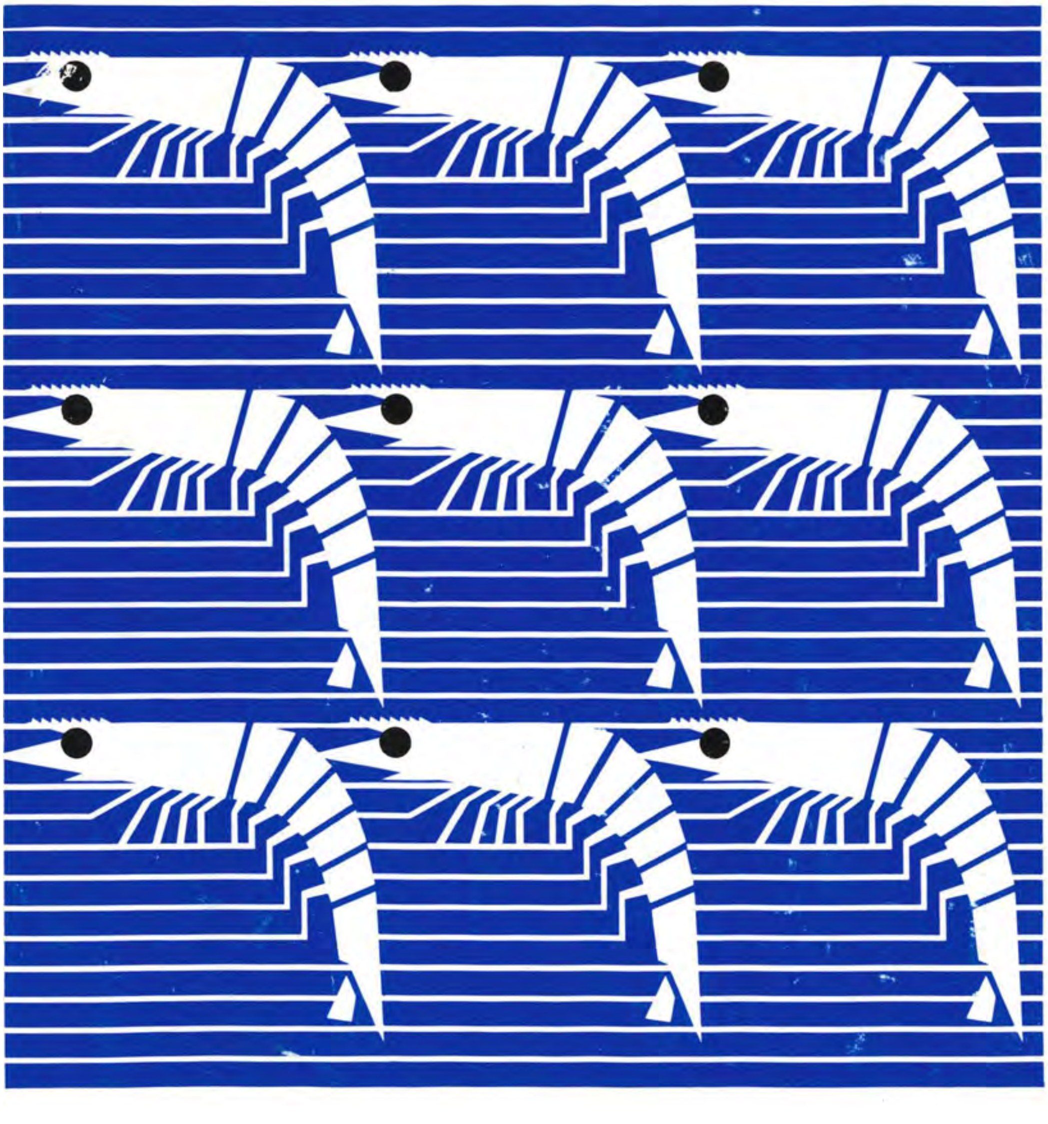
Second Australian National Prawn Seminar



Second Australian National Prawn Seminar

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Foreword

Since the First Australian National Prawn Seminar in 1973, Australian prawn fisheries have grown in size and value to become Australia's most valuable fisheries resource. In the same period the number of people involved in the fishing industry, research and management has also increased. Major new research centres have been established and several new programs implemented. A wide array of management regimes have been introduced including limited entry, seasonal and area closures coupled with sampling regimes to optimise the size at which prawns are harvested. Recently there has been a resurgence of interest in penaeid aquaculture which has been stimulated by the marked increase in pond production in South America and South East Asia, and the impact the product is having on world markets.

Because of the wide geographic separation of the various Australian prawn fisheries, there is little opportunity for those involved in the industry to meet and discuss topics at the national level. Accordingly it was felt that an update of developments and progress in research, management, economics, marketing, and aquaculture was necessary. We formed an organising committee and obtained funds to cover conference and publication expenses.

The Second Australian National Prawn Seminar was held at Kooralbyn, Queensland from 22 to 26 October 1984. Altogether 147 people attended, 51 papers and nine posters were presented. These covered life histories, ecology, fisheries biology, aquaculture, commercial fisheries, population dynamics and management. Papers included reviews of key topics, several of which were given by overseas speakers who helped to put the Australian work into an international perspective. Two workshops were held, one dealing with future research and one with aquaculture. Persons attending, papers and posters, are listed in the appendix. Following the seminar, the organising committee became an editorial committee to arrange for publication of selected papers from the seminar. Ted Middleton assisted the committee in the role of technical editor. This book presents 34 papers arising from the seminar.

We express our appreciation to the Fishing Industry Research Committee and to CSIRO for the financial support necessary for organising the seminar and publishing the book; to Michael Bryce, Jenny Conde and Ann Stirling who designed the logo, conference material and book layout; to Elizabeth Wallis of CSIRO and to Jenny Marsden and other staff of Kooralbyn Valley Resort for assistance in organising and running the seminar; to all the seminar participants and speakers; and to the referees and authors who made it possible to publish the book so soon after the seminar.

Peter Rothlisberg
Burke Hill
Derek Staples
Cleveland, August 1985

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A review of penaeid prawn biological research in Australia

Abstract: By 1974 the present day penaeid fisheries were almost fully developed in New South Wales (NSW) (*Penaeus plebejus, Metapenaeus macleayi*); Queensland (*P. plebejus, P. esculentus* and lesser commercial species); Northern Territory (*P. merguiensis, P. esculentus, P. semisulcatus* and lesser commercial species); Western Australia (*P. latisulcatus, P. esculentus*); South Australia (*P. latisulcatus*). Research groups existed in all these areas and most of the research was on problems directly related to management—defining fisheries, population dynamics including tagging studies, recruitment of juvenile prawns and reproductive biology. NSW had established the Brackish Water Fish Culture Station at Port Stephens in 1971, which has included major studies on *M. macleayi.* In 1974, the Commonwealth Scientific and Industrial Research Organization (CSIRO) phased out the East Coast Prawn Project (mainly on *P. plebejus*) and the Northern Prawn Project (*P. merguiensis*) and started the Tropical Prawn Research Project. The latter aimed to study those aspects of prawn biology which affect the yield of the fishery, namely larval, juvenile, adult ecology, population dynamics, feeding and nutrition, behaviour and physiology. The ensuing decade has seen an overall maturing of prawn research in Australia. Various projects in universities were started on prawn ecology, behaviour and larval development and CSIRO started a field project on *P. esculentus* and *P. semisulcatus.* Major achievements have been in larval and postlarval biology, juvenile recruitment into the fishery and prediction models, population dynamics, tagging and migration, and aspects of behaviour and physiology. In addition to these applications, the research has provided management with the information necessary for nursery ground and seasonal closures and optimisation of yield.

Introduction

The period 1948 to 1974 saw the rapid expansion and development of Australia's penaeid prawn fisheries associated with offshore trawling. At the time of the First National Prawn Seminar in November 1973, fisheries were well established in New South Wales, Queensland, Northern Territory, Western Australia and South Australia (Ruello 1975a). The research in the ensuing decade is, in general, a reflection of this development and the expansion of these fisheries, particularly in the north (Fig. 1). Thus New South Wales (NSW) Department of Fisheries continued management related research on the eastern king prawn, *Penaeus plebejus* and the school prawn, *Metapenaeus macleayi*; Queensland (Qld), in conjunction with the Commonwealth Scientific and Industrial Research Organization (CSIRO), completed the East Coast Prawn Project; Northern Territory (NT) carried out resource surveys and monitoring on various species; Western Australia (WA) continued research on the western king prawn, *P. latisulcatus,* and South Australia (SA) developed a highly regulated fishery in Gulf St Vincent and Spencer Gulf, based on research done by the Department of Fisheries. The total number of personnel, however, engaged in this research, was small with only one or two professional officers in each state government department. Consequently, while much has been achieved with the resources available, a good deal remains to be done if the prawn fisheries are to be properly managed.

At the time of the First National Prawn Seminar CSIRO had two projects on penaeid prawns: the East Coast Prawn Project, run jointly with Queensland Fisheries, and the Northern Prawn Project, both of which ended in 1974. The East Coast Prawn Project was mostly an investigation of the biology of the eastern king prawn, *P. plebejus,* in southeastern Queensland, and the Northern Prawn Project was a study of

Figure 1. Location of marine laboratories where penaeid prawn research is carried out in Australia(●) and principal areas where field research has been done(✱), in the period 1973 to 84.

the population dynamics and juvenile recruitment of the banana prawn, *P. merguiensis,* in the Gulf of Carpentaria. In July 1974 a new project, the Tropical Prawn Research Project was officially started by CSIRO. This project aimed to make a broadly based study of prawns in the Gulf of Carpentaria and by 1975 a team of six research scientists, five experimental officers, and support staff was assembled, and research started on the ecology of larvae, juvenile and adult prawns, population dynamics, feeding and nutrition, behaviour and physiology. It was by far the largest prawn research project launched in Australia, and this is reflected in the number of papers published by this group. The project at first concentrated mainly on *P. merguiensis,* although data on other species were also collected, but in 1981 research, which is still continuing, began on the two tiger prawn

Table 1. Research topics reviewed and number of papers published from 1974 to 1984.

Topic	No. of papers
Taxonomy (including larvae)	7
Adult populations	
Distribution and stock density	4
Tagging	5
Population dynamics	7
Recruitment to the fishery—juveniles	21
Larval studies	4
Reproductive biology	4
Behaviour	8
Functional morphology	3
Physiology	17
Population genetics	4
Total	84

Table 2. The commercially important Australian prawn species, corresponding common names, occurrence by state in order of importance and status of research. NSW = New South Wales; NT = Northern Territory; Qld = Queensland; SA = South Australia; WA = Western Australia.

Scientific name	Australian official common name	Commercial occurrence by state	Published research 1974 to 1984
Major commercial species			
Penaeus esculentus	brown tiger prawn	Qld, NT, WA, NSW	+
P. indicus	red legged banana prawn	NT, WA, Qld	+
P. latisulcatus	western king prawn	WA, SA, NT, Qld	+
P. merguiensis	banana prawn	Qld, NT, WA	+
P. plebejus	eastern king prawn	NSW, Qld.	+
P. semisulcatus	grooved tiger prawn	NT, Qld, WA	+
Metapenaeus endeavouri	blue endeavour prawn	Qld, NT, WA, NSW	+
M. ensis	red endeavour prawn	Qld, NT, WA	+
M. macleayi	school prawn	NSW, Qld	+
Minor commercial species			
Penaeus longistylus	red spot king prawn	Qld, NT, WA	+
Metapenaeus bennettae	greentail or greasyback prawn	NSW, Qld	+
M. dalli	western school prawn	WA, NT	—
M. eboracensis	york prawn	Qld, NT	—
M. insolitus	greasyback prawn	NT, Qld, WA	—
Parapenaeopsis sculptilis	rainbow prawn	Qld, NT, WA	—
Trachypenaeus fulvus	bay prawn	Qld, NT	—
Haliporoides sibogae	royal red prawn	NSW, Qld	+

species, *P. esculentus* and *P. semisulcatus.* In addition, the CSIRO Division of Food Research has investigated problems associated with processing prawns for marketing. Aquaculture research was started in 1971 by the NSW Fisheries Department, which established the Brackish Water Fish Culture Station at Port Stephens, with much of the effort devoted to the school prawn, *M. macleayi* (Maguire 1980).

Apart from government instrumentalities there has been little sustained research on penaeid prawns. The University of Queensland has had two post-graduate student projects on prawn ecology, while at James Cook University of North Queensland both students and staff have done laboratory studies on prawn biology.

This review is grouped under topics as in Table 1 and the locations of prawn research laboratories and field research are shown in Fig. 1. Since there are other review papers dealing with fishery development and management in this volume, these topics will not be included. In general, only biological research that has been published is reviewed here, except for areas where there is little or no existing data, and non-published reports are included. More than 50 penaeid species have been described from Australian waters (Grey et al 1983) of which nine are of major and eight of minor commercial importance (Table 2). Those on which research has been published since from 1974 to 1984 are shown. Because the use of common names may cause confusion, particularly since Australia and FAO official common names may differ (Grey et al 1983) only scientific names will be used. Scientific names and corresponding Australian common names are listed in Table 2.

Taxonomy

Only one new species, *Solenocera australiana* has been described from Australian waters since 1974 (Perez-Farfante and Grey 1980). An illustrated guide, with keys, to Australian penaeid prawns has been published (Grey et al 1983), and Miguel (1982) has included Australian species in his review of the genus *Metapenaeus.* Identification of early juvenile stages of penaeids is often difficult and Young (1977) has devised a working key for Moreton Bay species. While progress in adult and juvenile taxonomy has been modest, there has been considerable progress in description of larval stages. Fielder et al (1975) have given a detailed account of the development of *P. esculentus,* and a large number of species from the Gulf of Carpentaria have been reared at sea or in the laboratory (Rothlisberg et al 1978, 1983). Because of the close similarity of the zoeal stages within the genus *Penaeus*, these authors have developed a discriminant analysis technique for their identification.

Adult populations

Distribution and stock density surveys

Surveys have been undertaken primarily to ascertain the extent of the resource and are mostly descriptive but data on depth distribution and time of occurrence have often been included. Unfortunately, although the results have become available for management purposes and to industry, few have been published even as in-house publications of fisheries departments. The NSW Fisheries Department has continued survey work on deepwater prawns off the NSW coast, from the edge of the continental shelf down to 750 m depth (Gorman and Graham 1974; NSW Fisheries, Kapala Cruise Reports 25, 26, 28, 45, 46, 47, 48, 51 to 55, 59, 61, 72[1]). *Haliporoides sibogae* is the principal species, and the main grounds are between 30° and 34° S latitude (Sydney to Port Stephens).

In the eastern Gulf of Carpentaria, CSIRO conducted monthly trawl sampling in the Albatross Bay, Cape Keerweer and southeastern Gulf during 1976, 1977 and 1978. All species were recorded, measured and sexed. Reports were made to the research sessions of Northern Fisheries Committee in 1976, 1977 and 1978, but this research has not yet been published[2].

D.L. Grey of the Northern Territory Fisheries Division investigated the ecology of prawns in Shoal Bay during 1972 to 1978. Data on distribution and abundance of 21 species were collected and this demonstrated the presence of large numbers of smaller species of *Parapenaeopsis* and *Metapenaeus* as well as juvenile *Penaeus* spp. Surveys were also made of Van Diemen Gulf and Fog Bay. Results of those studies were reported to the research sessions of Northern Fisheries Committee for 1976, 1977 and 1978, but have not been published.

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[2] CSIRO Division of Fisheries Research, Cleveland, Qld. 4163, Australia.

Grey (1981) reported the first occurrence in Australia of *P. indicus* in commercial quantities. *Penaeus longistylus* has attracted interest as a potentially commercial species and Penn (1980b) has described its length to weight relationships and made some observations on its distribution.

Collection of data on *P. latisulcatus* in South Australia by the Fisheries Department was started in 1968, and is still continuing. The work done has included studies on recruitment, growth, migration, mortality and yield and has served as the basis for a very closely managed fishery, but so far only preliminary data have been published (Carrick 1982).

Tagging

Tagging is of key importance in penaeid population studies for estimates of stock size, for understanding movements and migrations and for mortality estimates. Experiments on the effects of tagging on mortality and behaviour are therefore essential. Prior to 1974, Ruello (1970) and Lucas et al (1972) using modified Atkins and Petersen disc tags, respectively, had examined the effects of tagging on mortality in the laboratory. The Atkins tag was used extensively in New South Wales (Ruello 1975b), and the latter in Queensland; subsequently Glaister (1978b) also measured the mortality due to Atkins tags on *M. macleayi.*

A more extensive set of experiments was done by Penn (1975b) on *P. latisulcatus* comparing the effects of Atkins and toggle tags both in the field and in the laboratory. Little difference was found in the effects of the two tags on survival and growth, and the toggle tag was used subsequently because of its speed and convenience. Penn (1981) has reviewed prawn tagging in Australia up to 1980.

Meanwhile, CSIRO felt that the pin and Petersen disc used by Lucas was unsatisfactory and used the Floy streamer tag in extensive tagging of *P. esculentus* and *P. semisulcatus* at Groote Eylandt (Somers 1981). Although this tag appeared to cause minimal mortality, there were conflicting reports on testing done in USA. Accordingly, the effects of the tags on mortality and growth over 70-day periods, as well as on moulting and emergence times of *P. esculentus* were studied, and found to have only negligible effects or none at all (Hill and Wassenberg in press). This tag was later used in extensive tagging in the Gulf of Carpentaria.

Population dynamics

Population estimates of *P. plebejus* in southeastern Queensland were made by Lucas (1974) using commercial catches and tag and recapture experiments. A natural mortality rate (M) for the offshore fishery was estimated at 0.05 week^{-1} with a fishing mortality (F) of 0.02. Penn (1976) carried out an intensive study of the *P. latisulcatus* population in Cockburn Sound (near Perth), which was closed to commercial fishing, using tag and recapture and controlled fishing effort. Various methods of estimating population size were evaluated. Petersen estimates of M were much lower than those of Lucas, ranging from 0.015 to 0.033. A stock assessment of *P. merguiensis* in the Gulf of Carpentaria by Lucas et al (1979) estimated M as 0.05 week^{-1}, with total mortality during the fishing season as 0.22 to 0.35 week^{-1}.

Ruello's (1975b) research on growth and breeding migrations of *P. plebejus* had been submitted for publication at the time of the First National Prawn Seminar. The most interesting feature of this research was the recapture of eight prawns more than 500km north of their release point. Montgomery (1981) has reported even more extensive migrations.

A mark and recapture study of *P. esculentus* and *P. semisulcatus* in the Groote Eylandt area by Somers et al (1982) was successful in obtaining growth data and demonstrating that the migration patterns of the two species were different, but satisfactory mortality estimates could not be made. Tagging and logbook data on *P. latisulcatus* have been collected in South Australia by M.G. King and N.A. Carrick since 1972 and used to manage the fishery, but although reported annually to the technical session of Western Fisheries Research Committee, results have not yet been published .

An analysis of recorded prawn catches in south Queensland to determine long term trends, annual and other cycles, and correlations with abiotic factors was made by Stephenson and Williams (1981). Fluctuations in catches were best modelled by log-transformed catches, rainfall with lag and temperature with lag. Temperature was found to be the predominant abiotic factor.

Recruitment to the fishery—juveniles

Juveniles of all the commercially important penaeids occupy estuarine or inshore areas (usually called nursery grounds) and most studies of this phase of the life cycle have included aspects of the environment.

The primary problem in these studies was to sample the juvenile populations quantitatively and this has been approached in various ways. Penn and Stalker (1975) devised a net for daytime sampling of the nocturnal *P. latisulcatus* thus overcoming some of the problems of water column sampling of mobile prawns. Staples and Vance (1979) studied the effects of tidal, diurnal, lunar and seasonal cycles on the catchability of juvenile *P. merguiensis* in the Norman River and concluded that tide had the most effect. Coles (1979) found that environmental effects depended on the species, light being more important than tide for *P. plebejus* whereas tides were more important for *M. bennettae* and *M. macleayi.*

The environment and biology of juvenile *P. plebejus* in Moreton Bay was described by Young (1978). The entry of the postlarvae into Moreton Bay and the distribution in relation to habitat type and annual recruitment of this species and *P. esculentus* and *M. bennettae* were described in detail by Young and Carpenter (1977). Penn (1981) reviewed nursery ground habitat requirements of juvenile Australian penaeid prawns.

Ruello (1977) studied the migration of *M. macleayi* from various NSW estuaries using mark and recapture methods and concluded that the movements were generally northerly but not as extensive as those of *P. plebejus.* Glaister (1978b) in a more detailed study of *M. macleayi* in the Clarence River obtained similar results, together with some growth data. This study also included the effects of environmental factors on juvenile populations and Glaister (1978a) concluded that river discharge was of major importance to the offshore catch of *M. macleayi.* Coles and Greenwood (1983) examined seasonal movement and size distribution of juvenile *P. plebejus, M. macleayi* and *M. bennettae* in the Noosa River (Qld) system. Immigration and emigration patterns differed for the three species, with salinity influencing distribution within the estuary, and season and size of prawn determining emigration patterns.

The most detailed studies of juvenile penaeid populations that have been conducted were those of Staples and colleagues who collected data on immigration and emigration of

P. merguiensis together with detailed hydrological and meteorological data, for four years in the Norman and adjacent rivers in the Gulf of Carpentaria, starting in late 1974 (Staples 1979; 1980a, b; 1983a, b; Staples et al 1984; Staples and Vance 1985; Vance et al 1983, in press). Earlier papers are descriptive, but the later papers examine the effects of the environment, both short and long term, on the immigration of postlarvae and the emigration of juveniles. Rainfall was shown to be the predominant effect and a model was developed for predicting catches in the southeastern Gulf of Carpentaria, based on rainfall up to February (for a commercial season commencing between 1 and 15 April).

An interesting study of the infestation of juvenile *P. merguiensis* in the Norman River by a trypanorhych cestode was made by Owens (1981). The level of infestation was related to size and behaviour and to salinity, and the possibility of using the parasite as a biological tag was discussed. This concept was later extended to a bopyrid parasite on the same prawn species (Owens 1983).

Larval studies

Taxonomic descriptions aside, larval biology is a much more difficult area in which to obtain data and this is reflected in the smaller number of papers. Penn (1975a) suggested that nocturnal tidal patterns in Shark Bay (WA) combined with larval vertical migration would provide a mechanism for transport of larvae into nursery grounds, and proposed that his model might have a general application.

An extensive larval sampling program in the Gulf of Carpentaria was undertaken during 1975 to 1977 by CSIRO and the distribution and abundance of zoeal stages of four *Penaeus* spp. was described (Rothlisberg, Jackson and Pendrey 1983). During this survey, data were also collected on vertical migration of all stages of larvae at 24 h stations, and this information was combined with data on tidal- and wind-driven currents to produce a model for larval transport of *P. merguiensis* for the southeastern Gulf (Rothlisberg 1982; Rothlisberg, Church and Forbes 1983). It is apparent from this work that sophisticated current modelling, together with a detailed knowledge of the vertical migration patterns of the various larval stages, is essential for understanding larval transport.

Reproductive biology

There have been few studies on reproductive biology of prawns, mainly because of difficulty of systematic collection of material and the labour of preparing large numbers of histological sections necessary to define ovarian stages. Penn (1980a) studied spawning and fecundity in *P. latisulcatus* and used an index of population fecundity to give estimates of relative levels of spawning throughout the year. Spawning was found to occur throughout the year in the north with a maximum from April to October and in the south it was over the October to May period with a peak in February. Crocos and Kerr (1983) used a similar index of population fecundity for *P. merguiensis* in the Gulf of Carpentaria and found two main spawning periods, one in August to November and the other in February to May. The relative importance of these peaks varied from north to south and the maximum peak of reproductive output did not forecast maximum recruitment of postlarvae into estuaries in the various regions. On the other hand, O'Connor (1979) found only one spawning peak, from February to May, in a *P. esculentus* population, near Low Islets, North Queensland (16° 23′S, 145° 34′E).

Behaviour

Many of the publications on prawn ecology include observations on behaviour or have behavioural implications (eg Coles 1980), but this section deals essentially with experimental studies in the laboratory. *Penaeus latisulcatus* was found to respond to flashes of high intensity white light of short duration (electronic flash) but not flashes of red light (Hindley and Penn 1975). *Penaeus merguiensis* shows a persistent dark phase of activity in red light (but not in continuous bright white light), but there is no endogenous tidal rhythm (Hindley 1975b). In this prawn, food is not found visually but is detected by chemosensory mechanisms which respond to 10^{-5} to 10^{-6}M amino acids, the prawn moving rheotactically to seek the food (Hindley 1975a). The process of implantation of sand grains into the statolith cavity immediately after moulting in *P. merguiensis* was described by Haywood and Alexander (1982). Aziz and Greenwood (1982) experimented with substrate preference of *M. bennettae* and found that particle sizes below 250 μm were preferred.

Moulting behaviour of *P. esculentus* was investigated by Wassenberg and Hill (1984) using time lapse video equipment and red to infrared light. Ecdysis was nocturnal and took only an average of 18.1s. The authors suggest that this prawn has reduced catchability during pre- and post-moult, due to its behaviour.

No systematic studies of predation of prawns appear to have been made, but Maguire and Bell (1981) studied the effect of fish on growth and survival of *M. macleayi* in ponds. Sparids appeared to be predators, but mullets, silver-biddies, gobies and grapsid crabs did not appear to be competitors.

Functional morphology

Using the scanning electron microscope and observations on feeding, Hindley and Alexander (1978) and Alexander et al (1980) have described the structure and function in feeding of the elaborate chelate periopods and the third maxillipeds of *P. merguiensis.*

Moult staging by setal development of the pleopods has been described by Longmuir (1983) who also gives a brief account of the process of ecdysis.

Physiology

Under physiology are included studies on physiological ecology, those relevant to aquaculture (metabolism, nutrition and induction of spawning), and food technology (tissue chemistry and flavours).

Temperature and salinity tolerance limits of *M. bennettae* were found to be 8 to 33°C and 1 to 62‰, respectively (Aziz and Greenwood 1981).

Dall (1981) and Dall and Smith (1981) examined osmotic and ionic regulation in *P. merguiensis, P. esculentus, P. plebejus,* and *M. bennettae.* Juveniles of all four species were able to osmoregulate at low salinities although the adults varied in this capability. All species were able to regulate ions over the salinity range 10 to 50‰. Calcium was accumulated and magnesium and sulphate reduced. Smith and Dall (1982) measured extracellular fluid space using a molecular size range of radioisotopic labels, in *P. esculentus* and *P. plebejus* and found evidence of separate blood and tissue fluid compartments.

The only study related to the effects of pollution on prawns has been made by Denton and Burdon-Jones (1982) who examined the effect of temperature and salinity upon the acute toxicity of heavy metals to *P. merguiensis.*

The foregut contents of five prawn species were analysed for carbon, nitrogen and bacterial carbon by Moriarty (1977) and related to the substrate content of these substances. In a later study, the food was analysed from prawns in the Gulf of Carpentaria and found to consist mainly of foraminifera, small molluscs, crustaceans and polychaetes (Moriarty and Barclay 1981). From 48 to 77% of organic carbon and 42 to 77% of organic nitrogen were assimilated.

Nutritional requirements of *M. macleayi* were investigated by Maguire and Hume (1982) who found that high calcium levels depressed growth, whereas phosphorus was without effect. The optimum level of protein when given as prawn tail meat was estimated to be 270g kg^{-1} dry weight of food. The utilisation of body lipid and protein by *P. esculentus* during 21 days of starvation was measured by Barclay et al (1983). Protein provided the main source of energy and digestive gland lipid appeared to have a role in late pre-moult stages.

Experimental studies of induction of spawning of *P. latisulcatus* have been reported by Kelemec and Smith (1980, 1984). Holding wild-caught prawns at 10 to 15°C, or enucleation of eyestalks had no significant effect on spawning index, egg fertilisation or hatching.

Generally, processing of prawns for consumption is a straightforward process, but one of the recurring problems, resulting in dumping of catches in some areas, is off-flavours. These are varied and have been described as garlic, rotten onion, metallic, solvent and iodoform-like. These have been investigated by Whitfield and Freeman (1983); Whitfield, Freeman and Bannister (1981); Whitfield, Freeman, Last and Bannister (1981); Whitfield et al (1982); Whitfield et al (1983); Whitfield and Tindale (1984). Most of the organic compounds responsible for these off-flavours have been identified and microbial spoilage, environmental pollution and diet were the most likely sources of the off-flavours.

Population genetics

Population genetics differs from the preceding topics in that there had been no research in this area at the time of the First National Prawn Seminar. Subsequent research has employed slab gel electrophoresis and staining of various enzymes, to identify polymorphic loci. Redfield et al (1981) found that *P. merguiensis* from the Gulf of Carpentaria had very low levels of heterozygosity. Mulley and Latter (1981a, b) examined geographic differentiation in nine commercially important species, and found that differences in gene frequency were minor in all cases and geographic differentiation was appreciable only between widely separated populations of *P. latisulcatus* and *M. endeavouri.* However, Richardson (1982) suggested that there may be two allopatric subpopulations of South Australian *P. latisulcatus* from Investigator Strait and Gulf St Vincent, respectively, possibly separated by time of spawning, but there was no evidence of genetic isolation of these stocks, in spite of their geographical separation from other areas. Thus, it appears that, for management purposes, the commercially important penaeid prawn species in Australia can be considered homogeneous throughout their range. Also, the prospects of obtaining genetically different individuals for selective breeding for aquaculture does not appear encouraging.

Discussion

A large part of the biological research of the last decade has been aimed at providing prawn management authorities with essential scientific information. Some of this has been direct problem solving research, such as distribution and stock density surveys, tagging and population dynamics. Other research, on juvenile prawns and larvae has wider biological implications, but has running through it the essential management theme of recruitment to the fishery, with the underlying causes of fluctuations in annual abundance. One of the studies in the Gulf of Carpentaria enabled a quantitative prediction model to be developed, a unique achievement for penaeid prawn research. Another research project in the same area, in conjunction with physical oceanographers, has shown, for the first time, how prawn larvae are transported. The broadly based nature of much of this research has also proved its value to both management and to the industry. Research on juvenile prawns has enabled nursery grounds to be accurately defined and legislation has been enacted to protect these areas from fishing. The data from population dynamics research has been used to develop yield per recruit models so that both industry and management can be advised on the optimum time for harvest and appropriate seasonal closures recommended.

While it is true to say that prawn research has reached a high level of sophistication over the last ten years, there has been considerable unevenness in research effort (Table 1). It is, of course, essential for the fishery that the main effort should continue to concentrate on the recruitment into the fishery, that is, the juvenile stages. The earlier stages of the life cycle (reproducing adults and larvae) have received relatively little attention, yet at least a major part of the causes of long term fluctuations in abundance must lie with these stages. The larval stages of the major species have now been described and studies on the growth and survival of these stages are urgently needed. More work is needed on maturation and fecundity of the reproducing adults of major species and these, together with larval stages, will become of crucial importance in establishing any relationship between stock and recruitment.

At the fishable stock level, much more data are needed on growth rates and estimates of mortality, particularly the latter. Yield curves are sensitive to changes in rates of natural mortality, but most studies on population dynamics have had to rely on approximations, often crude or even derived from another fishery.

Perhaps our greatest lack is a real understanding of prawn ecology at the individual, rather than at the population level. Very little is understood of basic functions such as digestion and assimilation, energy metabolism or the endocrinology of moulting and maturation. The food organisms on which prawns feed have not been described, much less their ecology and production studied. Behaviour is receiving increasing attention, but a wide range of behavioural studies are urgently needed, since a fisherman is effectively an applied behaviourist. Substrate preferences are known, for example, but there is no real understanding of why a particular substrate is preferred. Many prawns are nocturnal but the role of light, both diurnal and lunar, is poorly understood. Studies of physiology and behaviour will become more critical as aquaculture develops, together with pathology, and it seems likely that aquaculture research will be the biggest development in the next decade.

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Distribution and abundance of early penaeid larvae in the Gulf of Carpentaria, Australia

Abstract: The present larval ecology study has three broad aims: to understand the factors affecting distribution and abundance; dispersal; and survival of penaeid larvae in the Gulf of Carpentaria. Underlying all these is the need to identify larvae of individual species from field collections. The three zoeal stages of *Penaeus esculentus, P. latisculcatus, P. merguiensis* and *P. semisulcatus* have been distinguished using a reference collection and numerical taxonomic methods. Patterns of zoeal abundance for the four species are widespread, yet discontinuous and discrete. *Penaeus merguiensis* larvae are abundant in only three areas along the eastern Gulf in March. The larvae of *P. latisulcatus* occur mainly in the western Gulf, with a broad peak of abundance from September to June. *Penaeus esculentus* larvae occur in the eastern and western Gulf in low numbers almost year round. The larvae of *P. semisulcatus* are widespread, occur in deep water, and appear in two peaks, September and January.

Introduction

An understanding of larval ecology aids in the understanding of: stock size and distribution; spawning time, location and frequency; density dependent and independent factors affecting recruitment patterns and strength (Sherman et al 1983). Further, knowledge of dispersal pathways, mechanisms and distances helps define geographic management boundaries and measures. In spite of the economic importance of penaeid prawns to Australian fisheries their larval ecology has been studied only superficially (Dakin 1938; Racek 1959; Kirkegaard 1972). The primary reason the larval ecology of penaeids has not been pursued in Australia, and indeed world-wide, is the lack of taxonomic resolution of the early larval stages. The problem has recently been overcome with the development of techniques for identifying the early larval stages of the common or brown tiger prawn, *Penaeus esculentus,* the western king prawn, *P. latisulcatus,* the banana prawn, *P. merguiensis* and the green or grooved tiger prawn, *P. semisulcatus* (Rothlisberg, Jackson and Pendrey 1983). In this paper we will summarise the distribution and abundance of the zoeal stages of *P. esculentus, P. latisulcatus, P. merguiensis* and *P. semisulcatus* and thereby broadly delineate the temporal and spatial patterns of reproductive activity of these four species in the Gulf of Carpentaria.

Materials and methods

Reference collection

Larvae used for identification were established in a reference collection at the Commonwealth Scientific and Industrial Organization (CSIRO) Marine Laboratories, Cleveland (status as of January 1985, Table 1). The methods for the shipboard rearing, as well as egg and larval transport are detailed in Rothlisberg, Jackson and Pendrey (1983). Additional larval rearings have been made in the laboratory at Cleveland using 3 l capacity Pyrex tubes (100mm diameter, 500mm length) with airlift circulation, housed in environmental cabinets to control temperature and photoperiod.

Larval identification

Sixteen morphological measurements were made on each of 2 316 individual larvae in the reference collection (485, *P. esculentus*; 358, *P. latisulcatus*; 451, *P. merguiensis*; and 1 022, *P. semisulcatus*). Data for each of the three zoeal substages were analysed separately by discriminant analysis, as described for the first

Table 1. Species and stage of development of penaeid larvae in CSIRO Marine Laboratories, Cleveland reference collection.

Species	Nauplius	Zoea 1	Zoea 2	Zoea 3	Mysis 1	Mysis 2	Mysis 3	Postlarva
Penaeus								
P. merguiensis	+	+	+	+	+	+	+	+
P. indicus	+	+	+	+	+	+	+	+
P. latisulcatus[1]	+	+	+	+	+	+	+	+
P. longistylus	+	+	+	+	+	+	+	+
P. plebejus	+	+	+	+	+	+	+	+
P. japonicus[2]	+	+	+	+	+	+	+	+
P. esculentus	+	+	+	+	+	+	+	+
P. semisulcatus	+	+	+	+	+	+	+	+
P. monodon[3]	+	+	+	+	+	+	+	+
Metapenaeus								
M. endeavouri	+	+	+	+	+	+	+	+
M. ensis	+	+	+	+	+	+	+	+
M. eboracensis	+	+	+	+	+	+	+	+
M. insolitus	+	+	+	+	+	+	+	+
M. bennettae	+	+	+	+	+	+	+	+
Trachypenaeus								
T. anchoralis	+	+	+	+	+	+	+	+
T. fulvus	+	+	+	+	+	+	+	+
T. granulosus	+	+	+	+	+	+	+	+
Atypopenaeus								
A. formosus	+	+	+	+	+	+	+	+
Parapenaeopsis								
P. cornuta	+	+	+	+				
Metapenaeopsis								
M. palmensis	+	+	+	+	+	+	+	+
M. novaeguineae	+	+	+	+	+			
Genera	6	6	6	6	5	5	5	5
Species	21	21	21	21	20	19	19	19

Source of material: [1]Port Broughton, Australia. [2]Yamaguchi Pref., Japan. [3]Iloilo, Philippines.

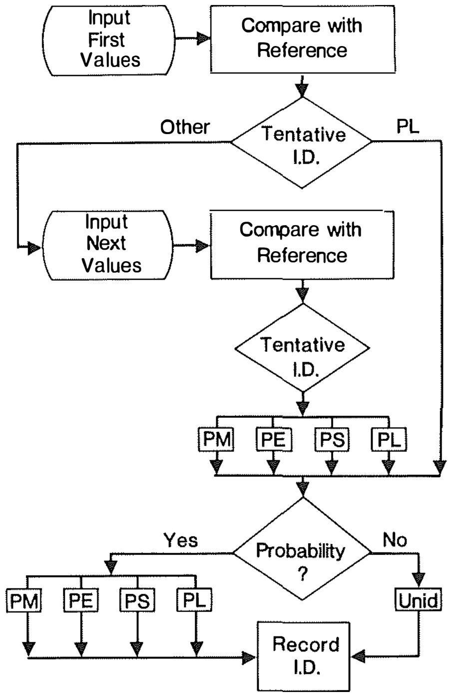

Figure 1. Flow diagram of interactive larval identification procedure. PM = *Penaeus merguiensis*, PE = *P. esculentus*, PS = *P. semisulcatus*, PL = *P. latisulcatus*, I.D. = Identification, Unid = Unidentified.

zoeal substage in Rothlisberg, Jackson and Pendrey (1983). All three zoeal substages of *P. latisulcatus* were found to be quite distinct from those of the other three species, and could be distinguished by measurements of four characters in the first zoea (Z_1) (lengths of the carapace, second segment of the first antenna, second antenna exopod and first segment of the second antenna endopod); three characters in the second zoea (Z_2) (lengths of the carapace and first segment of the second antenna exopod, and the number of setae on the second antenna exopod); and two characters in the third zoea (Z_3) (length of first segment of the second antenna exopod, and the number of setae on the second antenna exopod). To separate the remaining three species, an additional four characters were required for Z_1 (total length, lengths of the second and third segments of the second antenna exopod, and the diameter of the first segment of the first antenna), and an additional three for Z_2 (lengths of the second antenna exopod and the proximal part of the second segment of the first antenna, and the distance between telson rami) and two for Z_3 (length of the second antenna exopod and the distance between telson rami).

An interactive computer program was written to identify unknown larvae using the results produced by discriminant analysis. An identification is accomplished in one or two steps (Fig. 1). The operator first enters the zoeal substage and is then prompted to make the first set of appropriate morphological measurements on the unknown larva; these are the characters, described above, which are sufficient to distinguish the *P. latisulcatus* larvae from the other species. If the unknown is not *P. latisulcatus*, the second set of measurements is requested and the most likely identification, *P. esculentus, P. latisulcatus, P. merguiensis* or *P. semisulcatus* is determined. Once a tentative identification has been made in this way, the

Table 2. Effect of threshold probability on accuracy of larval identification, for three zoeal substages. The bold type shows percent of reference collection which is identified correctly at three threshold probability levels; normal type shows percent of reference collection which remains unidentified.

Species	Threshold probability level		
	Low	Operational	High
Penaeus latisulcatus			
Z_1	**95.6**	**97.0**	**98.4**
	0.0	1.5	4.4
Z_2	**100.0**	**100.0**	**100.0**
	0.0	0.0	0.0
Z_3	**99.1**	**100.0**	**100.0**
	0.0	0.9	0.9
Penaeus merguiensis			
Z_1	**89.1**	**94.7**	**98.8**
	0.0	13.6	26.0
Z_2	**95.0**	**97.7**	**99.2**
	0.0	7.2	12.2
Z_3	**85.1**	**89.8**	**91.4**
	0.0	6.4	13.8
Penaeus semisulcatus			
Z_1	**81.5**	**86.1**	**90.8**
	0.0	12.2	31.5
Z_2	**85.5**	**88.8**	**92.1**
	0.0	15.1	29.1
Z_3	**84.4**	**89.7**	**93.6**
	0.0	**13.3**	**30.4**
Penaeus esculentus			
Z_1	**80.8**	**86.8**	**93.6**
	0.0	15.5	41.6
Z_2	**69.4**	**73.9**	**79.8**
	0.0	19.0	36.1
Z_3	**90.8**	**92.4**	**94.2**
	0.0	12.5	28.3
Overall			
Z_1	**85.4**	**90.1**	**94.7**
	0.0	11.0	27.6
Z_2	**85.6**	**89.2**	**92.7**
	0.0	12.7	24.0
Z_3	**88.6**	**92.4**	**94.8**
	0.0	9.7	21.8

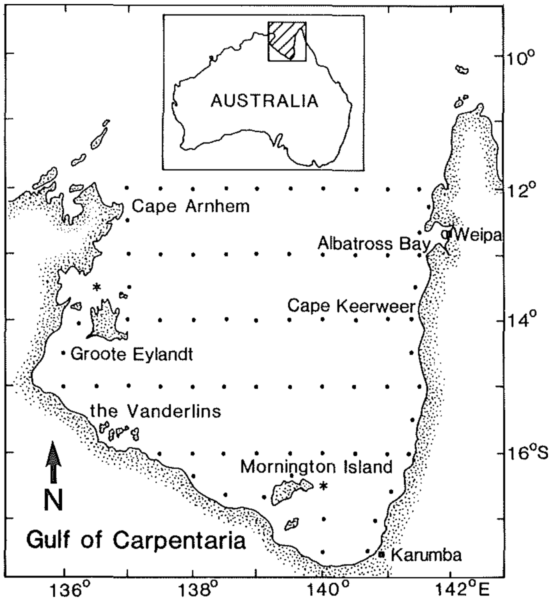

Figure 2. Gulf of Carpentaria station array for CSIRO Gulf-wide sampling cruises, 1975 to 1977. Position of stations for discrete depth sampling with plankton pump indicated by*.

program compares the probability level of the tentative identification with a threshold level. If the probability of the identification is not sufficiently high, then the tentative identification reverts to unidentified (Fig. 1).

To test the accuracy of identification, the program was applied to the larvae in the reference collection, with varying values of the identification threshold (Table 2). With a low identification threshold, that is accepting even those identifications with a very low probability, the accuracy of identifications ranged from 100% for *P. latisulcatus* Z_1, to 69.4% for *P. esculentus* Z_2. Averaged over all four species, the proportions of correct identifications were 85.4%, 85.6% and 88.6% for Z_1, Z_2 and Z_3 respectively. With a high threshold, the overall proportions of correct identifications increased to 94.7%, 92.7% and 94.8%, with the least accurate figure for *P. esculentus* Z_2 now 79.8%. However, a relatively high proportion of larvae remained unidentified, 27.6%, 24.0% and 21.8%.

An operational level, for use in identifying the larvae from the field collections, was chosen which is a compromise between these two extremes (Table 2). Using this threshold value, the overall proportions of correct identifications for Z_1, Z_2 and Z_3 were 90.1%, 89.2% and 92.4% respectively with 73.9% correct for the least accurate group, *P. esculentus* Z_2. This accuracy was achieved while leaving 11.0% of Z_1, 12.7% of Z_2 and 9.7% of Z_3 unidentified.

Plankton sampling

Penaeid larvae were sorted from the plankton samples obtained in the manner described by Rothlisberg and Jackson (1982). More than 2500 plankton samples have been taken in the Gulf of Carpentaria (Table 3, Fig. 2). A total of 1323 towed net samples (661, 142μm and 662, 500μm) were obtained from 10 Gulf-wide

Table 3. Number of plankton samples taken on CSIRO surveys of Gulf of Carpentaria, 1975 to 1978.

	Dates			Samples taken				Samples sorted			
Cruise	Start	Finish	Stations	142[1]	500[2]	Pump[3]	Total	142[1]	500[2]	Pump[3]	Total
Gulf-wide											
KL01	13 Jul 75	20 Aug 75	33	33	33	0	66	33	33	0	66
KL03	30 Sep 75	12 Oct 75	68	67	68	0	135	56	2	0	58
KL06	13 Nov 75	26 Nov 75	71	71	71	0	142	50	62	0	112
KL04	23 Apr 76	11 May 76	67	76	76	0	152	67	67	0	134
KL07	26 Jun 76	12 Jul 76	32	35	35	0	70	34	35	0	69
KL09	28 Aug 76	13 Sep 76	70	79	79	61	219	70	70	32	172
JB02	31 Oct 76	18 Nov 76	71	80	80	0	160	70	75	0	145
TP01	5 Jan 77	21 Jan 77	70	79	79	100	258	71	77	52	200
TP03	16 Mar 77	30 Mar 77	70	82	82	108	272	73	42	56	171
TP05	3 May 77	13 May 77	53	59	59	52	170	30	34	28	92
Sub-total			605	661	662	321	1644	521	464	168	1153
Southeastern Gulf											
TP10	10 Sep 78	17 Sep 78	60	60	60	0	120	59	59	0	118
TP11	23 Sep 78	30 Sep 78	60	60	60	52	172	59	57	28	144
TP12	8 Oct 78	14 Oct 78	60	60	60	40	160	58	58	20	136
TP14	21 Oct 78	28 Oct 78	61	60	60	52	172	60	58	28	146
TP15	4 Nov 78	10 Nov 78	60	60	60	34	154	59	58	18	135
TP16	18 Nov 78	23 Nov 78	40	40	40	0	80	40	39	0	79
Sub-total			341	340	340	178	858	335	329	94	758
Total			946	1001	1002	499	2502	856	793	262	1911

[1] 142μm mesh towed net
[2] 500μm mesh towed net
[3] vertically stratified pump samples with 142μm retention net

cruises. Of those, 985 (521, 142μm and 464, 500μm) have been sorted for penaeid prawn larvae. The zoeal stages sorted from the 142μm net samples for six cruises (KL04, April 1976 to TP03, May 1977) have been identified and quantified and the results are presented in summary fashion in this paper. In the figures that follow, both the overall spatial distribution and seasonal abundance of the three zoeal substages are combined for the four species (*P. esculentus, P. latisulcatus, P. merguiensis,* and *P. semisulcatus*). A map shows the larval abundance from the six cruises superimposed, not added together. Dots indicate actual station locations of samples which have been sorted and therefore, those without abundance rings represent real zeros. The standardised abundance, in number m^{-2}, is calculated from the number of larvae sorted from the sample, the fraction of the sample sorted, the volume of water filtered and integrated under one m^2 of sea surface by multiplying by the depth of the plankton tow (generally within 2 m of the bottom). The larval abundance histograms were calculated using the mean number of zoeae m^{-2} of that species, over all the stations sampled on that cruise. A more complete account of cruise by cruise differences of each zoeal substage is in preparation. In this account the spawning location and intensity for the four species is inferred by the location and abundance of the zoeal stage.

Results

The larvae of *P. merguiensis* had a coastal distribution (Fig. 3a). They were predominantly found in three areas of the Gulf: Albatross Bay in the northeast; south of Cape Keerweer on the mideastern coast; and the southern Gulf from the Sir Edward Pellew Group of islands (the Vanderlins) into the southeastern Gulf. Zoeae were seen in January, just north of Groote Eylandt in the western Gulf. The appearance of zoeae was seasonal with a large peak centred in March and a smaller one in September (Fig. 3b). No *P. merguiensis* zoeae were seen in the June or November samples.

The zoeal stages of *P. latisulcatus* were coastal, except for north of Mornington Island where they were found farther offshore (Fig. 4a). The larvae were restricted mainly to the southern and western Gulf with only small numbers in the northeast between Albatross Bay and Cape Keerweer. Zoeae appeared in samples year-round with two peaks of abundance, one in September, the other in January (Fig. 4b).

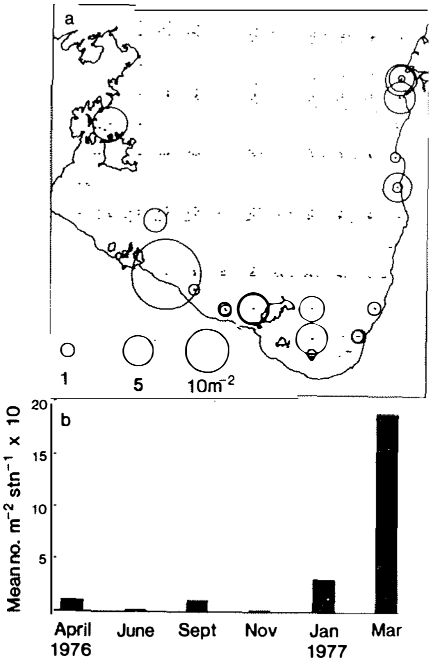

Figure 3. Distribution and abundance of combined zoeal stages for *Penaeus merguiensis*. **a.** spatial and **b.** seasonal.

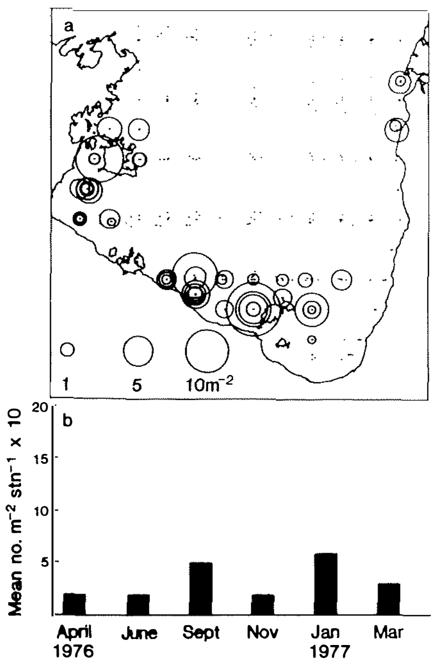

Figure 4. Distribution and abundance of combined zoeal stages for *Penaeus latisulcatus*. **a.** spatial and **b.** seasonal.

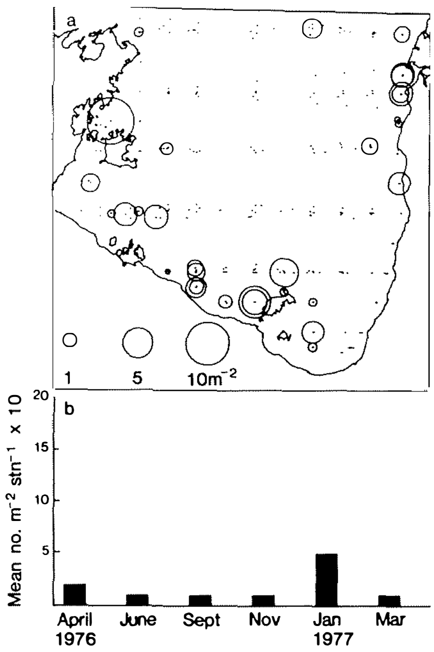

Figure 5. Distribution and abundance of combined zoeal stages for *Penaeus esculentus*. **a.** spatial and **b.** seasonal.

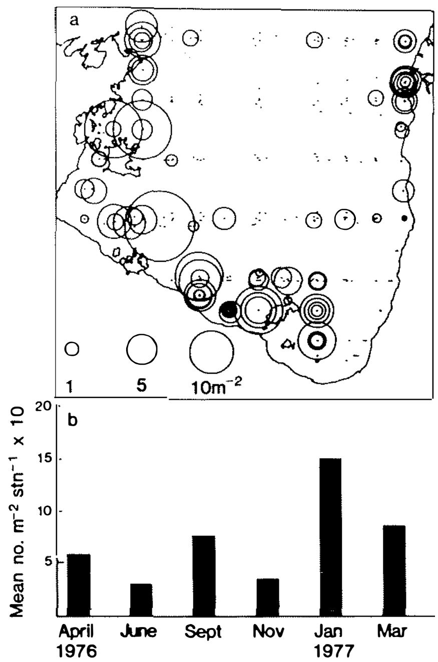

Figure 6. Distribution and abundance of combined zoeal stages for *Penaeus semisulcatus*. **a.** spatial and **b.** seasonal.

The early larvae of *P. esculentus* were also coastally distributed, but extended offshore in the northeastern and southwestern Gulf (Fig. 5a). Maximum concentrations occurred in Albatross Bay, around Mornington Island, north of the Vanderlins and just north of Groote Eylandt. Seasonally the larval abundance was relatively low, appearing year-round with a small peak in January (Fig. 5b).

The zoeal stages of *P. semisulcatus* were the most widespread and abundant of the four species considered (Fig. 6). Larvae were abundant near Albatross Bay, east and west of Mornington Island, north of the Vanderlins and north of Groote Eylandt (Fig. 6a). The larvae of *P. semisulcatus* were the only ones to be found north of Cape Arnhem. Also of note was the offshore extent of these larvae, particularly off Groote Eylandt and north of the Vanderlins. The larvae appeared year-round with a large and prolonged peak of reproductive activity from January to April and a smaller peak in September (Fig. 6b).

Discussion

Dakin (1938) was the first in Australia to elucidate the reproductive seasonality of a penaeid prawn based on larval abundance. At the time of his study the spawning adults were rarely if ever seen due to the lack of an offshore commercial fishery. He predicted the prolonged nature of the *P. plebejus* reproductive season from the appearance of early larvae offshore and late larvae and postlarvae near river mouths in northern New South Wales. Dakin's conclusion was somewhat fortuitous as the description he gives for the zoeal (=protozoeal) stages of *P. plebejus* is incorrect, since the larvae figured in his Plate 1 are not *Penaeus* but *Metapenaeus.* The strength of his assessment is his correct identification of the postlarval stages, which were more abundant in his collections. This prolonged reproductive season has been substantiated by Young and Carpenter (1977) who monitored the ingress and settlement of postlarvae in Moreton Bay, Queensland.

In Dakin's study area off New South Wales there was likely to be only one or two members of the genus *Penaeus (P. plebejus* or *P. esculentus).* In areas such as this where the numbers of species are limited or the seasonality of reproduction is known and non-overlapping, tentative larval identifications can be made based on the probabilities of occurrence in the plankton. In the tropical Gulf of Carpentaria eight species in the genus *Penaeus* have been recorded: *P. esculentus; P. indicus; P. japonicus; P. latisulcatus; P. longistylus; P. merguiensis; P. monodon* and *P. semisulcatus.* Kirkegaard (1972) made a preliminary report of the penaeid larval sampling carried out during the initial Gulf survey (Munro 1972, 1975) from 1964 to 1968. More than 200 offshore plankton samples were taken over a 3.5 year period, mostly in the southeastern Gulf, with a few samples off Weipa and Groote Eylandt in 1967. Kirkegaard (1972) found zoeae (=protozoeae), mysis and postlarvae of *Penaeus, Metapenaeus, Trachypenaeus, Parapenaeopsis* and *Sicyonia* but could not ascribe any of these to species. This result was similar to those of a number of workers world wide (see Rothlisberg, Jackson and Pendrey 1983 for full discussion). In an area like the Gulf with so many species, with overlapping spatial distributions and prolonged reproductive activity, a robust taxonomic technique is required to identify larvae.

The larval distributions described in this account correspond to adult distributions based on catch statistics for *P. merguiensis* (Somers and Taylor 1981) and the two tiger prawns around Mornington Island (Robertson et al 1985) and Groote Eylandt (Somers and Kirkwood 1984). The larval distributions and abundances are also useful in predicting adult distributions and abundances in areas that have not been surveyed or have large amounts of untrawlable bottom. The large numbers of *P. latisulcatus* and *P. semisulcatus* larvae between Mornington Island and the Vanderlins and extending into deep water north of the Vanderlins are an example. These results could also be used to add resolution to fisheries logbook data in which species are not separated. Some caution must be exercised with the interpretations of the larval distributions since the identifications are based on probabilities. This is especially true with the two species of tiger prawns (*P. esculentus* and *P. semisulcatus)* where there is a 7.6 to 13.9% chance of misidentification, dependent on species and zoeal substage. Further, we have dealt only with the four most abundant commercial species. Although other species can be and have since been incorporated into the identification scheme, there will always be a percentage of larvae that cannot be identified with absolute assurance.

Where comparisons can be made, the

reproductive dynamics, as inferred from zoeal abundance, agree quite closely with surveys of adults (Crocos and Kerr 1983; Crocos[1] pers. comm.) but are not fraught with the difficulties of interpretation of the histological data. The largest amount of reproductive activity, as assessed by larval abundance, occurs in the summer months; January for *P. latisulcatus*, *P. esculentus* and *P. semisulcatus* and March for *P. merguiensis*. Three species had secondary peaks in September; a very small one for *P. merguiensis*, a larger one for *P. semisulcatus* and for *P. latisulcatus* the September peak is nearly as large as the one in January. *Penaeus merguiensis* has the most well defined peaks of reproduction with periods of no larvae present in the plankton. The other three species appear to reproduce at some level year round.

While the results presented here are in summary form analysis is continuing to give higher spatial resolution to the seasonal changes in larval abundance. Different patterns of larval abundance around the Gulf are becoming apparent. By coupling these studies with histological studies of population fecundity (Crocos and Kerr 1983) a more complete picture of a species reproductive output is gained. Further, with studies of larval behaviour and oceanography (Rothlisberg 1982; Rothlisberg, Church and Forbes 1983) the effect of the reproductive output, in establishing postlarval recruitment patterns (Staples 1979), can be assessed. An example of this interdisciplinary approach of combining oceanography, larval ecology, reproductive biology and recruitment dynamics for *P. merguiensis* is presented by Rothlisberg, Staples and Crocos (1985).

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The effects of temperature and salinity on survival and growth of larval *Penaeus plebejus, Metapenaeus macleayi* and *M. bennettae*

Abstract: The combined effects of temperature and salinity on the hatching success and survival, growth and development of the larval stages of *Penaeus plebejus, Metapenaeus macleayi* and *M. bennettae* were investigated using controlled experiments in the laboratory. Response-surface analysis showed that, for all species, maximal hatching success and survival of larvae always occurred at the ambient levels of temperature and salinity at which spawning took place. *Metapenaeus bennettae* was the only species to spawn in both brackish and marine conditions. This species showed an adaptive response to ambient temperatures and salinities during early development. In each species tolerance to different temperatures and salinities was least during the development of the protozoeal stages and greatest during the development of the mysis stages.

Introduction

Most species of penaeid prawns which occur in shallow, coastal waters migrate to offshore waters as they approach maturity. This is a breeding migration. The distance that maturing stocks move offshore, away from estuarine areas, varies among species (Kutkuhn 1966). As a result, the extent to which the planktonic larvae encounter differences in temperature and salinity varies according to the species. In species which spawn well offshore, the entire larval development may be completed in oceanic waters at levels of temperature and salinity that do not vary greatly. In contrast to this, the larvae of species which spawn in, or close to, estuarine areas may encounter rapid changes in temperature and salinity. Temperature and salinity are two of the principal abiotic factors that may affect hatching success and the survival, growth and distribution of marine organisms (Kinne 1964). In many species, tolerance to changes in temperature and salinity is lowest during early development (Kinne 1964). Laboratory and field studies of the response of eggs and larvae of marine organisms to the combined effects of temperature and salinity should therefore lead to a greater understanding of the significance of these factors in determining survival during early development.

The common penaeid prawns of southeastern Australian coastal waters are *Penaeus plebejus, Metapenaeus macleayi* and *M. bennettae.* Indirect evidence from studies of the distribution of fertilised females (Racek 1959) and the movement of tagged adults (Ruello 1975; Montgomery 1981) indicates that *P. plebejus* spawns 3 to 20 nautical miles offshore at depths of 50 to 200 m and that larval development takes place in oceanic waters where temperature and salinity are relatively stable (Aurousseau 1959). Similar studies of *M. macleayi* have indicated that this species spawns in relatively shallow (30 m) water (Racek 1959; Ruello 1977). Early larval development in this species probably takes place in coastal waters. Because of the proximity of the spawning grounds to the coast, the late larval stages of *M. macleayi* may encounter irregular changes in temperature and salinity at the entrance to coastal lagoons or estuaries. *Metapenaeus bennettae* is unusual because it can complete its whole life cycle in shallow coastal lagoons (Morris and Bennett 1952). Surveys of the plankton of coastal lagoons in New South Wales (NSW) by Morris

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and Bennett (1952) and experiments done in the field (Preston 1985) have shown that *M. bennettae* spawns in both marine conditions (temperature range 25 to 29° C, salinity range 30 to 35‰) and brackish conditions (temperature range 20 to 23° C, salinity range 20 to 22‰).

Penaeus plebejus, M.macleayi and *M. bennettae* differ in the length of their spawning migrations. They also differ in the tolerance of juveniles and adults to changes in salinity (Dall 1964; Dall and Smith 1981). I therefore wanted to determine whether the eggs and larvae of these species differ in their response to the combined effects of temperature and salinity.

Laboratory studies have shown that the survival and growth of marine and estuarine decapod larvae may change markedly during development (Sandoz and Rogers 1944; Costlow et al 1966). The effects of temperature and salinity on laval mortality may also vary according to previous temperature and salinity history (Lucas 1972; Rosenberg and Costlow 1979), or the amount of food available (Anger et al 1981). In rearing decapod larvae for laboratory studies, considerable variation in survival may occur between broods of larvae with apparently no difference in culture conditions (Scheltema and Williams 1982).

Previous studies of hatching success and the survival of the larval stages of penaeid prawns have found wide variation in the survival of different batches of larvae (Hudinaga 1942; Ewald 1965). Hudinaga (1942) studied temperature and salinity effects separately and found that the eggs and larvae of *P. japonicus* were less tolerant to changes in salinity than to changes in temperature. The protozoeae had the lowest tolerance to changes in salinity and the mysis stages were the least affected. Gopalakrishnan (1976) observed similar effects in *P. marginatus.* However, experiments in which temperature and salinity are treated as separate factors cannot provide information on interactive relationships between these factors which may be biologically important (Alderdice 1972). In the present study, laboratory experiments were designed to determine the nature of the response of eggs and larvae to the combined effects of temperature and salinity and the extent of variation between cohorts, different species and spawning conditions.

Experiments with *P. plebejus* were done in the laboratory at the NSW State Fisheries research station at Port Stephens (32° 45'S, 152° 04'E). Experiments with *M. macleayi* and *M. bennettae* were done at the University of New South Wales research station at Smiths Lake (32° 15'S, 152° 22'E) and at the University of Sydney.

Materials and methods

Mature female *P. plebejus* (size range 160 to 180mm total length) with implanted spermatophores were caught with an otter trawl northeast of Tweed Heads in NSW (170m, 27° 55'S, 153° 51'E). On arrival at Port Stephens, healthy females were transferred to 250 l fibreglass tanks containing fresh filtered (50 μm filter) seawater (32 to 35‰). Temperature in the spawning tanks was maintained at 19 to 20° C until individuals were induced to spawn by raising the water temperature to between 22 and 25° C.

Mature female *M. macleayi* (100 to 150mm TL), with implanted spermatophores were captured with an otter trawl from Stockton Bight, NSW (30m, 32° 45'S, 153° 15'E). On arrival at Smiths Lake, the prawns were immediately transferred to 100 l tanks containing fresh filtered seawater (33 to 35‰).

Mature female *M. bennettae* with implanted spermatophores were caught in hand nets at Smiths Lake. Prawns (75 to 80mm TL) from the same area within the lagoon were used for each set of experiments. Temperature and salinity at the place of capture in Smiths Lake were measured using a Hamon temperature and salinity probe. Captured females were held in 100 l tanks containing lagoon water at ambient temperature and salinity. Laboratory experiments with *M. bennettae* were done at intervals throughout the spawning season.

A balanced factorial design of combinations of temperatures and salinities was used in the hatching and rearing experiments. Preliminary experiments were done to determine the levels of temperature and salinity at which there was reasonable potential for hatching success and survival of the larvae of each species. Factorial combinations of temperature and salinity were then set within an ecologically relevant range, at levels of survival that would ensure meaningful statistical analysis of treatment effects and comparisons between individuals and species. Temperatures were maintained to within 0.2° C using thermostatically controlled water baths. The salinity of filtered seawater (lagoon water for *M. bennettae*) was reduced with distilled water or increased with synthetic salts (Instant Ocean, Aquarium Systems Inc) to produce the required salinities.

Stages of development (eggs, nauplii (N), protozoeae (P) and mysis (M)) were treated separately. Batches of larvae from each spawning were reared to the stage required for each experiment in 5 l glass beakers containing fresh, filtered sea or lagoon water at the ambient temperature and salinity of the place of capture of the spawning females. Stocking densities in the 5 l beakers were 100 nauplii l^{-1}, 50 protozoeae l^{-1} and 20 mysis l^{-1}. In the experimental design, four replicate, 1 l plastic containers were placed in each of the temperature and salinity combinations. To avoid abrupt changes in temperature and salinity, eggs or larvae were initially placed in 200 ml of water at ambient rearing conditions. The temperature and salinity were then adjusted to the desired levels over a period of 2 h. Stocking densities in the containers used in the temperature and salinity experiments were the same as those in the rearing containers. These densities were below the growth-limiting densities for penaeid larvae (Emmerson and Andrews 1981) but greater than natural densities (Preston unpubl.).

The diatom *Skeletonema costatum* was found to be the most suitable algal species for rearing protozoeae. *Skeletonema costatum* cultured in enriched seawater (Loeblich and Smith 1968), was introduced to the 5 l glass beakers at a concentration of 1×10^4 cells ml^{-1} as soon as larvae had reached the last naupliar stage. Algal concentrations were monitored using haemocytometer counts and maintained at about 1×10^4 cells ml^{-1} during the development of the protozoeal stages, and above 1×10^5 cells ml^{-1} during development of the mysis stages.

Artemia nauplii were added at a concentration of 10 nauplii ml^{-1} to the containers used for rearing mysis stage larvae. The same concentrations were used when larvae were reared in the various combinations of temperature and salinity.

In one of the laboratory experiments with *M. bennettae*, the effects of algal concentration on the survival of the protozoeal stages in the various combinations of temperature and salinity was examined.

Response-surface methods (Box and Youle 1955; Alderdice 1972) were used to examine and compare results from individual prawns. Percent survival, the time taken for each stage to develop, and the size attained by first stage protozoea larvae (P_1) were plotted against temperature and salinity using response-surfaces generated by multiple regression equations containing linear (T, S), quadratic (T^2, S^2) and linear by linear (T x S) interaction terms. The level of significance of the component variables (T, T^2, S, S^2 and T x S) was determined using the appropriate F-ratios. The contribution that the component variables made in reducing the variance in each response-surface equation was assessed in terms of r^2 = (sum of squares due to regression)/(total sum of squares). Each experiment was continued until larvae at the lowest temperature had developed through the required number of stages (eg N_1 to P_1) or were dead (ie when all limb movement had ceased). During the experiments the containers were inspected every 2 h and the times taken for eggs to hatch or for larvae to reach a given stage of development were recorded. For each species, 400 P_1 larvae (20 from each temperature and salinity combination) were measured (TL) using an ocular micrometer.

Results

In preliminary experiments with each species, eggs and larvae were exposed to 20 combinations of four temperatures (15, 20, 25 and 30° C) by five salinities (10, 20, 30, 40 and 50‰). The results of these pilot experiments showed that the hatching success of eggs and the survival of larvae was poor at all salinities at the lowest temperature (15° C). At higher temperatures survival was least at extreme salinities (10‰ and 50‰). Because of the poor survival at 15° C and salinity extremes these levels were eliminated from subsequent experiments. Later experiments were done at four temperatures (19, 24, 29 and 34° C) and five salinities (20, 25, 30, 35 and 40‰).

Hatching

Response-surface analysis showed that both temperature and salinity significantly affected the hatching success of *P. plebejus* eggs. These eggs were less resistant to differences in salinity than to differences in temperature (Fig. 1a). Minor variations in response that occurred when there were variations in the ambient temperatures and salinities at spawning, did not result in differences in the level of significance of temperature and salinity (T, S^2, $P<0.05$). Maximum hatching success for

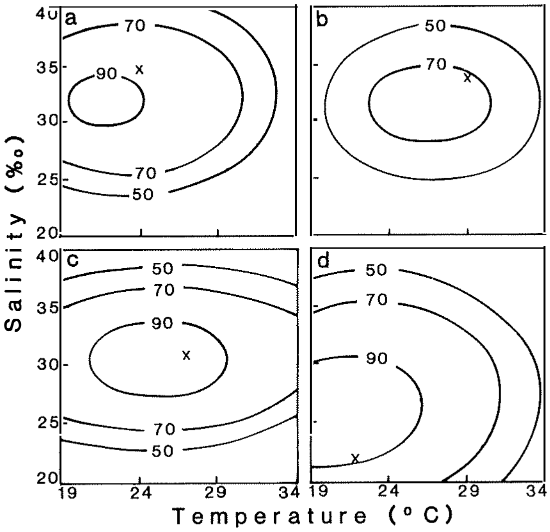

Figure 1. The combined effects of temperature and salinity on hatching success for eggs of **a.** *Penaeus plebejus,* **b.** *Metapenaeus macleayi* and **c.,d.** *M. bennettae.* Contours are the percentage of eggs that hatched. x = temperature and salinity at spawning.

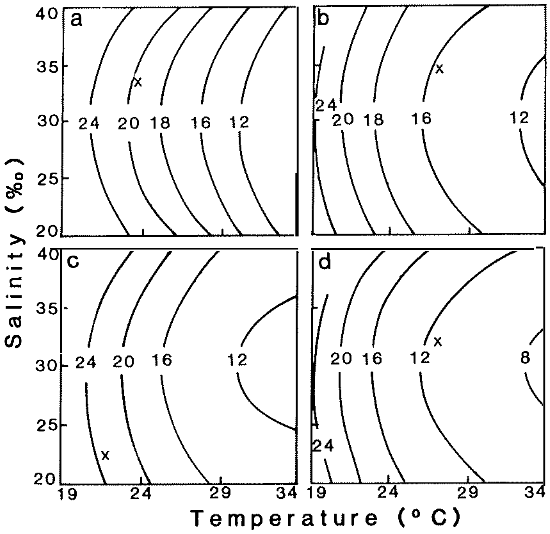

Figure 2. The combined effects of temperature and salinity on hatching time for eggs of **a.** *Penaeus plebejus,* **b.** *Metapenaeus macleayi* and **c.,d.** *M. bennettae.* Contours are the time taken to hatch (h). x = temperature and salinity at spawning.

all temperature and salinity combinations occurred when individuals spawned within 72 h of captivity.

The eggs of *M. macleayi* and *M. bennettae* spawned in marine conditions showed the same response to temperature and salinity combinations, and this differed from the response shown by *P. plebejus* eggs (Fig. 1a,b,c). Hatching success was strongly affected by temperature and salinity (T^2, S^2, $P<0.01$). At all temperatures, hatching success decreased in high or low salinities with no significant interaction between temperature and salinity. Eggs of *M. bennettae,* which were spawned in brackish conditions, showed a different response from those spawned in marine conditions (Fig. 1d). Hatching success was strongly affected by temperature, but the effect of salinity was less pronounced (T, T^2, S^2, $P<0.01$; S, $P<0.05$). Maximum hatching success occurred at combinations of low temperature and low salinity. Tolerance to a range of salinities decreased as temperatures increased (Fig. 1d).

The rate of embryonic development (mean time taken to hatch) of each of the species increased as temperature increased (Fig. 2a,b,d). Salinity alone had no significant effect. The results for *M. bennettae* and *M. macleayi,* showed that salinity interacted with temperature resulting in a decrease in development rate at combinations of high temperatures and high or low salinity (Fig. 2b,c). Eggs of *M. bennettae,* spawned in marine conditions, hatched more rapidly in all temperature and salinity combinations than those spawned in brackish conditions (Fig. 2c,d). These eggs were, however, initially exposed to higher temperatures than eggs spawned in brackish conditions and were therefore at a more advanced stage of development at the start of the experiment.

Naupliar stages

Survival from N_1, hatched in marine conditions to P_1 was strongly dependant on salinity (Fig. 3a,b,c). In addition to the pronounced effect of salinity alone (S^2, $P<0.01$) in each species, there was a significant interaction between temperature and salinity (T x S, $P<0.05$). This interaction resulted in maximal survival of larvae at the ambient temperature and salinity at hatching (Fig. 3a,b,c). The combined effects of temperature and salinity on survival of nauplii of *M. bennettae,* hatched in brackish conditions, differed from the effects on nauplii of this species, hatched in marine conditions (Fig. 3c,d). The survival of nauplii hatched in brackish conditions was more strongly determined by temperature than salinity (T, T^2, $P<0.01$; S, $P<0.05$).

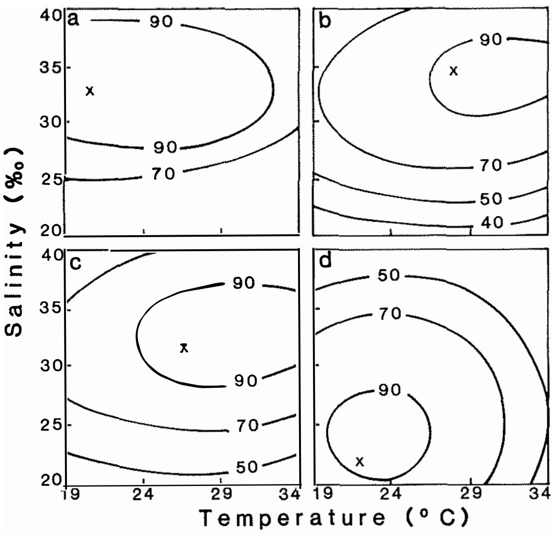

Figure 3. The combined effects of temperature and salinity on survival from the first nauplius to first protozoea of **a.** *Penaeus plebejus*, **b.** *Metapenaeus macleayi* and **c.,d.** *M. bennettae.* Contours are survival percentage. x = temperature and salinity at hatching.

For each species the rate of development from N_1 to P_1 was determined by temperature alone (Fig. 4a,b,c,d). The size attained by protozoeae of all three species was significantly affected by

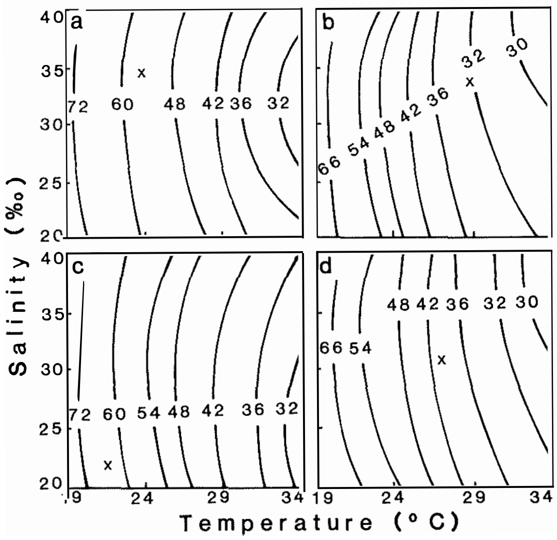

Figure 4. The combined effects of temperature and salinity on development time from the first nauplius to first protozoea of **a.** *Penaeus plebejus*, **b.** *Metapenaeus macleayi* and **c.,d.** *M. bennettae.* Contours are the median development time (h).

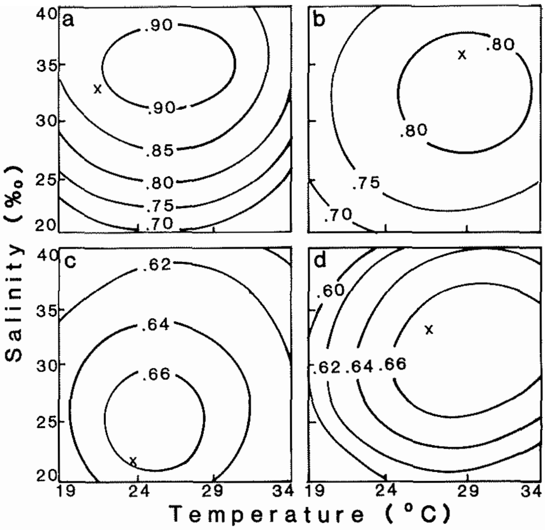

Figure 5. The combined effects of temperature and salinity on size of first protozoeae of **a.** *Penaeus plebejus*, **b.** *Metapenaeus macleayi* and **c.,d.** *M. bennettae.* Contours are the total body length (mm).

temperature and salinity (Fig. 5a,b,c,d; T^2, $P<0.01$; S^2; $P<0.05$). Larvae reared in temperatures and salinities that produced the highest survival attained a larger size.

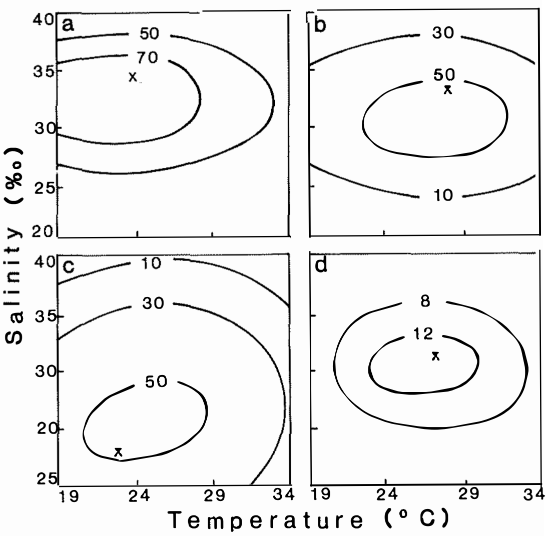

Figure 6. The combined effects of temperature and salinity on survival from first protozoea to first mysis of **a.** *Penaeus plebejus*, **b.** *Metapenaeus macleayi* and **c.,d.** *M. bennettae.* Contours are percentage survival. Diatom concentrations were 1 x 10^4 cells ml^{-1} in **a, b** and **c** and 1 x 10^2 cells ml^{-1} in **d.** x = temperature and salinity at hatching.

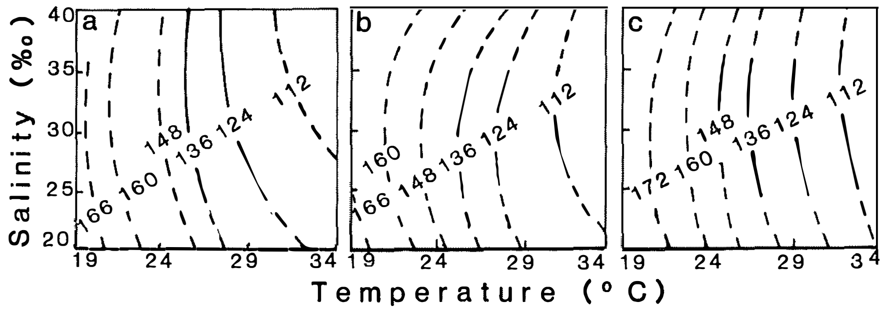

Figure 7. The combined effects of temperature and salinity on development time from first protozoea to first mysis of **a.** *Penaeus plebejus*, **b.** *Metapenaeus macleayi* and **c.** *M. bennettae*. Contours are development time (h). Broken lines are extrapolations (see text).

Protozoeal stages

Mortality was higher during the development of larvae from P_1 to M_1 than during the other stages of larval development for all species (Fig. 6a,b,c,d). Maximum survival from P_1 to M_1 was greater in *P. plebejus* than in *M. macleayi* or *M. bennettae*. In all species, maximum survival of protozoeae occurred at temperatures and salinities at which nauplii were reared prior to the experimental treatments (Fig. 6a,b,c,d). The response of the protozoeal stages of *M. macleayi* was similar to that of *P. plebejus*, as survival was significantly affected by salinity alone (S^2, $P<0.01$; Fig. 6b).

The survival of the protozoeae of *M. bennettae* was strongly affected by both temperature and salinity. Salinity had a more pronounced effect

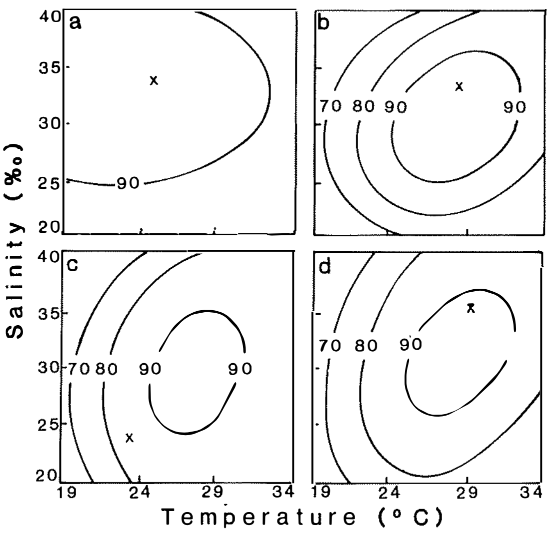

Figure 8. The combined effects of temperature and salinity on survival from first mysis to first postlarval of **a.** *Penaeus plebejus*, **b.** *Metapenaeus macleayi* and **c.,d.** *M. bennettae*. Contours are percentage survival. x = temperature and salinity at hatching.

on protozoeae initially exposed to brackish conditions than on those exposed to marine conditions before the experiments (Fig. 6c,d). Lower diatom concentrations (1×10^3 and 1×10^2 cells ml^{-1}) resulted in reduced survival (Fig. 6d) but no change in the level of significance of the temperature and salinity effects (T^2, S^2, $P<0.01$).

In all three species the duration of development from the first protozoea to the first mysis was determined by temperature alone (T, T^2, $P<0.01$; Fig. 7a,b,c). In sub-optimal conditions there were too few surviving larvae to determine accurately the range and median time taken for first protozoeae to develop to the first mysis. Response-surface analysis was therefore restricted to levels of temperature and salinity at which the survival of larvae was greater than 25%. Within this region (solid lines in Fig. 7a,b,c) the duration of the protozoeal stage was strongly temperature dependent. The development times of the few protozoeae that survived in sub-optimal conditions corresponded well with extrapolated estimates (broken lines in Fig. 7a,b,c).

Mysis stages

The mysis stages of *P. plebejus* showed a wider tolerance to temperature and salinity than larvae at earlier stages of development (Fig. 8a). Although there was a marked increase in survival through the mysis stages, the temperatures and salinities at which maximum survival occurred were similar to those for the protozoeae (Fig. 6a). In contrast, the mysis stages of *M. macleayi* and *M. bennettae* showed pronounced differences in survival in the various combinations of temperature and salinity (Fig. 8b,c,d) by comparison with the earlier stages of development (Figs. 1, 3 and 6). The myses of the *Metapenaeus* spp. had relatively high survival at all temperatures and salinities. Salinity alone had no effect on survival. At low temperatures, survival decreased but only to a level of about 70% at the lowest temperature. Maximum survival

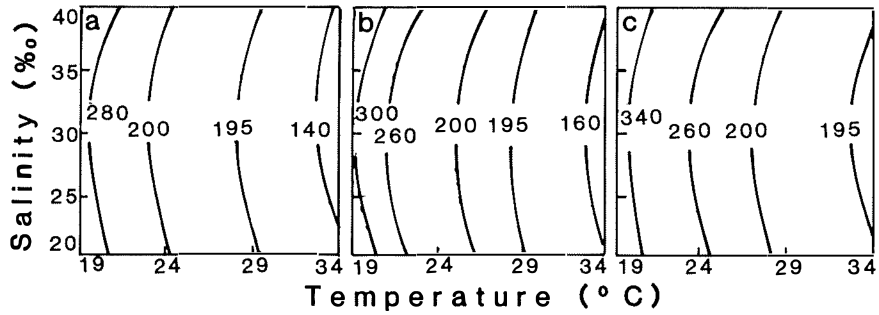

Figure 9. The combined effects of temperature and salinity on development time from first mysis to first postlarva of **a.** *Penaeus plebejus,* **b.** *Metapenaeus macleayi* and **c.** *M. bennettae.* Contours are development time (h).

(90%) of myses occurred at combinations of high temperature and low salinity, and low temperature and low salinity. This tendency was reflected in significant interactions between temperature and salinity effects as determined by response-surface analysis (T, T^2, TxS, $P<0.01$; Fig.8c,d,e).

The development time of the mysis stages of the three species was determined by temperature alone (Fig.9a,b,c), but the three species developed at different rates. *Penaeus plebejus* myses developed more rapidly to the first postlarval stage than in the *Metapenaeus* spp. *Metapenaeus bennettae* showed the lowest rate of mysis development at all combinations of temperature and salinity.

Discussion

Maximal hatching success and survival of the larvae of *P. plebejus, M. macleayi* and *M. bennettae* always occurred at the ambient levels of temperature and salinity at which spawning took place. It is evident that the strong influence of the ambient temperatures and salinities at spawning, is a factor which could explain differences in responses among and within species.

Preston (1985) suggested that the developing embryos of *M. bennettae* adapt to the temperature and salinity levels of the spawning medium, and that tolerances, defined during embryogenesis influence the tolerances of subsequent stages. The ability to adapt to environmental conditions at an early stage of development has been observed in other crustaceans (Crisp and Costlow 1963; Lucas 1972; Rosenberg and Costlow 1979). In the estuarine crab, *Rhithropanopeus harrisii,* adaptation to both temperature and salinity during embryogenesis was found to persist through larval development to the first crab stage (Rosenberg and Costlow 1979). Kinne (1963) proposed that non-genetic, embryonic adaptation to salinity may be attributed to irreversible conditioning by the spawning medium. In the absence of any known regulating mechanism operating during embryonic development, it has been suggested that salinity and temperature limits are determined by cellular responses (Crisp and Costlow 1963; Ushakov 1968). The results of the present study showed that the eggs of *M. bennettae,* initially exposed to brackish conditions, subsequently tolerated a wider range of salinities than those initially exposed to marine conditions. Cellular responses during embryonic development do not explain this difference. Instead, limits of tolerance may have been partly determined by the temperatures and salinities at which the parent stock developed gonads and the internal osmotic environment in which ovaries developed and yolk deposits were formed.

The response of nauplii to temperature and salinity was similar to the response of hatching eggs in that the temperatures and salinities at which maximum survival occurred were those at which nauplii were hatched. On moulting to the first protozoea the larvae of each of the three species attained the greatest size at temperatures and salinities optimal for survival. Laboratory studies of other decapods have shown that larvae attained a maximum size at temperatures optimal for survival (Rothlisberg 1979; Johns 1981). During the naupliar stages of penaeid prawns, yolk reserves are progressively depleted (Omori 1979). The difference in size attained by *P. plebejus*, *M. macleayi* and *M. bennettae* first protozoeae, at different temperatures and salinities may reflect differences in yolk utilisation during the development of nauplii. Laughlin (1983), found that utilisation of yolk during the early development of *Limulus polyphemus* varied significantly with both temperature and salinity. Yolk reserves were most efficiently utilised at temperatures and salinities optimal for survival. Further studies are needed to determine whether the size attained by protozoeae affects their efficiency in capturing food particles (Brooks and Dodson 1965) or their vulnerability to predators (Dodson 1974; Kerfoot 1975).

The development time from N_1 to P_1 was strongly determined by temperature. Although there were no statistically significant salinity effects, at combinations of high temperature and high salinity, nauplii of *M. bennettae*, hatched in marine conditions, tended to develop more rapidly than nauplii hatched in brackish conditions.

In all three species mortality was higher during the development of the protozoeae than at any other stage of development. At optimal temperatures and salinities, survival through the protozoeal stages was higher in *P. plebejus* than in the two *Metapenaeus* spp. Previous studies in which penaeids have been reared in the laboratory have found that the mortality of protozoeae was high, particularly at the first and third stages (Hudinaga 1942; Ewald 1965; Gopalakrishnan 1976; Omori 1979). In the present study, the survival of protozoeae was measured by recording the number of first stage protozoeae that survived through to the first mysis stage. No test was made to determine the response of the first, second and third stages independently. The shape of the response-surface contours of survival indicated that the mechanisms determining the limits of tolerance to combinations of temperature and salinity were similar to those at earlier stages.

The proportion of survival of protozoeae attributable to either temperature or salinity varied among species. In *P. plebejus*, mortality was principally due to the effects of salinity (95% of the variation accounted for). The mortality of *M. macleayi* protozoeae was also principally due to the effects of salinity (71%). In *M. bennettae*, survival was determined by both temperature and salinity (but only 68%). This indicates that mortality was not due to these factors alone. The nutritional quality of *Skeletonema costatum* and the level of food reserves of the larvae may have contributed to mortality. Hudinaga (1942) reared the first protozoeae of *P. japonicus* through to the first mysis on a diet of *S. costatum* alone, with an average survival of 27.9% and a maximum of 64.8%. The latter was similar to the maximum values obtained for *P. plebejus* in the present study. More recent studies have shown that *Thalassiosira* spp. may be more suitable for rearing the protozoeal stages of penaeid prawns (Thomas et al 1976; Emmerson 1980). Mixed algal cultures may also enhance survival, and in addition, protozoeae may feed on micro-zooplankton (Gopalakrishnan 1976; Omori 1979; Emmerson 1984). Having depleted their yolk reserves, first protozoeae are in a poor nutritional state before feeding commences (Omori 1979). The extent to which the survival of protozoeae was dependent on the availability of food was shown in the present study. At a diatom concentration of 1×10^3 cells ml^{-1}, maximal survival of *M. bennettae* first protozoeae was approximately 40%, whereas at 1×10^2 cells ml^{-1}, maximal survival was reduced to approximately 12%. The onset of feeding was clearly a critical stage in the larval development of these penaeid species, as has been found in studies of other decapods (Paul and Paul 1980; Anger et al 1981; Lang and Marcy 1982).

In the present study the mysis stages of all three species, showed an increased tolerance to differences in temperature and salinity in comparison with earlier stages. The relative indifference of the mysis larval stages to a range of salinities suggested a fundamental change in the mechanisms determining the limits of tolerance of larvae to salinity. Increased tolerance to a range of salinities was most pronounced in the mysis stages of *M. macleayi* and *M. bennettae.* In these species, salinity alone had no significant effect on mortality. Differences in the level of salinity had a significant effect on the survival of the mysis stages of *P. plebejus* but the mysis larvae were more tolerant to the range of salinities than the earlier larval stages.

There is a significant difference in size of the mysis larvae of these species (Preston, unpubl). *Penaeus plebejus* are the largest and *M. bennettae* the smallest. More efficient capture of *Artemia* nauplii by the larger mysis larvae may have speeded development.

The present laboratory experiments showed that when spawning occurred in marine conditions, the response of the eggs, nauplii and protozoeae to temperature and salinity was similar for the three species. Hatching success and the survival of larvae was less than 50% at salinities less than 20‰. These data indicate that the effects of salinity may be important in determining survival during early development and that low salinities would present a physiological barrier to eggs and larvae previously exposed to marine conditions.

There are no records of *P. plebejus* spawning in areas of reduced salinity. Dall and Smith (1981) found that adult *P. plebejus* were poor osmoregulators. The evidence from the present study was that high salinity (>25‰) was required for the successful development of eggs, as suggested by Allen (1966). The osmoregulatory ability of *M. macleayi* has not been studied, but there are no records of this species spawning in areas of reduced salinity. Dall and Smith (1981) found that adult *M. bennettae* were highly efficient osmoregulators. The results of the laboratory experiments in the present study provided strong evidence that the eggs and larvae of *M. bennettae* showed an adaptive response to the effects of temperature and salinity, associated with changes in spawning conditions. During the spawning season of *M. bennettae,* the rates of change of temperature and salinity are normally slow, with a graduation of environments from brackish to marine (Gordon 1981). In these conditions, an adaptive response to ambient levels of temperature and salinity during early development would enhance survival through to the first mysis. Subsequent survival during development from M_1 to the first postlarva was found to be relatively independent of temperature and salinity. Extreme floods in Smiths Lake or similar lagoons, although short-lived, can result in major changes in salinity (Gordon 1981). Laboratory experiments showed that few eggs hatched and no larvae survived at combinations of low temperature (<20°C) and low salinity (<10‰) indicating that mortality would be great in flood conditions.

The data from these experiments showed that the direct effect of temperature, although significant, was of secondary importance to salinity in determining the survival of eggs and larvae. At the lowest temperature tested at which eggs and larvae survived (19°C), the total development time from eggs to postlarvae was from 22 to 25 days depending on the species. At the highest temperature (34°C), development time was reduced to 12 to 14 days. The indirect effect of temperature may, therefore, significantly affect the survival of prawn larvae by determining the length of time that larvae are exposed to planktivores.

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Identification of the postlarvae of the commercially important *Penaeus* species in Australia

Abstract: Techniques for identifying postlarval *Penaeus* spp. taken during ecological studies in the Gulf of Carpentaria were examined on the basis of both field-collected and laboratory-reared material. A working key was then developed and later extended to include the six main commercial prawn species in Australia. Three groups of species can be identified: (a) banana prawn group, (b) tiger prawn group and (c) king prawn group based on easily observed and quantified morphological characteristics. The distinguishing characters used were carapace: rostrum length ratio and the ratio of two distances measured between telson spines. Species identification within these three main groups is more difficult and uses multivariate numerical identification based on discriminant analysis of known species. At present, *P. esculentus* and *P. semisulcatus,* can be separated within the tiger prawn group, and *P. latisulcatus, P. longistylus* and *P. plebejus* with a lower degree of accuracy within the king prawn group. The only banana prawn species included in the analysis is *P. merguiensis.*

Introduction

The taxonomic status and identification of the adult stage of the genus *Penaeus* from Australian waters has been well reviewed by Dall (1957) and Racek and Dall (1965). Identification of these species has been simplified by the key of Grey et al (1983) but the identification of their postlarvae remains much more difficult. Young (1977) developed a key for the identification of juvenile penaeid prawns of Moreton Bay, southeastern Queensland which included *Penaeus esculentus* and *P. plebejus.* A key by Paulinose (1982) identified the early postlarval stages of *P. merguiensis, P. indicus, P. monodon,* and *P. semisulcatus* in Indian Ocean waters. Motoh and Buri (1981) also used a key to identify four groups of *Penaeus* postlarvae from Philippine waters. Both the keys of Paulinose, and Motoh and Buri, however, refer only to a narrow range of postlarval sizes and do not cover all the species found in Australian waters. The present study was initiated to develop a working key for the identification of *Penaeus* postlarvae found during ecological studies in the Gulf of Carpentaria. The main species involved were *P. merguiensis, P. esculentus, P. semisulcatus, P. latisulcatus* and *P. longistylus.* With the inclusion of *P. plebejus* in the key, all the main commercial species in Australia have been covered. Postlarvae of *P. canaliculatus, P. indicus, P. japonicus, P. marginatus* and *P. monodon* are not included at present.

Materials and methods

Both pelagic and benthic prawns <3mm carapace length (CL) were considered as postlarvae in this study. Data from both field-collected and laboratory-reared animals were used to provide reference material. Field specimens were taken in both plankton trawls (1mm mesh) and benthic beam trawls (2mm mesh body with 1mm mesh codend). Samples included postlarvae of *P. merguiensis* (from the Norman River, Gulf of Carpentaria), *P. plebejus* (from Southport, southeastern Queensland) and *P. latisulcatus* from Gulf Saint Vincent, South Australia. The identification of field collected material was checked by rearing postlarvae through to juvenile stages in the case of *P. merguiensis* and by detailed comparisons of all stages throughout their development for the other two species. Animals which were reared in the laboratory from females of known species included *P. longistylus*

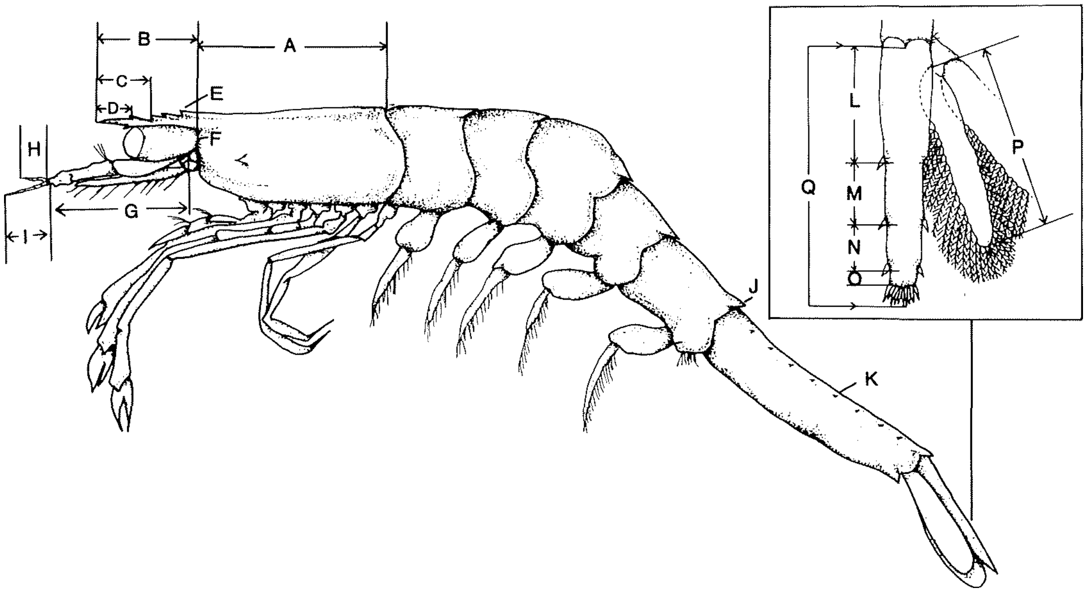

Figure 1. Postlarval *Penaeus* specimen showing morphological characters used for identification of the main commercial species in Australia. Symbols A to Q are described in full in Table 1.

(from Groote Eylandt, Gulf of Carpentaria), *P. esculentus* (from Moreton Bay, southeastern Queensland), *P. semisulcatus* (from Cairns, northern Queensland). Some *P. latisulcatus* specimens were also obtained from a prawn culture farm at Port Broughton, South Australia. All specimens were preserved in 10% formaldehyde in buffered seawater. A stratified subsample covering a representative size range of animals was mounted on slides and a series of morphological characters was quantified (Fig. 1 and Table 1). Many of the characters selected have previously been shown to be useful for postlarval identification by other workers (Cook 1966; Ringo and Zamora 1968; Young 1977; Motoh and Buri 1981). Measurements were made to an accuracy of 0.02 mm using an ocular micrometer at 180x magnification. Specimens were first classified into broad groups on examination of the more easily measured and quantified characters. Identification to the species level within these groups, was then carried out using numerical taxonomy based on a discriminant analysis of known reference material (Sneath and Sokal 1973). All measurements were first converted to ratios by dividing by CL to remove the slight differences in initial size of the reference material for each species. Initially, a stepwise analysis was conducted to select the characters most useful in discriminating between species. The classification scores for these characters were then calculated and the reference material re-analysed as unknowns and the success of the classifications and the probability of correct identification calculated. Classification scores for an individual of species j are calculated as

$$Cscore_j = a_j + b1_j x1 + b2_j x2 + \ldots\ldots\ldots$$

where $Cscore_j$ is the classification score based on the classification functions comprised of the constant a_j and coefficients $b1_j$, $b2_j$ etc. for characters x1, x2 etc. The specimen is classified to the species having the highest classification score. The probability P_j of an individual belonging to species j out of q species is calculated as

$$P_j = \frac{\exp(Cscore_j)}{\sum_{k=1}^{q} \exp(Cscore_k)}$$

Results

Postlarval identification

Group identification

Several ratios of the more easily measured characters were first examined in order to determine whether species or species groups could be separated without resorting to detailed numerical analyses. The ratio of CL to rostrum

Table 1. Description of characters considered for *Penaeus* postlarvae identification. Symbols as in Figure 1.

	Description
A	Carapace length
Rostral characters	
B	Rostrum length
C	Distance from base of penultimate dorsal rostral tooth to rostral tip
D	Distance from base of last rostral tooth to rostral tip
E_1	Number of dorsal rostral teeth (includes epigastric)
E_2	Number of ventral rostral teeth
F	Position of dorsal rostral teeth relative to orbital socket (expressed as ordered multi-state variable ranking 0 to 5)
First antennae characters	
G	Antennal length
H_1	Exopod length
H_2	Number of exopod segments
H_3	Number of spines on exopod tip
I_1	Endopod length
I_2	Number of endopod segments
Abdominal characters	
J	Presence and relative size of fifth abdominal spine (0 to 3, absent to large)
K	Presence or absence of spines on sixth abdominal segment
Telson and uropod characters	
L	Upper telson base to first spine base
M	Distance between bases of first (proximal) and second lateral telson spines
N	Distance between bases of second and third lateral telson spines
O	Distance between base of third (distal) lateral spine and base of outer terminal spine
P	Inner uropod length
Q	Telson spine formula (bilateral spine count eg 8+8=16)

length (Fig.2a and b) for all species ranged from 0.82 to 5.07 (Table 2a). However the ratio ranged from 2.96 to 5.07 in the king prawns species, (*P.latisulcatus, P.longistylus* and *P.plebejus*), effectively separating this group from the other species whose ratios ranged from 0.82 to 2.41. The point of separation between king prawns and others was set at 2.69, the midpoint between the highest combined banana and tiger prawn group and the lowest king prawn group ratio recorded. The banana and tiger prawn groups were then separated without overlap by differences in ratio of telson spine distances M:N (Fig.3a and b), 0.98 to 1.07 for the banana prawn group,

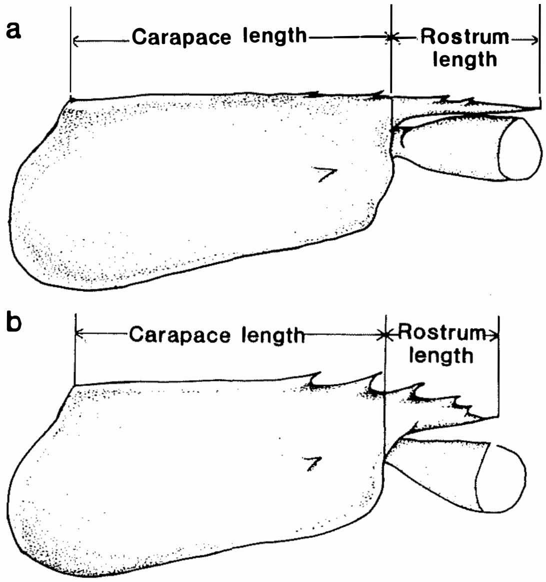

Figure 2. *Penaeus* postlarvae showing **a.** banana and tiger prawn group with long rostrum relative to carapace length (*P.merguiensis, P.esculentus* and *P.semisulcatus*), **b.** king prawn group showing short blunt rostrum relative to carapace length (*P.latisulcatus, P.longistylus* and *P.plebejus*).

P.merguiensis (Table 2b), and 1.48 to 2.34 for the tiger prawn group, *P.esculentus* and *P.semisulcatus* (Table 2a). The point of separation between the banana and tiger prawn groups was set at 1.28, the midpoint between the highest banana prawn group ratio and the lowest tiger prawn group ratio.

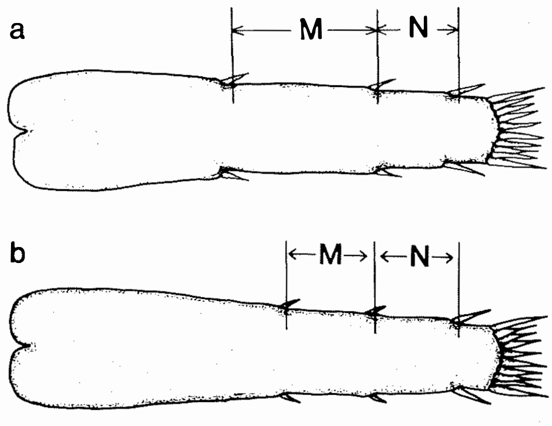

Figure 3. Telson of *Penaeus* postlarvae showing **a.** tiger prawn group with a high M:N ratio (*P.esculentus* and *P.semisulcatus*), **b.** banana prawn group with low M:N ratio (*P.merguiensis*).

Table 2. Ratios of **a.** carapace length to rostrum length **b.** first telson spine distance (Table 1, M) to second telson spine distance (Table 1, N) in postlarvae of six Australian *Penaeus* species. SE is the standard error of the ratio based on n observations.

	Carapace length (mm)											
	1.0-1.49			1.5-1.99			2.0-2.49			2.5-2.99		
	Ratio	SE	n	Ratio	SE	n	Ratio	SE	n	Ratio	SE	n
a. Carapace length: rostrum length												
Banana prawn group												
P. merguiensis	2.02	0.01	30	1.40	0.03	55	1.01	0.02	9	0.82	—	4
Tiger prawn group												
P. esculentus	2.41	0.03	70	1.87	0.08	31	1.20	20.05	10	1.07	—	4
P. semisulcatus	2.12	0.05	48	1.56	0.04	40	1.25	0.02	19	1.28	0.01	9
King prawn group												
P. latisulcatus	4.27	0.03	67	5.07	—	1	4.63	0.28	5	3.62	—	1
P. longistylus	3.63	0.08	35	4.01	0.06	55	3.53	0.05	33	3.07	0.06	9
P. plebejus	2.96	0.07	22	3.50	0.05	50	3.49	0.03	51	4.11	—	2
b. Telson spine ratios (M:N)												
Banana prawn group												
P. merguiensis	1.07	0.01	104	1.01	0.01	163	0.99	0.02	18	0.98	—	4
Tiger prawn group												
P. esculentus	2.34	0.06	75	1.89	0.03	32	1.63	0.04	9	1.56	0.02	8
P. semisulcatus	2.31	0.09	52	1.65	0.02	45	1.65	0.04	20	1.48	0.03	18
King prawn group												
P. latisulcatus	1.80	0.02	66	2.06	—	4	1.41	0.03	11	1.56	—	1
P. longistylus	1.58	0.04	35	1.32	0.01	55	1.41	0.01	34	1.29	0.01	11
P. plebejus	1.60	0.03	22	1.41	0.01	51	1.33	0.01	58	1.29	—	3

Table 3. Characters and their classification parameters used for the identification of *Penaeus esculentus* and *P. semisulcatus* from within the tiger prawn group. Characters are listed in order of importance together with their F-values used to enter the variable into the model (n=191). Character symbols as in Figure 1 and Table 1.

Character	F-value	Classification coefficients: *Penaeus esculentus*	Classification coefficients: *Penaeus semisulcatus*
Number of exopod spines $\mathbf{H_3}$	126.84	3.073	1.980
Telson spine distance **M**	16.24	91.816	142.369
First antennal length **G**	13.38	69.797	57.230
Telson spine distance **N**	22.77	5.438	34.762
First antennal exopod length $\mathbf{H_1}$	8.41	119.158	132.185
Constant		-56.924	-54.586

Table 4. Characters and their classification parameters used for the identification of *Penaeus latisulcatus*, *P. longistylus* and *P. plebejus.* Characters are listed in order of importance together with their F-values used to enter the variables into the model (n=307). Character symbols as in Figure 1 and Table 1.

Character	F-value	Classification coefficients: *Penaeus latisulcatus*	Classification coefficients: *Penaeus longistylus*	Classification coefficients: *Penaeus plebejus*
Telson spine distance **L**	79.34	172.856	217.621	59.851
Telson spine distance **M**	22.39	-83.793	-2.931	-10.917
Inner uropod length **P**	24.16	248.255	222.186	206.626
First antennae endopod length $\mathbf{I_1}$	16.18	50.211	47.827	79.708
Relative size fifth abdominal spines **J**	10.12	-2.813	-3.504	-2.665
First antennal length **G**	8.67	-15.879	-5.353	-2.319
Telson spine distance **O**	12.21	113.273	99.160	89.683
Constant		-97.299	-92.585	-82.713

The following key separates the six species of *Penaeus* postlarvae in the size range of 1 to 3 mm CL into three prawn groups, king, tiger and banana.

1. Rostrum slender, extending beyond or level with eyes (Fig. 2a), (ratio of carapace length: rostral length <2.69); usually with ventral rostral teeth if CL greater than 1.8 mm **2**

Rostrum coxcomb and blunt, not extending beyond eyes (Fig. 2b), (ratio of carapace length: rostral length ≥ 2.69); no ventral rostral teeth .... **King prawn group**

2. Telson spine ratio M:N high (Fig. 3a), (ratio M:N >1.28) .... **Tiger prawn group**

Telson spine ratio M:N low (Fig. 3b), (ratio M:N ≤ 1.28) .... **Banana prawn group**

Species identification

Within the tiger prawn group the characters most useful for discriminating between the two species of tiger prawns in order of importance were the number of spines on the tip of the first antennal exopod, (Table 1, H_3) first telson spine distance (Table 1, M) first antennal length (Table 1, G), second telson spine distance (Table 1, N) and first antennal exopod length (Table 1, H_1) (Table 3). Other characters did not significantly increase the precision of the identification. Calculating the classification scores for each specimen in the reference material (multiplying each character value by its coefficient and adding the constant) resulted in correct identifications for 82% and 94% for *P. esculentus* and *P. semisulcatus* respectively. To verify the accuracy of the technique a random subgroup of the reference material was used to calculate the coefficients and then the remainder of the sample was treated as unknowns resulting in correct identifications in 81% and 96% of the cases. For the king prawn group the most useful characters were the upper telson length (Table 1, L) and the first telson spine distance (Table 1, M), inner uropod length (Table 1, P), first antennal endopod length (Table 1, I_1), relative size of fifth abdominal spine (Table 1, J), first antennal length (Table 1, G) and third telson spine distance (Table 1, O) (Table 4). Percentage correct identifications were 71%, 78% and 82% for *P. plebejus, P. latisulcatus* and *P. longistylus* respectively. Percentage correct identifications for the random subsample were 56%, 71% and 58%. The lowered accuracy for the king prawn group resulted from the close similarity of *P. plebejus* to the other two species making them difficult to separate. Percentage correct identifications for *P. latisulcatus* and *P. longistylus* alone were 94% and 96%. Therefore to identify the two species within the tiger prawn group and the three species within the king prawn group:

1. Calculate classification score using coefficients from either Table 3 (tiger prawn group) or Table 4 (king prawn group).

2. Compare classification scores. Highest value gives identification providing probability >0.95.

Discussion

Several field observations can be used to aid identification. These include geographical distribution, habitat preferences, and pigmentation. The geographical ranges of the species belonging to the banana, tiger, and king prawn groups are well described by Grey et al (1983). In general, settlement of postlarvae usually occurs inshore in the same region as is inhabited by adult stock (Staples et al 1985) and the presence of adult prawns adjacent to a postlarval sampling point may be used as a guide to the postlarval identification. The habitat type preferred by postlarvae and juveniles of many *Penaeus* species has also been described by Staples et al (1985). Pelagic postlarvae are widely distributed whereas benthic postlarvae typically select more restricted habitat types. Postlarvae of the banana prawn inhabit shallow (<3 m) bare mud substrate usually within the confines of mangrove lined creeks and rivers. Tiger prawn postlarvae, on the other hand, are found mainly in seagrass and algal areas on soft sandy mud substrate. King prawn postlarvae typically settle out on the shallow bare sandy substrates. Knowledge of the site of collection can therefore be of great assistance in making identifications. Motoh and Buri (1981) used the pigmentation pattern of fresh material for distinguishing the main groups of *Penaeus* in the Philippines. Postlarval banana prawns are typically white, opaque with little pigmentation. The tiger prawns (greater than 1.8 mm CL) are very heavily pigmented with reddish brown chromatophores especially on the tips of the telson and uropods. Chromatophores expand to colour most of the animal in older postlarvae. The king prawn postlarvae, in contrast, are more lightly pigmented on the uropods and telson. All pigmentation fades within two to three months in formaldehyde solution.

After a specimen has been keyed to within one of the major groups, detailed measurements and observations are necessary to derive a species identification. At present our key covers only six species of *Penaeus* and some care in its use is necessary. Using the classification score method of identification can give an identification for any unknown specimen unless one adopts the rule that if the probability of the identification is below critical level (say 95%) then the specimen is classified as unknown. Even with this imposed probability, without further development of the key it is not known whether the technique will work on morphologically similar species such as *P. merguiensis* and *P. indicus.* The present key must therefore be considered preliminary and further development and modification will be made as more reference material becomes available. A collaborative approach from several laboratories using similar techniques would speed the key's expansion and its usefulness.

Acknowledgements

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Habitat requirements of juvenile penaeid prawns and their relationship to offshore fisheries

Abstract: The habitat requirements of the juvenile stage of five major commercial penaeid prawn species and the resource partitioning of an estuary by these species were studied in the Embley River in northeastern Gulf of Carpentaria during 1981-82. Sampling was carried out over a series of 24 h stations with a small beam trawl. The maximum catch recorded during the 24 h period was taken as a measure of the relative abundance of prawns. For the five commercial species, seagrass flats, algal beds and mud banks immediately adjacent to the mangrove fringe (mud-mangrove banks) formed the main nursery areas. All species, with the exception of *Metapenaeus ensis,* were found predominantly in one habitat type. Juvenile tiger prawns, *Penaeus esculentus* and *P. semisulcatus,* were most common in seagrass whereas the juvenile banana prawn, *P. merguiensis,* was largely confined to mud-mangrove banks. *Metapenaeus endeavouri* occurred commonly on seagrass but with some spread to other habitats while *M. ensis* was widespread, occurring on seagrass, mud-mangrove, bare intertidal mud and open channel locations. Because of these specialised habitat requirements, especially of the *Penaeus* species, the regional distribution and long-term abundance of adult prawns of this genus in the Gulf appears to be related to the geographic distribution and size of their nursery areas.

Introduction

Five species of penaeid prawns make up more than 98% of the total commercial catch of prawns in the Gulf of Carpentaria (data of Commonwealth Department of Primary Industry for 1980 to 1983, Canberra). These are the banana prawn, *Penaeus merguiensis,* the tiger prawns, *P. semisulcatus* and *P. esculentus,* and the endeavour prawns, *Metapenaeus endeavouri* and *M. ensis.* The Gulf fishery commenced in the late 1960s and catches of banana prawns were high in the early years due to favourable environmental conditions and the discovery of new fishing grounds. Over the last decade, the catch of banana prawns has declined and tiger and endeavour prawns have become increasingly exploited. Tiger prawns now form the main component of the catch (Fig. 1). Initial research in the Gulf of Carpentaria concentrated on banana prawns but as the importance of tiger prawns increased, more research effort has been directed into tiger prawn life history and population dynamics.

A considerable amount of information is now available on juvenile stages of the banana prawn in the Gulf of Carpentaria (for review see Dall 1985) but little information exists on juvenile stages of the other important commercial species. A few studies on these species have been carried out in other areas, however, including the recruitment and distribution of *P. esculentus* in Moreton Bay, Queensland, Australia (Young and Carpenter 1977; Young 1978), postlarval and juvenile stages of *P. semisulcatus* and *M. ensis* in India (Silas et al 1984), Tongatapu (Braley 1979), Indonesia (Noor-Hamid 1976), and some work has been reported on *P. semisulcatus* in the Arabian Gulf (Van Zalinge 1984) and the Sinai Peninsula region (Tom et al 1984). The habitat requirements of several related species were examined in Mozambique by Hughes (1966).

The present study was initiated to examine the temporal and spatial variation in the distribution

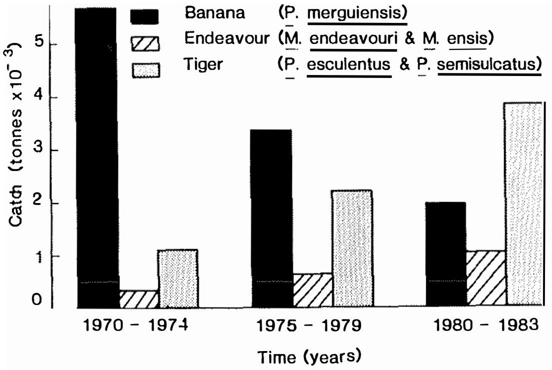

Figure 1. Mean annual commercial prawn catch for the three main species groups in the Gulf of Carpentaria, 1970 to 1983. (Data from Commonwealth Department of Primary Industry, Canberra).

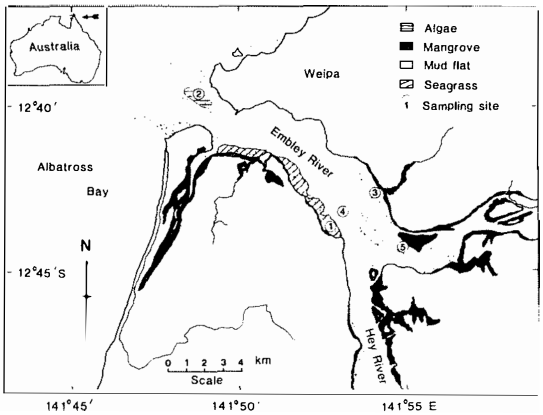

Figure 2. The Embley River estuary at Weipa. Sampling sites shown as: (1) intertidal seagrass flat, (2) shallow algal bed, (3) intertidal non-vegetated mud flat, (4) deepwater channel, (5) intertidal mud-mangrove bank.

of penaeid prawns inhabiting an estuarine system in the Gulf of Carpentaria. The Embley River in the northeastern Gulf was chosen as a study site mainly because of the presence of the five main commercial species in the offshore Albatross Bay region (Grey et al 1983). The seasonality in the distribution and abundance of these species has also been examined (CSIRO, unpublished data[1]) and the estuary contains a wide range of habitats likely to be suitable as nursery areas for juvenile prawns. Further, the narrow mouth of the estuary facilitated the monitoring of immigration and emigration of prawns.

This paper reports on some preliminary findings on the spatial distribution of the five major commercial species over scales ranging from within habitats (m) to Gulf-wide comparisons ($m \times 10^5$). Findings for other species and the temporal distribution of prawns on scales ranging from tidal and diel cycles (h) to seasonal comparisons ($h \times 10^3$) will be reported elsewhere.

Materials and methods

Juvenile prawns were collected from the Embley River estuary at three-weekly intervals from September 1981 to September 1982 using a 1x0.5m beam trawl fitted with a 2mm mesh net and a 1mm mesh codend. Five habitat types were selected for detailed sampling:
(1) seagrass flat, *Enhalus acoroides,* (2) shallow algal bed, mainly *Laurencia* sp. and *Sarconema* sp., (3) intertidal bare mud flat, (4) deep subtidal channel and (5) steep intertidal mud bank immediately adjacent to the mangrove fringe (mud-mangrove bank) (Fig.2). Trawls on the wide gently shelving intertidal banks were made at right angles to the shore while other samples were taken parallel to the shore in the direction of the prevailing current. Trawls were repeated every 2h throughout a 24h period and the maximum catch taken during the 24h period was used as the index of relative abundance. Larger specimens, >5 to 7mm carapace length (CL), were identified to species using morphological characters revised from Grey et al (1983). Smaller specimens were identified using numerical taxonomy methods based on known reference material (Heales et al 1985). For the between-habitats comparisons, only prawns >5mm CL were used.

Dispersion within a habitat was estimated from a series of 10 parallel 200m long trawls taken at random within a 20m wide strip on the intertidal flats and 10 consecutive 30m trawls along the steeper bank. All trawls were taken at the time of day and tide stage known to maximise catches (eg low tide for *P. merguiensis*—Staples and Vance 1979). Similar samples in the Norman River in the southeastern Gulf (17° 30′ S, 140° 50′ E) were also analysed for banana prawn dispersion patterns. In this case, eight random trawls were made each week for 40 weeks within a 500m length of the estuarine bank. Morisita's index of dispersion (Morisita 1959) was used to describe dispersion patterns of all species and was calculated as—

$$I_\delta = \frac{k \sum_{i=1}^{k} n_i (n_i - 1)}{T (T-1)}$$

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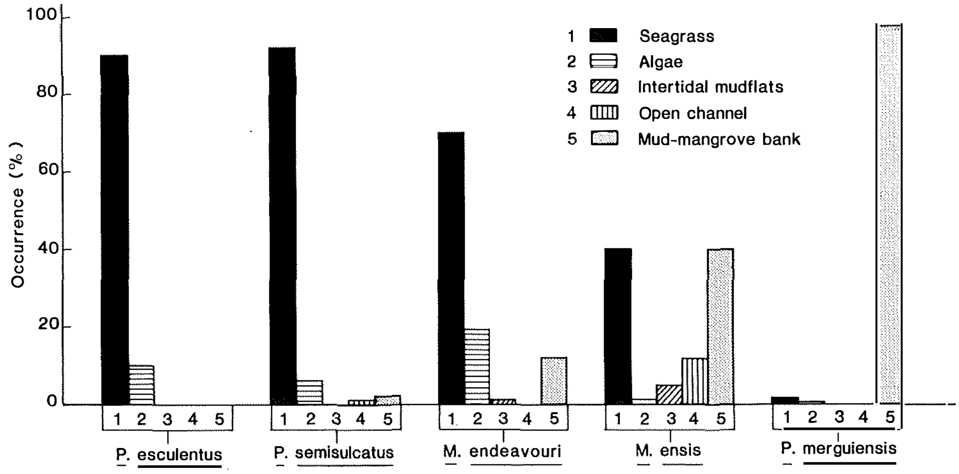

Figure 3. Percentage distribution of the catch of the five major commercial prawn species in each of five habitats in the Embley River estuary, 1981-82.

where k is the total number of samples taken, n_i is the number of individuals in sample i, and T is the total number of individuals taken. The significance of the departure from random is given by the variance ratio—

$$F = \frac{I_{\delta} \cdot (T-1) + k-T}{T-1}$$

for k-1 and ∞ degrees of freedom.

On a regional scale, the mean annual catch of banana and tiger prawns was estimated from landing figures and logbook returns for the 10 year period, 1973 to 1982 (data of Commonwealth Department of Primary Industry, Canberra). Geographic distribution of prawn catches was obtained from figures published by the Australian Fisheries Council (AFC 1982). The size of the estuarine mangrove systems within each region of the Gulf was estimated from Australian Topographic Survey Maps (1:100,000) for the Gulf coastal regions. The linear distance of the estuary fringed with mangroves, rather than mangrove area, was used as the best index of the available mangrove nursery area. Seagrass distributions within the Gulf were established from aerial surveys and subsequent transect sampling carried out in collaboration with I.R. Poiner (unpublished data[2]).

[2] I.R. Poiner, CSIRO Marine Laboratories, PO Box 120, Cleveland, Qld 4163, Australia

Results

Between-habitat distribution

Because habitats were in close proximity, temperature and salinity differences between habitats were negligible. Strong spatial partitioning existed among the five species, however, with all species, with the exception of *M. ensis* found predominantly in one habitat type (Fig.3). *Penaeus esculentus, P. semisulcatus* and *M. endeavouri* had their highest occurrence on the seagrass site while *P. merguiensis* was largely confined to the mud bank immediately adjacent to the mangrove fringe (mud-mangrove bank). The percentage occurrence within these habitats was more than 90% for the two tiger prawn species, 70% for the endeavour prawn and approximately 97% for the banana prawn. In terms of total habitats occupied, *P. esculentus* and *P. merguiensis* showed the narrowest range followed by *P. semisulcatus, M. endeavouri* and then *M. ensis.* Approximately 20% of *M. endeavouri* occurred on the algal bed and 10% were on the mud-mangrove bank while *M. ensis* was even more widespread occurring equally on the seagrass and mud-mangrove sites. *Metapenaeus ensis* was the only commercial species to occupy the bare intertidal mudflats and open channel locations.

Within-habitat distribution

In both the seagrass area and on the mud-mangrove bank, the index of dispersion used to describe the dispersion pattern of the different prawn species, did not differ significantly from

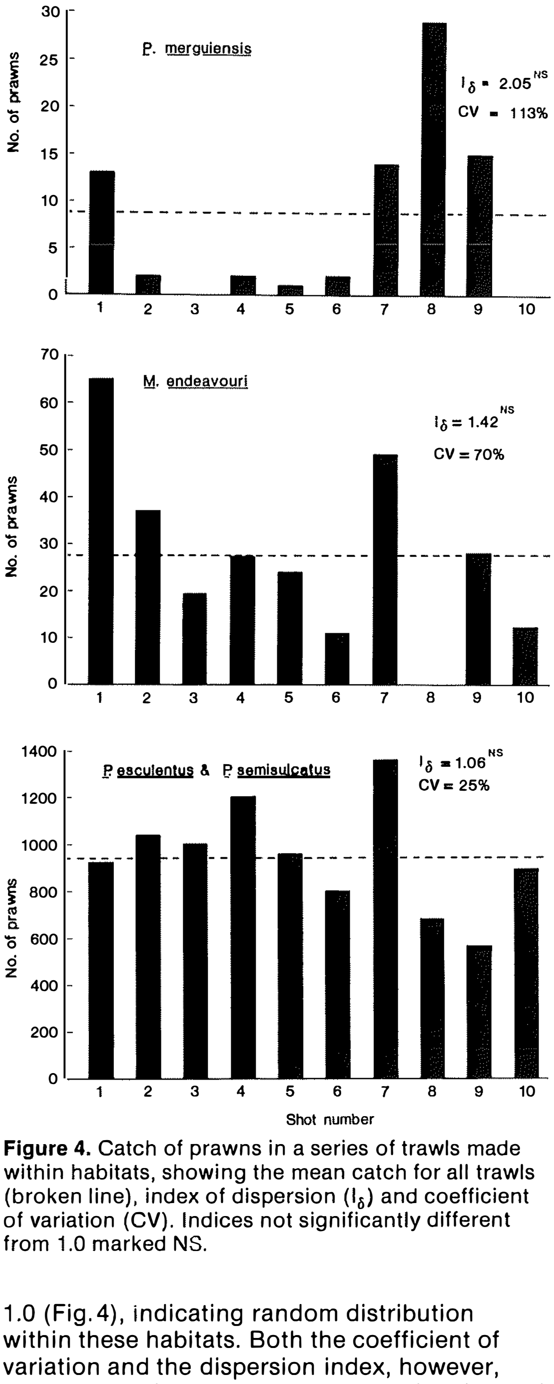

Figure 4. Catch of prawns in a series of trawls made within habitats, showing the mean catch for all trawls (broken line), index of dispersion (I_δ) and coefficient of variation (CV). Indices not significantly different from 1.0 marked NS.

1.0 (Fig. 4), indicating random distribution within these habitats. Both the coefficient of variation and the dispersion index, however, were greater for *P. merguiensis* than for either of the other groups indicating a greater tendency for clumping (Fig. 4). When juvenile and postlarval *P. merguiensis* were analysed separately, the dispersion index was significantly higher than unity within each stage ($P<0.05$). Because of the low sample numbers involved in this analysis we also tested 40 sets of random trawls taken in the Norman River between 1977 and 1979. The average dispersion index was 1.76 and ranged from 0.94 to 5.85. It was significantly greater than 1.0 on three occasions. We concluded that all species were essentially randomly distributed within habitats, although *P. merguiensis* was more variable and had a greater tendency for aggregation.

Distribution of nursery areas and catches

The main nursery area for juvenile *P. merguiensis* near the Embley River mouth was the mud-mangrove banks. Further sampling showed that both mangroves and juvenile banana prawns extended approximately 30 km inland, close to the upper limit of tidal influence. Similar mangrove lined estuarine rivers and creeks extend around the Gulf with a major concentration in the southeastern region (Fig. 5). Commercial catches of banana prawns are also widespread around the Gulf with the exception of a small area within the Limmen Bight region. Mean annual catch taken from 1973 to 1982 from each region of the Gulf was positively correlated with the size of the nursery area present inshore, calculated as the total length of available mangrove lined estuary ($r=0.76, df=5, P<0.05$; Fig. 6). The Limmen Bight region of the Gulf did not fit this relationship, and factors other than available nursery area presumably have more effect on catches in this region. Omitting Limmen Bight from the analysis resulted in a correlation coefficient of 0.96, ($df=4, P<0.01$) for the other five regions.

Seagrass areas in the Gulf are much patchier than mangroves in their distribution and are confined largely to the western Gulf. Catches of tiger prawns are also more discontinuous than banana prawns and are restricted to regions where seagrass nursery areas occur (Fig. 7). Complete quantitative data on seagrass areas are not yet available although considerable mapping and some analyses have been carried out. Preliminary analyses suggest that regional catches of tiger prawns are related to the area of available seagrass habitat with again the exception of the Limmen Bight region.

Discussion

Four of the five commercially most important species of prawns in the Gulf of Carpentaria, were closely associated with some form of vegetation during the juvenile phase of their life

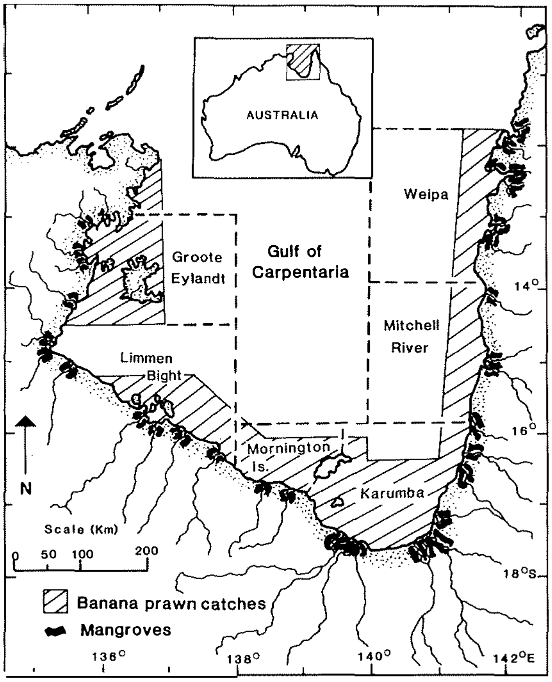

Figure 5. Distribution of mangrove lined rivers and extent of commercial catches of banana prawns *Penaeus merguiensis* in the Gulf of Carpentaria. Boundaries of the statistical catch regions are defined by broken lines.

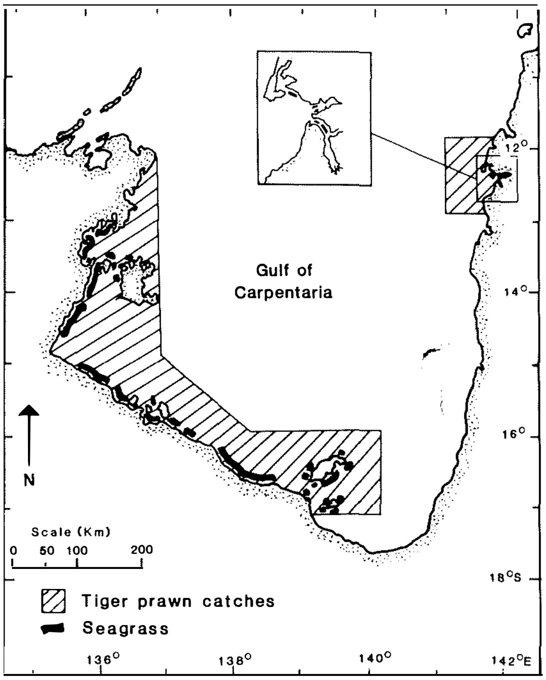

Figure 7. Distribution of seagrass areas and extent of commercial catches of tiger prawns *Penaeus esculentus* and *P. semisulcatus* in the Gulf of Carpentaria. Seagrass areas in the northeastern Gulf are mainly confined to estuaries and are shown in the inset.

history in the Embley River estuary. The most important nursery habitats were the intertidal seagrass flats, algal beds and mud-mangrove banks of the estuary. The three species of the genus *Penaeus* were more restricted in their habitat requirements than the two *Metapenaeus* species. Within the *Penaeus* species there was little overlap between tiger prawns (both species) which were found mainly on seagrass, and banana prawns which were largely confined to the mud-mangrove banks. Of the two *Metapenaeus* species, *M. endeavouri* was found most commonly in the typical tiger prawn seagrass habitat but a significant percentage was also found in the algal and mud-mangrove areas. *Metapenaeus ensis* occurred equally in the seagrass and mud-mangrove areas and was also the only species to occur in any numbers on the bare intertidal mudflat and open channel. In comparing the distribution of the different species among habitats, it must be remembered that not all habitats are equally stable in time. The relatively low use of algal areas by the tiger and endeavour prawns, for example, is in part a reflection of the instability of algal areas in the estuary. Good algal cover occurred only in spring (September to November) and autumn (March to May) and because prawn occurrence was calculated on an annual basis the importance of algal areas may be underestimated. The more dynamic interactions between prawn abundances and preferred habitats will be reported elsewhere.

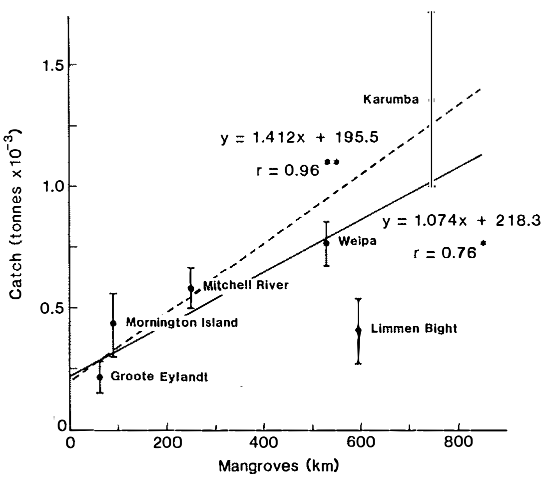

Figure 6. Mean annual commercial banana prawn catch (± standard error) and total length of mangrove lined rivers in each region of the Gulf of Carpentaria. The regression lines for all regions (solid line) and for all regions except Limmen Bight (broken line) are shown. $^*P<0.05$, $^{**}P<0.01$.

Many species of the genera *Penaeus* and *Metapenaeus* utilise the inshore coastal waters and estuaries as nursery areas during the juvenile phase of their life history (Kutkuhn 1966; Kirkegaard 1975). There is also considerable evidence to show that different species exhibit a strong spatial separation within this nursery area zone. Gunter (1961) and Gunter et al (1964) concluded that salinity was the most important factor in controlling the distribution of juvenile *P. setiferus, P. aztecus* and *P. duorarum* in nursery areas of the Gulf of Mexico, although more recent studies have suggested preferences of some species, in particular *P. aztecus,* for different vegetation types (Turner 1977; Zimmerman et al in press). It is obvious that salinity, vegetation type and prawn distribution will all be inter-related and arguments as to which is the controlling factor will tend to be circular. In the present study, however, study sites within the same estuary were in close proximity and temperature and salinity differences between sites were within ± 1%. On this scale, vegetation and substrate differences appeared to control prawn distribution. Similar observations have been made for some of these species in other parts of their range. *Penaeus esculentus,* in Moreton Bay in southeastern Queensland (27° 30′ S, 153° 20′ E), for example, occurred more commonly in seagrass areas than in adjacent bare substrates in areas of intermediate salinities (Young 1978). Basson et al (1977) suggested that *P. semisulcatus* in Saudi Arabia is dependent on algal and seagrass beds during its postlarval and juvenile stages. Price and Jones (1975) and Price (1979a, b) also recognised certain areas of Saudi Arabia as being important nursery areas for *P. semisulcatus* on the basis of their extensive algal and seagrass beds. In the Mediterranean, *P. semisulcatus* were also found over seagrass beds by Tom et al (1984). Mohamed et al (1981) reported that postlarval and juvenile *P. semisulcatus* were common in floating algal masses. In contrast, *P. merguiensis,* like the morphologically and ecologically similar *P. indicus,* appears to be much more closely associated with the mud-mangrove environment throughout much of its range (Hall 1962; Hynd 1974; Munro 1975; Chong 1979; Motoh 1981). These consistencies in the literature suggest that generalisations can be made concerning the habitat requirements of several species. Penn (1981) warns that considerable variation in nursery area requirements can occur in some instances and gives the example of White (1975), who reported that *P. esculentus* utilises highly turbid waters of Exmouth Bay in Western Australia (22° 20′ S, 114° 15′ E) in areas where little seagrass exists.

Based on our findings on the restricted nature of the habitat requirements of the main commercial species in the Embley River, especially for the genus *Penaeus,* we examined whether the large-scale distribution of the adult stocks of these species was in any way related to the distribution of their nursery grounds. For both tiger and banana prawns, the distribution of the main fishing grounds in the Gulf coincided with the presence of the appropriate nursery habitat inshore to the fishery. Thus, on a regional scale, nursery area distribution appeared to be controlling the major distributional patterns of the different prawn species. As a corollary, we suggest that the generalisations concerning the habitat requirements of these species appear to hold within the Gulf of Carpentaria, at least on a qualitative basis. Other factors, such as substrate and the distribution of food organisms will then affect the smaller scale distribution of prawns within these wider limits.

On a more quantitative basis, there is evidence that the mean catch of banana prawns over 10 years in each region of the Gulf depended on the amount of mangrove habitat available in estuaries within the region. While considerable year-to-year variation in catches has occurred, the highest mean catches have been made in regions with more available mangrove estuaries. A similar relationship for prawn catches (total of several species) and mangrove area has been found in Indonesia (Matsubroto and Naamin 1977) and the catch of several species and the area and type of estuarine vegetation in several regions of North America (Turner 1977). In our study, the Limmen Bight region of the Gulf was an obvious outlier with a much lower mean catch than expected on the basis of its rather extensive mangrove system. Catches fluctuated from 0 to 1400t over the 10 years which could only in part be explained by rainfall fluctuations (Vance et al in press). The behaviour of prawns in this region serves as a useful reminder that the distribution and abundance of animal populations cannot be described on the basis of one or two physical parameters observed in only one part of their range. Further work in the Limmen Bight region should elucidate which factors affect long-term catches of *P. merguiensis* throughout its range.

The relationship between mangroves, seagrass and prawn catches has obvious implications for the management and future wellbeing of Australian prawn fisheries. The first conclusion is that, because these nursery areas are limited in their distribution, the offshore prawn fisheries are also limited resources. Any changes to the nursery habitat will have a corresponding effect on the offshore catch. Apart from the five main commercial species, many other species of penaeid prawns utilised the Embley estuary during part of their life history. The more common species included *M. dalli, M. conjunctus,* and *M. eboracensis,* all of which were often found on the wide bare intertidal mudflats. If the amount of vegetation in an estuary is reduced through its destruction for alternative land use (eg housing canals, aquaculture) then a corresponding decrease in the commercial species offshore can be expected and a replacement by less important non-commercial species is possible.

The restricted niche of each species must also be borne in mind in the consideration of pond siting and design in future aquaculture applications. It should also be considered in any re-stocking scheme of natural populations from hatchery postlarvae. Because only limited areas of suitable habitat are available around the Australian coast, and these areas will have upper limits to their carrying capacity, indiscriminate release of hatchery-reared postlarvae could be wasteful and costly.

Acknowledgements
Mr S. Garland, formerly of the CSIRO Marine Laboratories, Cleveland, Australia, provided invaluable assistance in the collection and sorting of all field samples. The present study was funded by the Fishing Industry Research Trust Account.

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Juvenile prawn biology and the distribution of seagrass prawn nursery grounds in the southeastern Gulf of Carpentaria

Abstract: Fifteen consecutive monthly samples of juvenile prawns were collected in beam trawls from estuarine and inshore coastal waters around the Wellesley Islands. On seagrass beds, juvenile brown tiger prawns, *Penaeus esculentus,* and endeavour prawns, *Metapenaeus endeavouri,* formed 46.1% and 27.7% of the catch respectively. Where seagrass was absent *M. endeavouri* was more abundant (23.9% of the catch) than *P. esculentus* (0.1%). Other commercial species were caught in small numbers during the study. The non-commercial *M. dalli* was common on both bottom types. Immigration to nursery grounds of postlarval *P. esculentus* peaked in July with little recruitment between December and June. Larger prawns moved to the offshore fishery between October and January. Immigration of *M. endeavouri* and *P. latisulcatus* occurred in October and November and larger prawns of both species moved offshore between November and February. *M. dalli* postlarvae appeared earlier with a peak in April and another in September and emigrated between May and October. Of nine species of seagrass collected around the Wellesley Islands, four were common in tiger and endeavour prawn nursery grounds.

Introduction

The Gulf of Carpentaria on Australia's northern coast is a large shallow embayment approximately 900km by 500km with a maximum depth of only 70 m. Its waters and surrounding estuaries contain habitats important to a number of penaeid prawn species which are commercially important.

There are two identifiable commercial prawn fisheries in the Gulf. One is a daytime fishery that targets on schools of the banana prawn, *Penaeus merguiensis.* The other is a night trawl fishery whose catch is mainly the two tiger prawns, the brown tiger, *P. esculentus,* and the grooved tiger, *P. semisulcatus.* Other important commercial penaeids caught with these include the two endeavour prawns, *Metapenaeus ensis* and *M. endeavouri,* and two species of king prawn, the western king prawn, *P. latisulcatus,* and the red spot king prawn, *P. longistylus.*

Up until the late 1970s the banana prawn fishery was the most important in the Gulf. Northern prawn fishery logbooks show that since 1978, however, landings of tiger prawns have exceeded landings of banana prawns (Data supplied by Commonwealth Department of Primary Industry, Canberra). By 1982, tiger prawns alone made up 47% of the commercial catch compared with only 33% for banana prawns. In the 10 years up to 1982 fishing effort expended in the tiger prawn fishery increased from 8000 to 19000 boat days (Australian Fisheries Council 1982).

The area in the southeastern Gulf centred around the Wellesley Islands is the major fishing area for tiger prawns in Queensland state waters. From 1982 fishing logbooks, an estimated catch of 600000 kg of tiger prawns was taken from fishing grounds adjacent to these islands.

In response to concern over the lack of biological information with which to assess the likely effects of increasing effort in this fishery, a project was initiated by the Fisheries Research Branch of the Queensland Department of Primary Industries to study the biology of the commercial penaeid prawns in the Wellesley Islands region.

This study was designed to provide the information required for the long-term management of the tiger prawn fishery. Two field sampling programs were implemented to run concurrently. Adult prawns in the commercial fishery were studied during an offshore sampling program and the biology of juvenile prawns was investigated in inshore nursery habitats.

This paper describes the overall juvenile prawn sampling program. It presents the life cycle timing for four prawn species based on data from the Dugong River, Mornington Island, the species composition of juvenile penaeid prawns in inshore waters, and the distribution of seagrass prawn nursery grounds around the Wellesley Islands.

Materials and methods

The sampling method consisted of trawling for juvenile prawns during the night hours at selected inshore sites. Two 1.5 m wide by 0.5 m high beam trawls fitted with 2.0mm mesh net were towed at a speed of 0.5 m s^{-1} for 50 m over the bottom. The towing vessel was a 7.3m launch rigged to enable both nets to be towed simultaneously, giving two samples at each site.

Prior to each trawl, water temperature and salinity were measured with a Hamon temperature and salinity meter at 200mm above the substrate.

An initial survey of island waters was conducted to choose sampling sites representative of the range of inshore habitats found around several islands of the Wellesley group. Sixteen sites were selected in sheltered areas with depths of 5 m or less. Eight additional sites were located in deeper waters (Fig. 1).

Samples were taken on consecutive new moons commencing in October 1982 and continuing for 15 months. At a site in the Dugong River with dense seagrass and an abundance of juvenile prawns, samples were taken every 2 h for 24 h each month. Data from this site were used in the analysis of life cycles.

Carapace length measurements (CL) were taken of all prawns caught, and those with a carapace length greater than 3 mm were identified to species (Dall 1957).

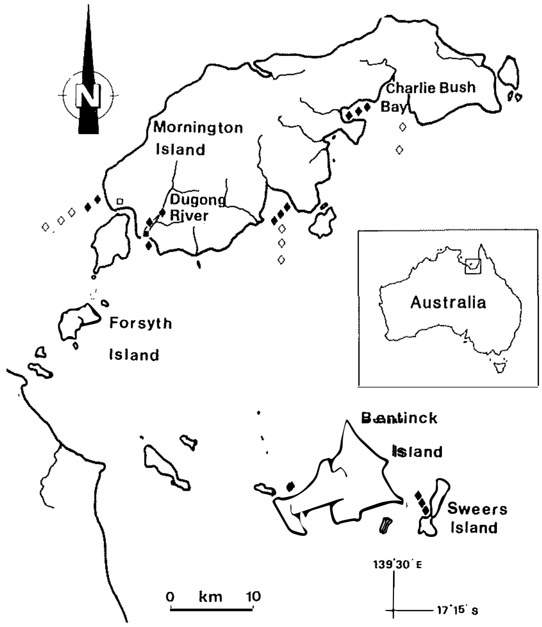

Figure 1. Juvenile prawn sampling sites ◇ around the Wellesley Islands in the southeastern Gulf of Carpentaria. Sites marked ◆ were in less than 5 m of water and 24-hour samples were taken at the site marked ■ in the Dugong River. Aboriginal mission is marked □ .

Studies of the seagrass beds around the Wellesley Islands were made in March and September of 1984. The total area of seagrass beds was determined using divers to check presence and absence of bottom vegetation along transects from deep water into the coast at approximately 0.5n mile intervals, with spot checks for continuity at intervals between transects. Where seagrass was found, a representative 1 m^2 sample of the bottom was taken. In the laboratory analysis seagrass samples were separated into component species and for each species the wet weights of both root and leaves were recorded.

Results

Temperature and salinity

Water temperatures at the 24 h sampling site in the Dugong River on Mornington Island exceeded 30° C during the summer months (December, January and February) with a maximum recorded temperature of 33.2° C (Fig. 2a). The lowest temperatures occurred in June and July 1982, with a minimum of 14.5° C in June. The winter drop in temperature, which

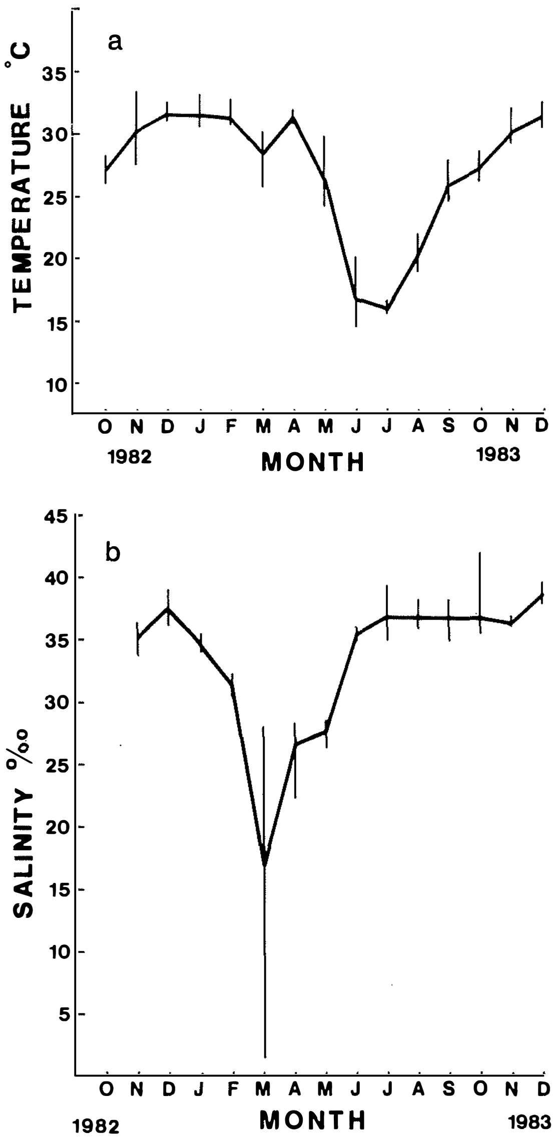

Figure 2. Mean and range of **a.** water temperature and **b.** salinity in the Dugong river from October 1982 to December 1983.

was of short duration, probably resulted from the cool southerly winds that blew from the mainland during these months.

With the exception of the February to May period when most rainfall occurred, salinities in the Dugong River remained relatively constant. The normal timing of monsoon rains in the southeastern Gulf is January-February.

Water salinity reached a minimum of 1.6‰ in March 1982 as a result of late monsoon rains and exceeded 40‰ at times in October (Fig. 2b).

Life cycle timing

The presence of prawns with CL≤ 5.0mm on sampling sites in the Dugong River entrance was used as an indication of recently settled postlarvae. As postlarvae and juveniles were found in inshore waters, a mixed life cycle was assumed with eggs fertilised offshore and postlarvae developing and appearing in inshore areas in three to four weeks. These would develop into juvenile prawns, move offshore to mature and spawn completing the life cycle (Kirkegaard 1975).

Penaeus esculentus

In the waters surrounding the Wellesley Islands there was evidence (Fig. 3a) of spawning by *P. esculentus* throughout the year, although at an extremely low level between October and May, 1982. We assume that a peak in spawning in June would result in the appearance of prawns with CL≤ 5.0mm on inshore grounds in July. Larger juveniles, CL≥ 5.1mm, peaked in abundance in September-October and then decreased to very small numbers on the inshore nursery grounds by January.

Metapenaeus endeavouri

Metapenaeus endeavouri prawns with CL≤ 5.0mm appeared on inshore grounds in November 1982 and again in January and October, 1983, suggesting offshore spawning between September and December (Fig. 3b). Numbers of larger juveniles peaked around October and November, decreasing to small numbers by March.

Penaeus latisulcatus

The number of *P. latisulcatus* prawns with CL≤ 5.0mm was very low throughout the year (Fig. 3c). Those caught in November, 1982, and October, 1983, suggest a September and October spring spawning with postlarvae settling in October and November. The numbers of larger juveniles peaked at the same time and after January were found in only small numbers on inshore prawn nursery grounds.

Metapenaeus dalli

The peaks in the curve for *M. dalli* prawns CL≤ 5.0mm in April and September suggest a March spawning followed by a smaller August spawning (Fig. 3d). Larger juveniles peaked in abundance in April, May and again in

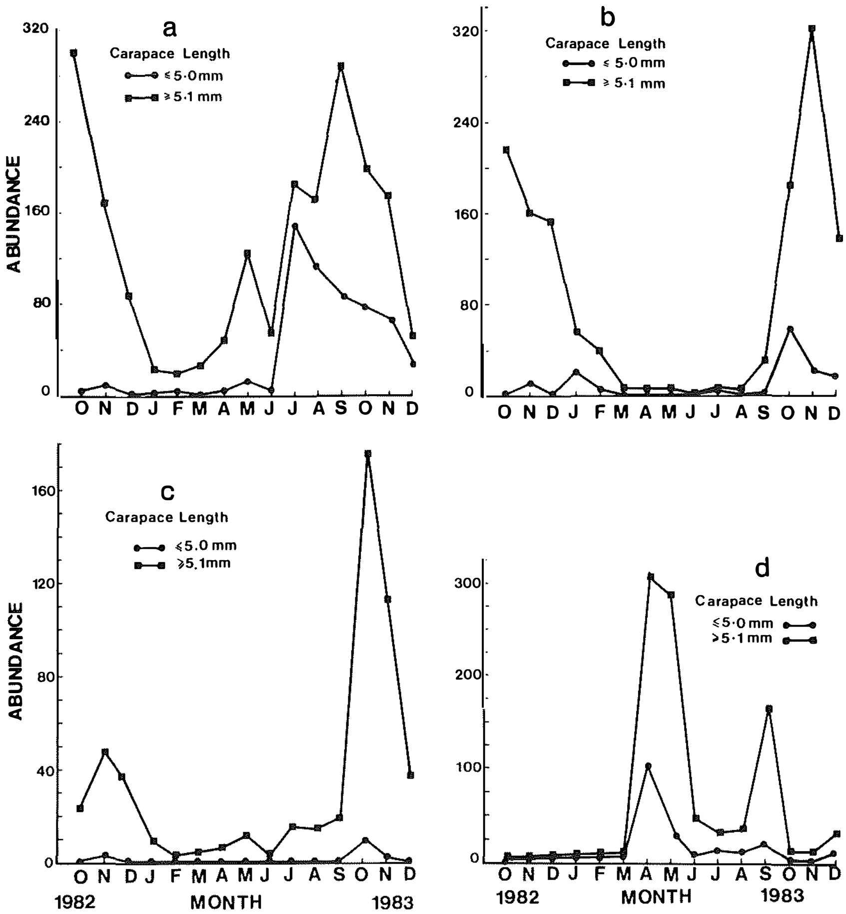

Figure 3. The number of **a.** *Penaeus esculentus*, **b.** *Metapenaeus endeavouri*, **c.** *Penaeus latisulcatus* and **d.** *Metapenaeus dalli* in the Dugong River each month from October 1982 to December 1983. The timing of the immigration of postlarvae and small juveniles to the nursery ground is given by the numbers of prawns with a carapace length of ≤ 5.0mm. The numbers of larger juveniles are given by the graph of ≥ 5.1 mm CL prawns.

September and had moved offshore from the nursery ground by October.

Species composition

Studies in southern Queensland (Young 1978; Young and Carpenter 1977) and preliminary investigations by Staples (1984) have shown that the density of some species of juvenile prawns in inshore areas is enhanced where seagrasses occur. As a preliminary analysis of species composition on prawn nursery grounds around the Wellesley Islands, data were compiled for two sites on Mornington Island: one at the entrance of the Dugong river where trawls were made through extensive beds of seagrass, and the other in Charlie Bush Bay where the bottom was free of seagrass cover.

Data for both sites are presented from samples taken each month during the 15-month sampling period. The density of commercially important prawns was far greater on the seagrass bed (Fig. 4a) where juvenile *P. esculentus* and *M. endeavouri* formed 46.1% and 27.7% of the catch respectively. In Charlie Bush Bay, *P. esculentus* represented only 0.1% of the total number of juvenile prawns and *M. endeavouri* 23.9% (Fig. 4b).

The non-commercial *M. dalli* was slightly more abundant on the bare substrate but relatively numerous at both sites. *Penaeus latisulcatus* and *P. semisulcatus* were few in number at both sites, mostly caught where seagrass occurred.

Only a few juvenile *P. merguiensis* were recorded from the samples. Such a low incidence is expected as juvenile *P. merguiensis* are most likely to be found within 2m of the shore (Staples and Vance 1979). Both Mornington Island sampling sites were more than 50m from the shoreline.

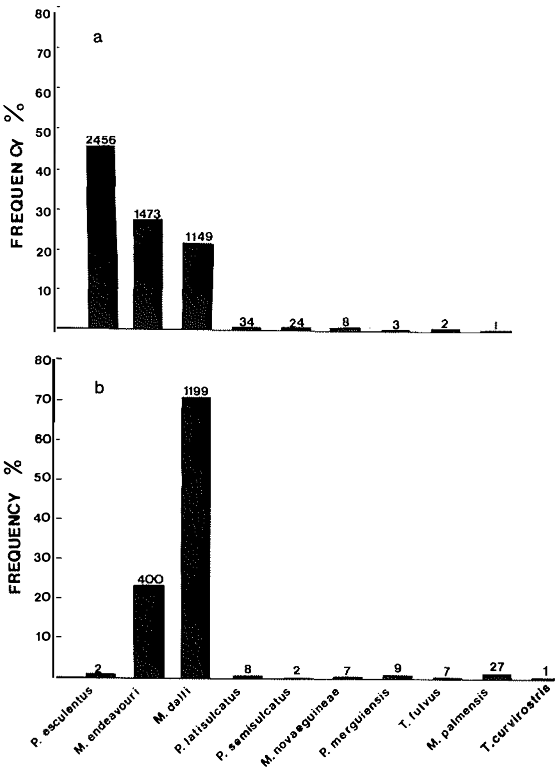

Figure 4. The species composition of juvenile prawns on **a.** seagrass beds in the Dugong River entrance and **b.** bare substrate in Charlie Bush Bay.

Table 1. Occurrence of seagrass species (+) around the Wellesley Islands and the adjacent mainland.

Sampling area	*Cymodocea serrulata*	*Halodule uninervis/pinifolia*	*Halophila ovalis*	*Halophila spinulosa*	*Halophila decipiens*	*Syringodium isoetifolium*	*Enhalus acoroides*	*Thalassia hemprichii*
Mornington Island	+	+	+	+	+	+	+	+
Denham Island	+	+	+	+		+		+
Sweers Island	+		+	+				
Bentinck Island	+	+	+	+	+	+		
Forsyth Island	+	+	+	+	+	+	+	
Allen Island	+	+	+	+		+		
Pains Island	+	+						
Adjacent mainland	+	+	+					

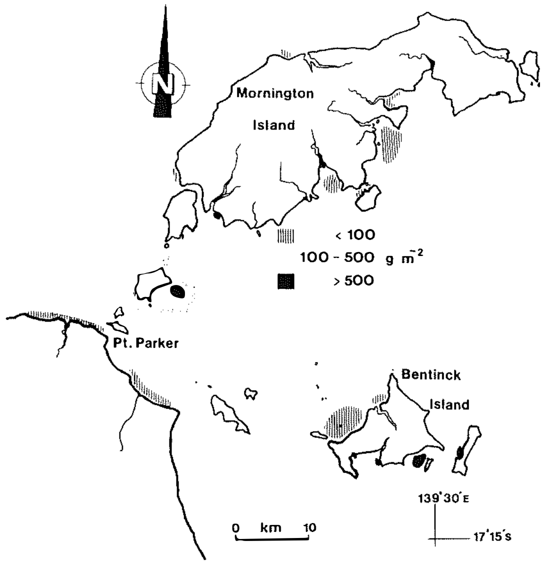

Figure 5. The distribution of seagrass beds around the Wellesley Islands and the adjacent mainland. Shaded areas represent the wet weight of all plant material collected from 1 m^2 of bottom.

Distribution of seagrass

Large areas of dense seagrass are restricted to the southwestern coast of Mornington Island, Government Bay on Forsyth Island, and the southeastern and northeastern coasts of Bentinck Island (Fig. 5). Seagrasses were sparsely distributed in depths greater than 5 m, possibly due to the generally high turbidity of the shallow Gulf waters.

Nine species of seagrass were identified from collections. The distribution of these species around the Wellesley Islands and the adjacent mainland coast is presented in Table. 1.

Discussion

Of the prawn species important to the southeastern Gulf of Carpentaria fishery, only two, *P. esculentus* and *M. endeavouri*, were common on the inshore nursery grounds of the Wellesley Islands. The small number of *P. merguiensis* in the two sites presented in this paper probably reflected the bias in sampling sites chosen with the intention of studying tiger prawn populations. During the sampling period, large numbers of *P. merguiensis* were present on shallow tidal banks near the aboriginal community (Fig. 1). *Penaeus semisulcatus* was present in the offshore fishery only in small numbers during 1983. Juveniles of this species were uncommon in Wellesley Island waters despite their presence around northern Gulf islands such as Groote Eylandt (Staples[1], pers. comm.).

Closures to fishing in the southeastern Gulf of Carpentaria have been implemented to prevent trawling of juvenile prawns. For such management to be successful an accurate estimation of the timing of the life cycle of the important commercial prawn species is needed.

There is evidence that the timing of the life cycle for *P. esculentus* may vary with latitude. In Moreton Bay, southern Queensland, recruitment to nursery grounds of *P. esculentus* postlarvae takes place in January and February (Young 1978), some five months later than in the southeastern Gulf of Carpentaria. Preliminary results from Weipa (Staples 1984), suggest a double recruitment to nursery grounds, one in September-October and one in March-April. Around the Wellesley Islands juvenile *P. esculentus* migrate to the fishery between September and January. A closure preventing trawling on the adjacent fishing grounds for any month between October and January inclusive would result in fewer juveniles caught incidental to the commercial catch of adult prawns. The timing of migration to the fishery of *M. endeavouri* (October to March) and *P. latisulcatus* (October to February) would be sufficiently similar to that of *P. esculentus* to enable a single closure time to be effective in reducing trawling of juveniles of all commercial prawn species common on the inshore nursery grounds. A closure during these times may not, however, be appropriate for other Queensland tiger prawn fisheries.

Approximately 26 km^2 of seagrass beds were mapped around the islands. Of the nine species of seagrass identified, five (*Cymodocea serrulata, Syringodium isoetifolium* and *Halophila spinulosa*) together with *Halodule uninervis* and *Halodule pinifolia* which were not separately identified, were common in the dense seagrass beds that characterised prawn nursery grounds. Detailed analyses of the relationship between the density of juvenile prawns and seagrass structure and composition are currently being undertaken.

A large proportion of the tiger prawns caught in the southeastern Gulf probably originate from seagrass nursery grounds around the Wellesley Islands. Otter trawling and dredging areas of seagrass, and changes to the environment that may limit size and growth of seagrass beds should be avoided.

The small total area of these seagrass beds emphasises the importance of conservation of these habitats for the long term maintenance of the tiger prawn fishery.

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The authors wish to acknowledge the assistance of L. and B. Squire and R. Shepherd in the collection and analysis of data and the preparation of figures for this manuscript.

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Prawn virus from juvenile *Penaeus esculentus*

Abstract: To enhance viral expression, 840 *Penaeus esculentus* from Moreton Bay and Groote Eylandt, Australia (27° 31'S, 153° 18'E and 14° 05'S, 136° 15'E respectively) and 2300 *Metapenaeus bennettae* from Moreton Bay, were kept under crowded conditions (0.5 to 1.5 kg m^{-3}) in batches of about 200 prawns each, at 20, 25, 30 or 35° C for up to six weeks. Wet mounts of digestive gland were examined for baculoviral inclusion bodies at intervals, and at the end of each experiment, small subsamples (usually five prawns) were fixed and sectioned for histological examination. No signs of infection were seen in wet mounts. Inclusion bodies identical to those caused by hepatopancreatic parvo-like virus (HPV) were found in sections of two *P. esculentus* from Moreton Bay. The infected prawns had been kept at 20 and 25° C. This is the first record of a marine virus from Australian waters. In addition, Y organ necrosis was observed in both species of prawns, and basophilic, Feulgen-negative, crystalline bodies were observed in the pancreatic nuclei of two *M. bennettae.*

Introduction

The rapid expansion of experimental and commercial culture of penaeid prawns has been accompanied by the recognition of the importance of penaeid diseases, particularly viral diseases, in limiting production. Six virus diseases have been described from penaeids, all within the last 11 years. Three are baculoviruses primarily infecting cells of the hepatopancreas. *Baculovirus penaei* (BVP) has been found in *Penaeus duorarum, P. aztecus,* and *P. vannamei* in Hawaii. It has been associated with high mortality and morbidity in larval shrimp culture (Lightner 1977). Monodon baculovirus (MBV) infects the tiger prawn, *P. monodon,* causing morbidity and mortality in juvenile and sub adult prawns (Lightner and Redman 1981). Baculoviral mid-gut gland necrosis (BMN) infects *P. japonicus* in Japan, and epizootics have resulted in high mortalities in larval shrimp, (Sano, Nishimura, Oguma et al 1981; Sano, Nishimura, Fukuda et al 1984). A probable picornavirus is the cause of infectious haematopoietic and hypodermal necrosis (IHHN) (Lightner, Redman and Bell 1983). This virus causes catastrophic losses in *P. stylirostris* and *P. monodon* but can be carried asymptomatically in *P. vannamei.* A reo-like virus has been found in the hepatopancreas of diseased *P. japonicus* in aquaculture facilities in southern France (Tsing and Bonami 1984). Finally a parvo-like virus, hepatopancreatic parvovirus (HPV), was found recently in the hepatopancreatic cells of *Penaeus merguiensis* in Singapore, *P. orientalis* in China, *P. monodon* in the Philippines, and *P. semisulcatus* in Kuwait (Lightner and Redman 1985).

Success in the intensive production of marine animals must be based in part on the development of methods for disease diagnosis and control (Sindermann 1984). The infant prawn aquaculture industry in Australia appears destined to become an important primary industry, providing disease and other problems can be overcome. The aim of this project was to find what viral infections, if any, were common in wild stocks of two Australian penaeids.

Materials and methods

Prawns were obtained using a one metre beam trawl towed across eel grass beds at Cleveland,

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Table 1. Total numbers of prawns held under the four different temperatures and their origin. Number of samples in parentheses.

	20° C	25° C	30° C	35° C
Penaeus esculentus				
Moreton Bay	102* (3)	370* (3)	100 (3)	250 (5)
Groote Eylandt			20 (1)	
Metapenaeus bennettae				
Moreton Bay	300 (3)	1000 (15)	400 (7)	600 (8)

*Groups in which HPV infections were found.

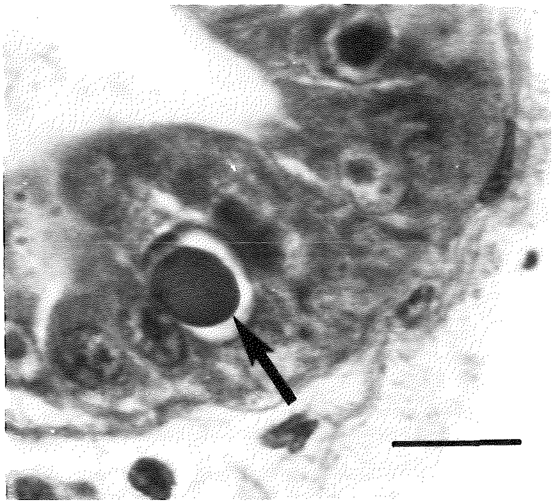

Figure 1. Tubule epithelium of the digestive gland of a *Penaeus esculentus* from Moreton Bay showing an HPV intranuclear inclusion body (arrow). Note the hypertrophied nucleus, chromatin emargination, and adjacent normal nuclei. H & E. Bar = 10 μm.

Moreton Bay (27° 31′S, 153° 18′E) and Groote Eylandt, Gulf of Carpentaria (14° 05′S, 136° 15′E). The animals were transported in aerated bins, counted, weighed and placed in aquaria under crowded conditions (0.5 to 1.5 kg prawn per m^3 tank water volume) at one of four temperatures (20, 25, 30 or 35° C, Table 1). Individual prawns weighed 0.1 to 1 g. Salinity was held at 35‰. A total of 20 *P. esculentus* from Groote Eylandt, 822 *P. esculentus* from Moreton Bay, and 2300 *Metapenaeus bennettae* from Moreton Bay were used. After periods of 4, 5 and 6 weeks, or earlier if prawns were lethargic or moribund, subsamples of five prawns were examined for the presence of inclusion bodies in the hepatopancreas using fresh squash preparations viewed under a light microscope. A 0.05% aqueous solution of malachite green was used to stain wet smears to aid detection of inclusion bodies. Tissues for histological examination were fixed in Davidson's fixative (Humason 1972). The fixative was injected directly into the digestive gland using a 1.1 mm diameter needle, and injected prawns were then immersed in fixative for 24 to 48 h. Prawns heavier than 1 g were cut along the mid dorsal line to facilitate fixative penetration. Wax sections (7 μm) were routinely stained with Harris's haematoxylin and eosin (H & E) (Humason 1972) and occasionally with Feulgen stain (Thompson 1966) to detect the presence of DNA.

Results and discussion

We observed three pathological conditions of possible viral etiology. Basophilic spherical inclusion bodies were found in the nuclei of epithelial cells lining the tubules of the hepatopancreas of two *P. esculentus* from Moreton Bay (Fig. 1, arrow). Infected nuclei were hypertrophied, the nucleolus was laterally displaced and nuclear chromatin was emarginated. In the first prawn, infected cells were found only towards the periphery of the hepatopancreas, most of the cells towards the centre having been destroyed. In the second, infected cells were evenly dispersed and most of the hepatopancreatic cells were intact. The histological appearance of the infected cells was identical to a condition caused by HPV, the virus described from four species of penaeids in Asia (Lightner and Redman 1985). These authors demonstrated using electron microscopy that the inclusion bodies of HPV contained virus. The moderately infected prawn had been kept at 20° C for two weeks and the severely infected prawn at 25° C for five weeks. The moderately infected prawn had become moribund but abnormal behaviour was not noted for the severely infected prawn. Infection in other prawns of the same batch was not detected, possibly because of the long incubation period of HPV (probably more than 33 days, Lightner, unpublished). As far as we are aware this is the first marine virus to be reported from Australian waters.

Clinical signs and mortality rates of HPV infected prawns are known only for *P. merguiensis* cultured in tanks and net cages

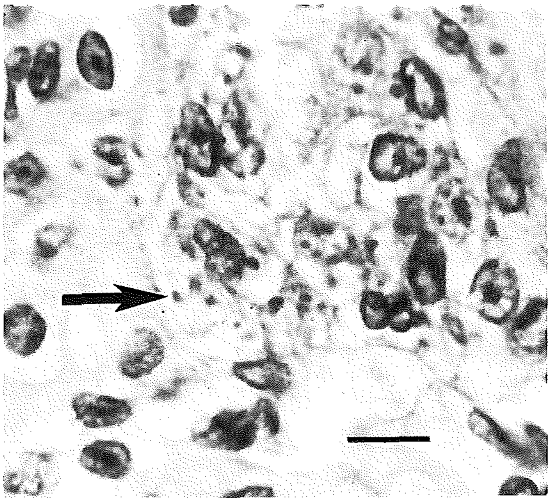

Figure 2. Focal necrosis in the Y organ of *Penaeus esculentus*. A group of affected cells occupies the centre of the photograph. Their cytoplasm contains basophilic granular bodies (arrow). H & E. Bar = 10μm.

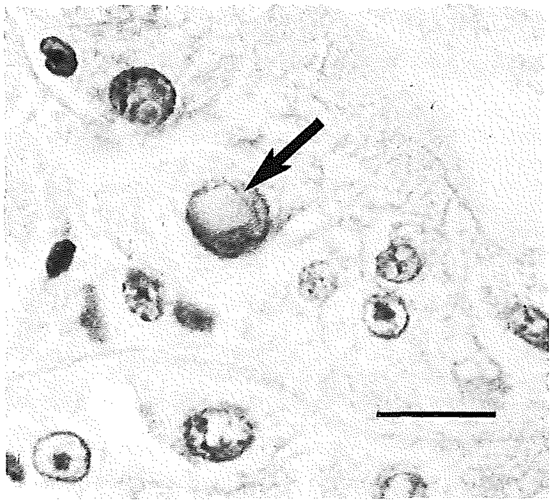

Figure 3. Tubule epithelium of digestive gland of *Metapenaeus bennettae* showing intranuclear crystalline body (arrow). Feulgen stain. Bar = 10μm.

in Singapore and for tank-reared *P. semisulcatus* in Kuwait. In these two species, gross signs of the disease included poor growth rates, reduced preening activity (hence, increased surface fouling by epicommensals), occasional opacity of abdominal muscles, and occasional presumed secondary bacterial and fungal infections. Mortalities accompanied by these signs most often appeared in juveniles after apparently normal development through the larval and postlarval stages. Weekly mortality rates of infected juvenile shrimp were moderate to high with accumulative mortalities reaching from 50 to 100% of the affected populations within four to eight weeks of disease onset (Lightner and Redman 1985).

The second condition, focal necrosis of the mandibular or Y organ, was noted in 15 *P. esculentus* kept at 20, 25 and 35° C and one *M. bennettae* kept at 25° C. The Y organ epithelial cord cells had highly vacuolate cytoplasm, pyknotic nuclei, and numerous cytoplasmic basophilic inclusions (Fig. 2, arrow). Similar lesions have been seen in *P. japonicus* and *P. stylirostris* (Lightner, unpublished). It is possible they are caused by a bunyavirus or rhabdovirus as both of these have been found in the Y organ of other crustaceans (Johnson 1984). Their pathogenicity is unknown.

A third condition was noted in two *M. bennettae* kept at 35° C for five weeks. Large basophilic intranuclear inclusion bodies (Fig. 3, arrow) in low to moderate numbers were found in otherwise normal-appearing digestive tubule epithelium cells. At first these were thought to indicate additional infections of HPV. However, in H & E sections the bodies differed in two ways from typical HPV inclusions: (1) some were clearly angular and in fact had a cubic symmetry, and (2) the host cell nucleolus was not present as a 'signet ring' pressed on to one side of the developing inclusion body. Feulgen staining indicated that the bodies did not contain DNA and therefore could not be HPV. They may be protein or RNA-protein crystals. Similar crystalline bodies have been reported from *P. stylirostris* in the United States where they were associated with a toxic disease syndrome linked to certain types of blue-green algae (Lightner and Redman 1984).

Representative histological sections of the three conditions have been lodged in the Queensland Museum (QM GL 4735 to 4737).

Acknowledgements

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Tagging of *Penaeus merguiensis* in the Gulf of Papua, Papua New Guinea

Abstract: During 1979 and 1980 a total of 1 111 adolescent banana prawns, *Penaeus merguiensis,* were tagged and released in coastal waters 3 to 5 m deep in the Gulf of Papua. From these releases 121 prawns were recaptured. Another 7 008 juvenile banana prawns were tagged and released in nursery zones of the Gulf of Papua with 113 recaptures. The lower proportion of recaptures from releases in the nursery zone can be related to the smaller size of prawns at tagging, increased time before recapture, and tag loss. The maximum period between tagging and recapture was 150 days the recapture rate declining steadily with time after release. Distance moved and depth of recapture was similar for both sexes, although prawns recaptured from the nursery tag releases were generally caught in shallower water. Of the recaptured prawns 46% moved in an easterly direction while 40% showed only localised movement (<10 km). *Penaeus merguiensis* was found to be able to undertake large migrations moving up to 80 to 150km from a major nursery ground to the main fishing grounds.

Introduction

The banana prawn, *Penaeus merguiensis,* forms the basis of many commercial fisheries in the Indo-West Pacific. Its distribution ranges from the Persian Gulf to Thailand, Hong Kong, the Philippines, Indonesia, Papua New Guinea, New Caledonia and the northern part of Australia (Grey et al 1983).

Since 1981, Papua New Guinea's most important commercial fishery has been the Gulf of Papua prawn fishery. The banana prawn is the dominant species contributing more than 50% to the total prawn catch (Gwyther 1980).

Extensive migrations have been documented for other penaeids by Linder and Anderson (1956) for *P. setiferus* (576 km) and Ruello (1970), and Montgomery (1981) for *P. plebejus* (640 and 1333 km, respectively). Lucas et al (1979) demonstrated that adult *P. merguiensis* exhibited limited movements in the Gulf of Carpentaria, Australia. This conclusion was supported by a study using biological markers which suggested that adult stocks came mainly from adjacent inshore estuaries (Owens 1983).

In the Gulf of Papua, the Aird Delta region (Fig. 1) has been identified as a major nursery area for *P. merguiensis* (Frusher 1984) and is separated from the main fishing grounds by 80 to 150 km. A tagging program was undertaken to determine the significance of the Aird Delta nursery site to the commercial fishery in comparison with other smaller sites situated closer to the grounds. The effectiveness of vinyl streamer tags as markers for prawn studies was also evaluated in this study.

Materials and methods

The vinyl streamer tag described by Marullo et al (1976) was selected for this study as it appeared to be an improvement over earlier techniques which have been summarised by Ruello (1970). Individually numbered vinyl streamer tags (Floy FTSL-73) were used. These tags were 95mm long, 3 mm wide with a central section of 22 mm in length and 1.5 mm in width which passed through the prawn. Tags were inserted between the first and second abdominal segments below the interconnecting hinge of the respective pleura using a

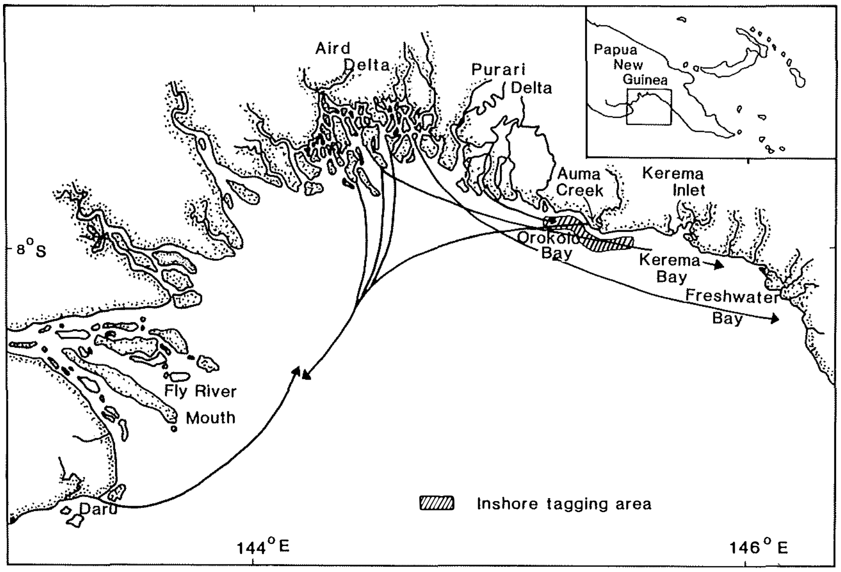

Figure 1. The Gulf of Papua showing the long distance movements by estuarine tagged *Penaeus merguiensis.*

disposable tagging needle. Prawns were tagged either as juveniles in estuarine nursery areas or as adolescents in the shallow nearshore areas prior to their migration to deeper water.

Prawns were caught in the inshore regions of the Gulf in and adjacent to Orokolo Bay in waters 3 to 5 m deep (Fig.1), using a single rigged 10 m trawler. The net was a 12 m flat otter trawl with 31 mm stretched mesh in the wings and 25 mm stretched mesh in the codend. Prawns of greater than 20 mm carapace length (CL) were retained. Shots of 5 to 10 minutes duration were taken and only the liveliest prawns from each shot were tagged. Prior to tagging the CL of prawns was measured to the nearest 0.1 mm using dial calipers, and the sex recorded. After tagging, a 10 to 15 minute recuperative period was allowed before prawns were released over the side of the vessel. During the recuperative period prawns were kept in plastic basins of 0.8 m diameter with seawater being continuously replaced. To minimise the danger from predators which follow prawn trawlers, a load of trawl fish was dumped before moving to a prawn release site, 0.5 km away. A total of 1111 adolescent banana prawns were released in 3 to 5 m of water. In estuarine nursery areas prawns were caught using a 35 m by 2m beach seine with 25 mm stretched mesh. This net retained prawns of >14 mm CL and 7008 were tagged in the Aird and Purari Deltas, Auma Creek and Kerema Inlet (Fig.1). After the recuperative period, prawns were released in 0.5 to 1.0 m of water.

Prawns were expected to be recaptured from the 14 commercial trawlers operating in the Gulf and the traditional dipnet fishery in the estuarine and coastal regions. Close liaison was maintained with the prawn trawling companies, and talks were held with village fisherwomen and councillors. Printed t-shirts advertising the program were used as rewards for tag returns.

Results

Tag effectiveness

To test for size selective effects of tagging, the mean size at release of all prawns tagged was compared with the calculated mean size at release for the recaptured prawns. In the inshore releases, 126 prawns were recaptured. The mean size of these prawns at tagging was 26.0 mm CL, which was significantly larger than the mean size of all tagged prawns released ($t=3.77$, $df=1235$, $p<0.001$). Of the 113 recaptures made from the estuarine releases, 24 were taken in the nursery creeks by traditional dipnetting and were excluded from the analysis. The mean size of the remaining 89 recaptures at the time of their release was 19.3mm CL which was also significantly larger than the mean size of all the estuarine releases ($t=8.24$, $df=7095$,

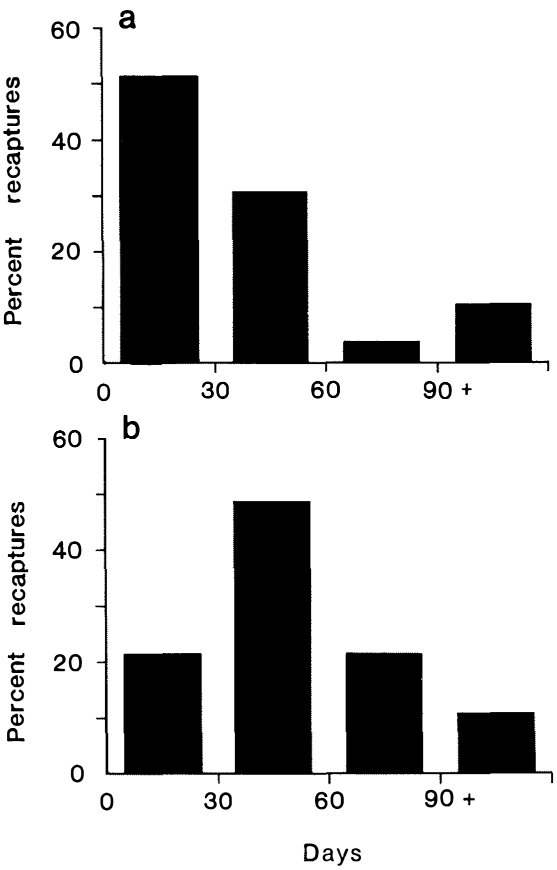

Figure 2. Time (days) at liberty for *Penaeus merguiensis* tagged in **a.** inshore and **b.** estuarine locations.

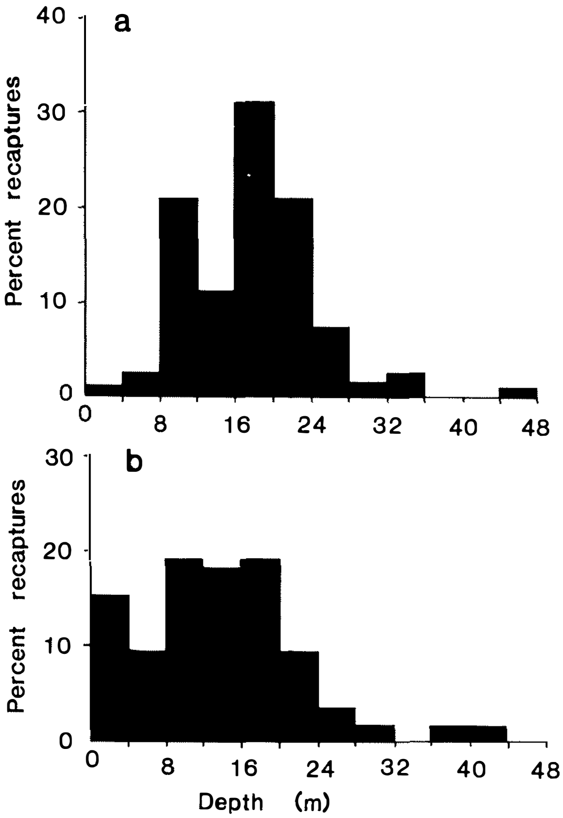

Figure 4. Depth (metres) at which tagged *Penaeus merguiensis* were recaptured from **a.** inshore and **b.** estuarine tagging locations.

p<0.001). This indicates that in both tagging locations smaller prawns suffered either greater mortality, tag loss or lowered catchability

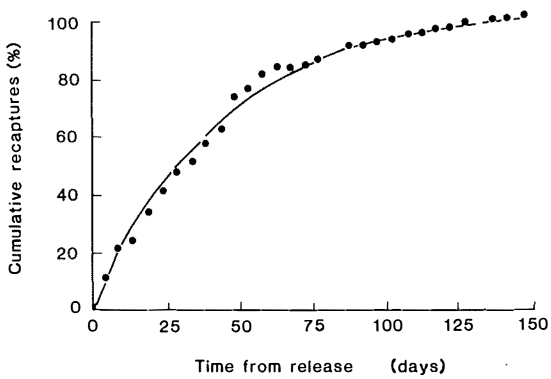

Figure 3. Percentage cumulative recaptures of tagged *Penaeus merguiensis* with time from release (days).

although the difference between the mean of releases for the inshore tagged prawns (0.8mm CL) was less than for the estuarine tagged prawns (2.2mm CL). For the inshore releases, the mean time at liberty for tagged prawns was 40 days during which time the mean size increased from 26.0mm CL to 28.3mm CL, a difference of 0.4mm CL week^{-1}. The mean time at liberty of estuarine prawns was 55.3 days, in which they increased in mean size from 19.3mm CL to 26.4mm CL, a difference of 0.9mm CL week^{-1}. The growth rate of pre-emigrant juvenile to adolescent banana prawns is more than twice that of adolescent to early adult banana prawns. These estimates fall within the confidence limits of *P. merguiensis* growth curves in the Gulf as determined by Frusher et al (in press).

Migrations

Of the tagging sites selected in the Gulf of Papua, the inshore releases were adjacent to

Table 1. Mean carapace length (CL, mm) of *Penaeus merguiensis* at tagging for all prawns released and those recaptured, together with mean carapace length and mean time at liberty (days) for recaptured prawns. SD = standard deviation. N = number of prawns measured.

	Inshore				Estuarine			
	Size at tagging				Size at tagging			
	All prawns (mm CL)	Recaptured prawns (mm CL)	Size at recapture (mm CL)	Time at liberty (days)	All prawns (mm CL)	Recaptured prawns (mm CL)	Size at recapture (mm CL)	Time at liberty (days)
Mean	25.2	26.0	28.3	40.0	17.1	19.3	26.4	55.3
SD	2.7	2.2	3.2	36.0	2.6	2.5	4.0	28.3
N	1111	126	103	123	7008	89[1]	93	89[1]

[1] excludes recaptures made in nursery creeks by traditional dipnetting.

and within the major commercial fishing grounds. Auma Creek, the Purari Delta and Kerema Inlet were in isolated estuaries and creeks fringing the coast which are considered small nursery grounds. The Aird Delta is considered the main nursery ground of the Gulf (Frusher 1984). Daru has a small beach seine fishery (C. Tenakanai[1], pers. comm.) and is located at the western extremity of the Gulf.

[1] C. Tenakanai, DPI Fisheries Research, PO Box 417, Konedobu, Papua New Guinea.

The extent of the long distance prawn movements is shown in Fig. 1.

A three-way factorial analysis of variance (Sokal and Rohlf 1969) was used to test differences between the number of recaptures in both tagging locations (estuarine and inshore) and time and distance travelled. There was no significant difference ($F = 1.66$, $df = 18$, $p > 0.05$). That is, prawns tagged in both inshore and estuarine locations moved comparable distances. However there was a significant

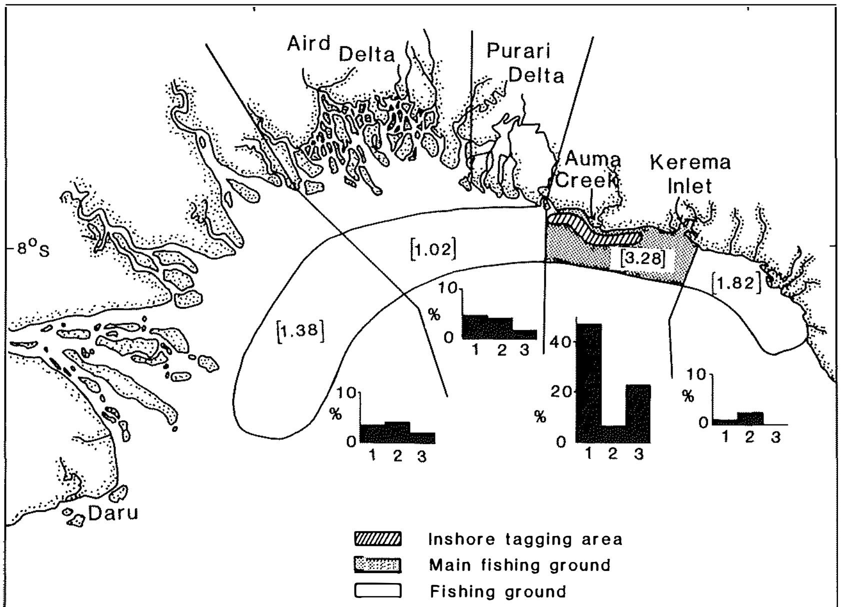

Figure 5. Origin of recaptures of *Penaeus merguiensis* expressed as percentage of total recaptures. (1 = Inshore releases, 2 = Aird Delta releases, 3 = Purari Delta, Auma Creek and Kerema Inlet releases. [numbers] = tags returned per 1000 hours of fishing.)

difference ($F=3.66$, $df=3$, $p<0.05$) in the number of recaptures from the different locations with time. From Fig. 2 it can be seen that the majority of prawns recaptured from inshore taggings were caught earlier (within 30 days) than prawns from estuarine tagging (between 30 and 60 days).

The maximum time between release and recapture was 150 days. A plot of the percentage cumulative recaptures against time shows a curvilinear line with a decreased probability of recapture with time (Fig. 3). As well as prawn mortality the decrease in recapture rate could be due to increased dispersion, decreased catchability or tag loss.

The maximum net displacement distance between site of release and recapture of male and female banana prawns was 167 and 190 km respectively. No significant difference ($G=32.67$, $df=21$, $p>0.05$) was found in the overall net displacement distances travelled by male and female *P. merguiensis* although the data suggested that females tended to be recaptured further from their release site. A total of 70% of females was recaptured more than 25 km from the release site in comparison to 40% of males. There also was no significant difference ($G=4.64$, $df=11$, $p>0.05$) in the depth at which male (mean = 15.9 ± 8.0mm CL) and female (mean = 16.0 ± 8.0mm CL) prawns were recaptured. Maximum recapture depths were 44 m for males and 40 m for females. There was a significant difference ($G=45.62$, $df=11$, $p<0.001$) between depths at which the estuarine (mean = 13.9 ± 8.8 mm CL) and inshore (mean = 17.7 ± 6.7 mm CL) recaptures were made. Prawns from estuarine tag releases were recaptured in shallower water (Fig. 4). The extra time required for prawns to migrate to deeper waters could allow for greater mortality and tag loss. The number of tags returned per hour for each of the recapture areas is shown in Fig. 5. The probability of recovery of tags would be expected to vary in direct proportion to the distance from the tagging site. The area of the main fishing grounds had the greatest number of returns per hour. The inshore tagged prawns, which accounted for 61.5% of the returns, were released in or adjacent to this ground. Auma Creek drains into the main fishing ground and a further 22.4% of the recaptures were from this release site. Only 16% of the recaptures were from nursery releases outside the main fishing ground. It is noteworthy that a small region within the fishing ground to the east of the main fishing ground produced 60% of the returns for this region, but received 20% of the effort. This region could have been fished at less than optimum during the study.

Although prawns from both the eastern and western ends of the Gulf moved both west and east, 46% of movement was in an easterly direction. In 40% of the cases, the recapture site was within 10 km of the release site. The main migration pathway for *P. merguiensis* was from the nursery creeks to Orokolo, Kerema and Freshwater Bays. The smaller western pathway was into the region adjacent to the Fly River mouth. This fishing area also received recruits from creeks on the mainland at the western extremity of the Gulf.

Discussion

Tag effectiveness

The use of vinyl streamer tags to mark penaeid prawns was highly recommended by Marullo et al (1976). The present study found the tag to be a satisfactory way of marking *P. merguiensis* although results suggest that more experimenting with the tags is required. *Penaeus merguiensis* of <17mm CL, the mean size tagged in the estuarine habitat, produced <2.5% of the recaptures. Lucas et al (1972), using Petersen discs, found that there was increased mortality of prawns <30 mm CL. Ruello (1970) showed a significant difference in recapture rates of large and small (<22 mm CL) *P. plebejus* using Atkins tags, although his sample size was small. Experiments to determine to what degree the mortality of small prawns (in this case *P. merguiensis* of <17mm CL) is due to the effect of tagging or natural mortality are recommended.

Tags were found to be settling sites for fouling organisms. Tags left suspended in a nursery creek for two weeks showed substantial growth of filamentous algae, increasing the tag thickness to 15mm. Most of the returned tags showed encrustations of bryozoan communities. The lack of algae on the returned tags compared with those suspended in the nursery creeks could be due to many causes such as abrasion on the substrate as the prawn moves, and different environmental conditions between the nursery and adult habitats (ie salinity, light penetration etc). Most of the returned tags had cuts along the sides. A single recaptured prawn kept in an aquarium fed off the fouling organisms of its tag suggesting that the cuts were caused by the chelae of the prawns. The period which a tag remains attached to a prawn is unknown, however it would decrease with increased time between release and recapture, as the prawn would have more time to cut the tag. Incorporation of a tougher material into the tag could increase the durability of the tag attached to the prawn.

The increased mortality of small prawns could be a result of either the increased time necessary before these prawns are recruited to the fishery, the increased distance they would have to travel to reach the fishing grounds, or the effect of tagging. Thus, size at marking, which can involve location (nursery or inshore regions) and capture method (prawn trawler or dinghy with seine net) and the proximity of the recapture site should be evaluated prior to initiating a tagging program. When there is a choice between tagging inshore or in nursery creeks, as was the case in this study, the value of obtaining more accurate data on prawn movements from nursery sites as well as the lower costs involved in tagging, should be evaluated against the lesser rate of tag returns.

Migrations

Although 88.4% of the inshore releases were captured within 40 km of their release site, the extent of migration prior to tagging is unknown as tagged prawns released in the Aird Delta in the west and Kerema Inlet in the east were recaptured in the vicinity of the inshore releases. Recaptures from Auma Creek accounted for 46.1% of the estuarine recaptures. As expected, the majority of these (61.9%) were recaptured in the main fishing grounds adjacent to the mouth of this creek, and thus migrations of these prawns would have been curtailed as they were caught moving through the prawning grounds.

Although the majority of the estuarine recaptures were from Auma Creek, this creek would be expected to contribute only a small proportion to the main catches in Orokolo and Kerema Bays due to its small size. This study showed that *P. merguiensis* were capable of large migrations and that prawns from the main identified nursery grounds of the Aird Delta do contribute to the main fishing grounds of Orokolo, Kerema and Freshwater Bays, 80 to 150 km to the east. Although returns from these grounds were small the time required to migrate this distance to the commercial fishery could account for the increased mortality.

From a fisheries point of view, the extensive migrations of penaeid prawns means that commercial fishing grounds need not be adjacent to nursery sites, and in fact can be located a considerable distance away.

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Distribution patterns of commercial prawns and reproduction of *Penaeus esculentus* around the Wellesley Islands in the southeastern Gulf of Carpentaria

Abstract: Species composition and distribution of commercially fished penaeid prawns were investigated in waters around the Wellesley Islands (139° 30'E, 16° 30'S). *Penaeus esculentus* was the most abundant species with *P. latisulcatus* the next major component and *Metapenaeus endeavouri, P. merguiensis* and *P. semisulcatus* less numerous. *Penaeus esculentus* migrated to the fishery from seagrass nursery grounds near southwestern Mornington Island and the Bentinck, Sweers Islands area. Juveniles, 18 to 26mm carapace length (CL), first appeared in November and major migration from nursery areas occurred in December. The minimum size of mature female *P. esculentus* was 26mm CL and 50% attained maturity at 31-32mm CL. Although there was a potential for spawning all year round, it is most likely to occur in July to September.

Introduction

Since 1977, the annual catch of tiger prawns, *Penaeus esculentus* and *P. semisulcatus,* and endeavour prawns, *Metapenaeus endeavouri* and *M. ensis,* in the Northern Prawn Fishery has exceeded 4000t (Anon. 1982). Because of this several studies of the biology of these species have been undertaken so that data could be provided for management purposes.

Growth and movement of tiger prawns were examined through tag and recapture experiments in the western Gulf of Carpentaria (Kirkwood and Somers 1984; Somers and Kirkwood 1984) and Grey and Buckworth 1983) studied the effect of seasonal closures on tiger and endeavour prawn populations in the western Gulf.

An extensive fishery for tiger prawns also exists around the Wellesley Islands (138 to 142° E, 16 to 18° S) in the southeastern Gulf of Carpentaria. Little biological information has been available for prawn populations in this region. The fishery surrounding the Wellesley Islands is relatively isolated from other prawning areas and may be considered a closed system. Most juvenile recruitment into the fishery is almost certainly derived from local sources.

Results of studies of juvenile penaeid prawns in inshore areas of the Wellesley Islands have been reported by Coles and Lee Long (1985). The present paper adds to this work by describing the distribution of the adult phase of the major commercial species around the Wellesley Islands as well as recruitment and aspects of the reproduction of the brown tiger prawn, *P. esculentus.*

Materials and methods

Sampling began in January 1983 using the fisheries research vessel Gwendoline May. Sampling was conducted with twin commercial otter trawls (11.0m headrope length Florida Flyers) on 37 trawlable sites (Fig. 1) selected around the Wellesley Islands at depths ranging from 9 to 42m. The sites were intended to encompass the extent of the fishery and incorporated transects which originated near to shore and terminated at the outer limits of the commercial grounds.

Each lunar month, duplicate 30 min trawls were made within four nights of the new moon. Surface temperatures were taken at the completion of each trawl.

Carapace length (CL) was measured to the

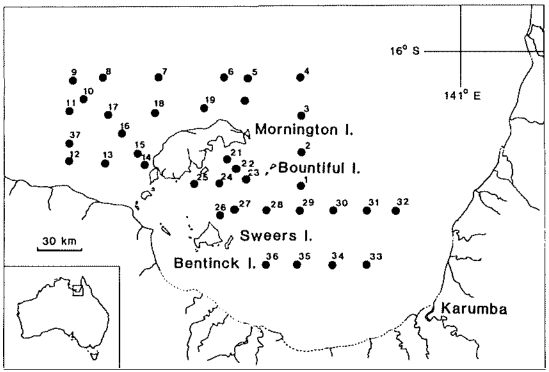

Figure 1. The southeastern Gulf of Carpentaria showing the group known as the Wellesley Islands and the position of sampling sites.

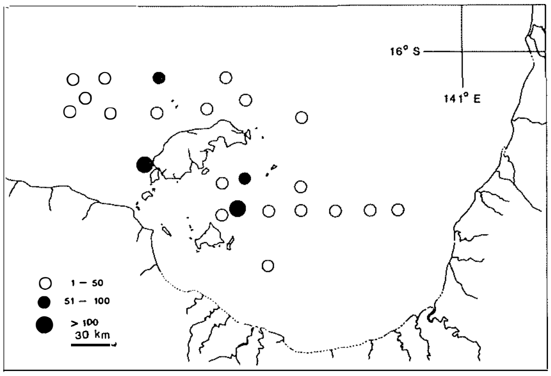

Figure 3. The number of *Penaeus latisulcatus* caught per hour at each site for 12 months (n = 5280).

nearest 0.1 mm for each prawn. Wet weights were recorded to the nearest 0.1 g. A visual assessment was made of ovarian development by examining the external appearance of the ovary. Four stages of development (immature, developing, early ripe, ripe) were distinguished using the criteria of Tuma (1967).

Results

Species composition

Six commercial species were found in the study area. A total of 39824 prawns was caught during the 12 months of sampling. The brown tiger, *P. esculentus,* was the most abundant (55% of the total catch), with *P. latisulcatus* and *M. endeavouri* comprising 22% and 10% of the total catch respectively. *Penaeus merguiensis* and *P. semisulcatus* made up less than 5% and only an occasional *P. longistylus* was caught.

Species distribution

Penaeus esculentus

Penaeus esculentus was abundant to the west and southeast of Mornington Island (Fig. 2). Southwest of Mornington and north of the Bentinck and Sweers Islands a large number of juvenile prawns was caught, possibly representing recruitment from adjacent nursery areas. Catches of *P. esculentus* of fewer than 100 prawns per hour were taken on the grounds to the north and to the east of Mornington Island, and to the southeast of Sweers Island.

Penaeus latisulcatus

Penaeus latisulcatus occurred in very small numbers throughout. The highest catch rate of this species was taken to the southwest of Mornington Island and to the north of Sweers Island (Fig. 3). Catch rates of 51 to 100 prawns per hour occurred on a sample station to the

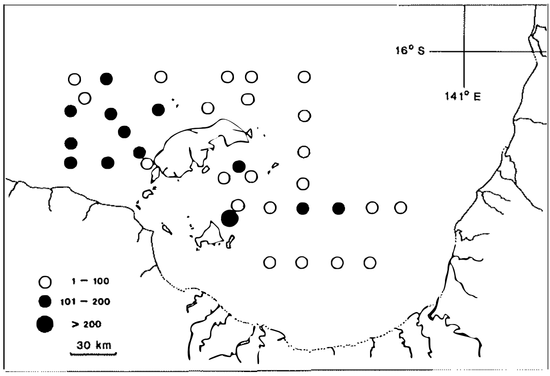

Figure 2. The number of *Penaeus esculentus* caught per hour at each site for 12 months (n = 14645).

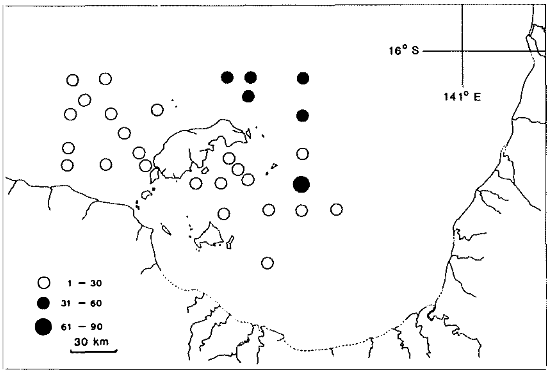

Figure 4. The number of *Metapenaeus endeavouri* caught per hour at each site for 12 months (n = 3020).

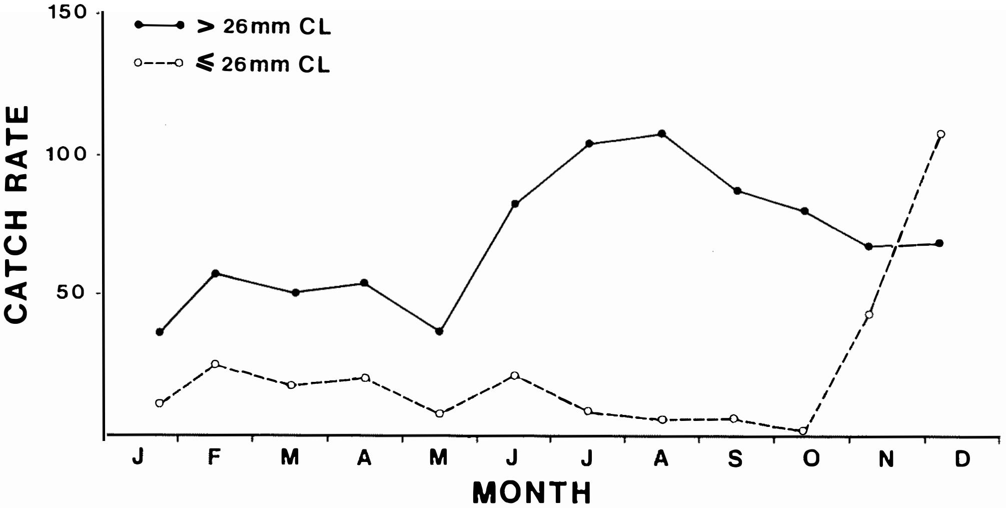

Figure 5. Catch rate (No. of prawns per hour) in each month for *Penaeus esculentus* >26 mm carapace length and ≤ 26 mm carapace length.

north of Mornington Island. Large catches of juvenile prawns also occurred to the southwest of Mornington Island.

Metapenaeus endeavouri

The highest catch rate of *M. endeavouri* was to the southeast of Mornington Island (Fig. 4). This species was found to be most numerous in the sites northeast of Mornington Island. It occurred in low catch rates throughout the rest of the study area.

Recruitment of *Penaeus esculentus*

Immigration to the fishery of juvenile *P. esculentus* (≤ 26 mm CL) was evident in November and continued into December (Fig. 5). The highest catch rate of 183 prawns per hour was in December. In earlier months of the year juvenile prawns were present but in small numbers. The catch rate for *P. esculentus* >26 mm CL exceeded 100 prawns per hour in July and August. It was less than the catch rate of *P. esculentus* ≤ 26 mm CL in December when immigration of juveniles occurred.

The highest catches of prawns ≤ 26 mm CL were taken to the north of Bentinck and Sweers Islands and to the west of Mornington Island in November and December (Fig. 6).

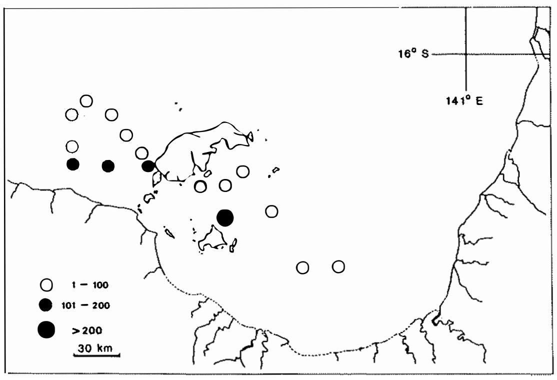

Figure 6. The number of *Penaeus esculentus* ≤ 26 mm carapace length caught per hour for November and December at each site (n = 2423).

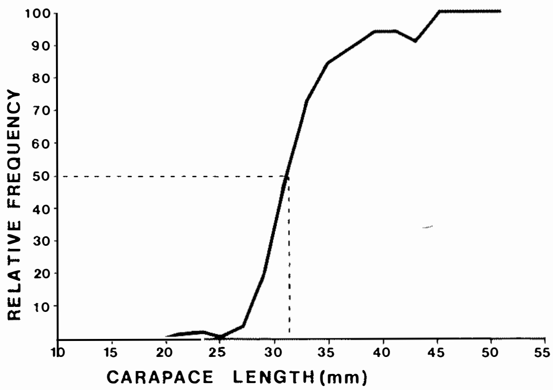

Figure 7. The size at maturity of female *Penaeus esculentus*. The graph shows the percentage of females with early ripe to ripe ovaries in each 2 mm size class. The size at which 50% were mature was between 31 and 32 mm carapace length.

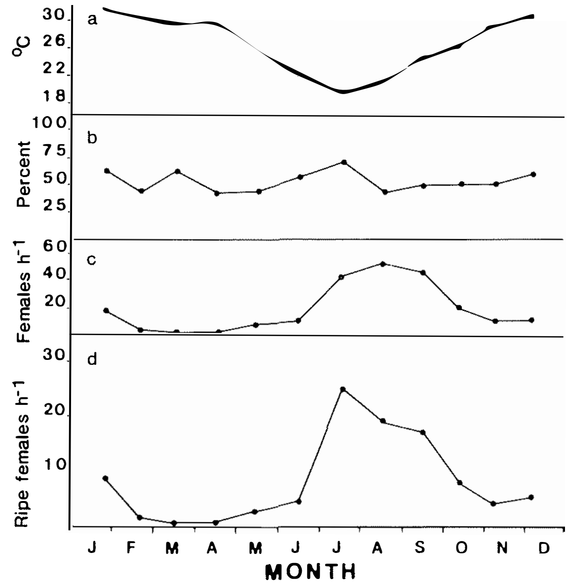

Figure 8. Data collected between January and December 1983 for **a.** the mean monthly bottom temperatures, **b.** proportion of ripe females, **c.** catch rate of females, **d.** the number of ripe females, for *Penaeus esculentus.*

Reproduction in *Penaeus esculentus*

The frequency of occurrence of early ripe to ripe ovaries increased sharply in females greater than 26mm CL (Fig. 7). At 31-32mm CL 50% of females were mature.

Throughout the year more than 40% of female *P. esculentus* had ripe ovaries, suggesting that spawning could occur at any time (Fig. 8b). However, ripe female catch rates were very low in February to May then increased from June through October (Fig. 8c).

When expressed as the number of ripe females within each month's catch, the greatest spawning potential occurred in July and extended to October (Fig. 8d). Spawning activity may be associated with bottom water temperatures (Penn 1980a). Around the Wellesley Islands mean bottom temperatures decreased from 31°C in January to 19°C in July and then increased in later months (Fig. 8a).

Discussion

Penaeus esculentus was the most numerous species in catches taken during this study and would probably be the largest component of the commercial catches. This differs from the catch in the western Gulf where *P. semisulcatus* and *M. endeavouri* are also numerous (Grey and Buckworth 1983; Somers and Kirkwood 1984). The choice of tiger prawn grounds as sampling sites may explain the small catch of *P. merguiensis. Penaeus longistylus* was rare in catches as this species is associated with areas close to coral reefs (Penn 1980b), unlike sites trawled in this study.

Juvenile *P. esculentus* (≤ 26mm CL) migrated from inshore nursery grounds to the nearshore fishery in November and December and then moved to the outer fishery in successive months. This timing is supported by studies of juvenile prawns on nursery grounds around the Wellesley Islands (Coles and Lee Long 1985). Studies on the east coast of Queensland in Trinity Inlet, Cairns (145°47′E, 16°55′S), showed that juveniles left the nursery grounds in December (Heasman 1983). Grey and Buckworth (1983) similarly found that recruitment to the fishery from nursery areas by *P. esculentus* in the western Gulf of Carpentaria began in November and that the major recruitment occurred in December and January. These studies all support a major recruitment to the fishery for *P. esculentus* between November and January. Results of tiger prawn life cycle studies in Weipa (Staples 1984) by contrast indicate that recruitment of juvenile *P. esculentus* to offshore areas occurs both summer and winter. No evidence of winter recruitment was found in the present study.

The juvenile *P. esculentus* entered the fishery at sites adjacent to the extensive seagrass beds around the Wellesley Islands which have been described by Coles and Lee Long (1985). This is evident from the high catch rates to the north of Bentinck and Sweers Islands where high numbers of juvenile prawns occurred.

Fifty percent of female *P. esculentus* were mature at 31-32mm CL. The high incidence of ripe females in the study area throughout the year raises the possibility that female *P. esculentus* have the potential for spawning during the entire year. It had been hoped that a spawning season could be determined from the abundance of females in a spent condition. Unfortunately spent females could not be positively recognised by external appearance of the ovary.

The percentage of ripe females appears to be a poor indicator of spawning as there were considerable changes in the size of the population of mature females throughout the year. This was quite marked between February and June when there was a high proportion of ripe females but a small population. In contrast, from August to October, the proportion of ripe females was similar but the population much larger. By combining the proportion of ripe females with relative abundance it was estimated that the peak spawning time is July to September.

The spawning seasons of some penaeids are closely associated with an increase in water temperature (Penn 1980a). As spawning of *P. esculentus* around the Wellesley Islands is most likely to have occurred in the coldest months, it is unlikely to have been triggered by the annual spring increase in temperature.

Acknowledgements
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Effect of temperature on duration of emergence, speed of movement, and catchability of the prawn *Penaeus esculentus*

Abstract: Continuous time-lapse video recordings were made of the brown tiger prawn, *Penaeus esculentus,* in 2 m and 6 m diameter tanks under controlled conditions. The mean duration of nocturnal emergence of prawns exposed to an annual cycle of temperature and night length was directly related to temperature and varied from less than 50 min night^{-1} at 16° C to more than 350min night^{-1} at 24 to 26° C. The regression model—

Emergence = 34.7 x Temperature – 488

accounted for 40% of the variation in emergence. Addition of night length as a second independent variable did not improve the fit of the model significantly. Independent observations of *P. esculentus* in temperature controlled tanks showed no significant correlation between duration of nocturnal emergence and night length in the range 600 to 780 min. Comparison of laboratory results with published field data on *P. esculentus* from Exmouth Gulf, Western Australia, suggest that this relationship between temperature and emergence can be used to correct abundance indices for differences in catch rate with changes in temperature. At low temperatures *P. esculentus* moved almost continuously when emerged, but as temperature rose there was an increasing tendency to remain stationary for part of the night. At 24±1° C, prawns moved for 75% of their total emerged time. There was a significant positive linear relationship between speed of movement and temperature with speeds of 40 to 50 m h^{-1} at 25° C dropping to less than 15 m h^{-1} at 16° C. The reported extent of migrations of tagged *P. esculentus* indicate a requirement for sustained high speed walking or swimming with a strong directional component of a type not seen in the laboratory experiments.

Introduction

Penaeid prawns and shrimps form the basis of several important tropical and sub-tropical fisheries. Many of these fisheries show marked daily, weekly, monthly and annual variation in catch. This variation results from a combination of those factors which determine the number of prawns present in an area and those which affect the catchability of individual prawns. Some species of penaeids bury in the substrate for part of the day or night. During this time their probability of capture by trawls is low and thus factors which influence the relative time spent emerged or buried, are important in determining catchability. The most obvious of these factors is light. Numerous authors have shown circadian rhythms of burying and emergence in penaeid species (Dall 1958; Racek 1959; Hughes 1968; Hindley 1975; Wickham and Minkler 1975). Another factor which affects the duration of emergence is temperature. Williams (1955) suggested that the reason for low catches of the shrimp *Penaeus duorarum* in winter was because it remains buried during periods of cold. Penn (1976) caught *P. latisulcatus* each month over a year and observed the behaviour of the newly captured prawns in aquaria. He found a seasonal cycle of emergence which he said was caused by temperature and he suggested that this cycle would affect catchability. Fuss and Ogren (1966) found a positive correlation between nocturnal activity of *P. duorarum* in tanks and water temperature in the range 10° to 26° C. These authors have not quantified the relationship between temperature and duration of emergence. White (1975) attempted to do so by relating temperature to commercial catch of *P. esculentus* in Exmouth Gulf, Western Australia. He found that although temperature affected catch, he could not calculate directly the magnitude of the effect from field data because of variation in catch resulting from immigration, emigration and mortality. An alternative approach is to quantify the effect of temperature by laboratory based experimental techniques.

Two distinctly different aspects of activity behaviour have been measured under laboratory conditions. These are the duration of emergence and the duration of locomotory activity. The first of these refers to the total time spent above the surface of the substrate regardless of what the prawn may be doing. Fuss and Ogren (1966), in a study of *P. duorarum,* classified all shrimp that were not buried as active even if they were motionless on the substrate. Locomotory activity by contrast refers specifically to periods when the prawn is moving. This measurement is not a good indicator of catchability because it does not take account of time when the prawn is stationery on the surface and therefore vulnerable to capture. A better measure of catchability is the duration of emergence.

Measurement of duration of emergence requires either frequent observations or continuous monitoring. Early studies involved intermittent direct observation—a technique which can cause disturbance to the experimental animals. Wickham and Minkler (1975) introduced the use of a low-light television system for remote viewing of behaviour of penaeids. This technique has been improved by the use of time-lapse recorders as described by Wassenberg and Hill (1984). Recorders allow for continuous monitoring, they also reduce the time required for playback and analysis and provide a permanent record. It was decided to use continuous time-lapse television recording for studying the effect of temperature on the behaviour of *P. esculentus* kept in large tanks.

The brown tiger prawn, *P. esculentus,* is a commercially important penaeid which is endemic to northern Australia. White (1975) showed that catches of *P. esculentus* dropped in winter and suggested that this was caused by the lowering of temperature. Since both temperature and night length vary seasonally, the behaviour of *P. esculentus* was monitored in a system having an annual cycle of both night length and temperature. Additional experiments under controlled conditions of light and temperature were used to separate the two effects. By recording behaviour of individual prawns in large tanks, it was possible to partition total emergence time into active and stationary periods as well as to measure the effect of temperature on speed of movement.

Materials and methods

Brown tiger prawns, *P. esculentus,* were collected from commercial trawlers operating in Moreton Bay (27° S, 153° E), Queensland. Active prawns were selected from the catch and transferred to the laboratory in bins of aerated seawater. They were held for at least two weeks to overcome the effects of the trawling stress described by Hill and Wassenberg (in press). Prawns used in experiments at ambient temperatures were held outdoors in two 1.1 × 0.7 m holding tanks supplied with flowing seawater and subject to ambient day and night length and temperature. Seawater temperature fluctuations in these tanks were dampened by 70 mm thick foam insulation. The holding tanks had a sand substrate into which the prawns could bury. This substrate consisted of 50% medium (0.25 to 0.5 mm diameter) and 50% fine and very fine sand (0.063 to 0.25 mm diameter).

The effect of an annual cycle in temperature and night length on the behaviour of *P. esculentus* was investigated in a 6 m diameter tank containing 800 mm depth of water and 200 mm of sand. The tank was monitored continuously by a closed-circuit television camera (National WV-1350A) connected to a time-lapse recorder (National NV-8030). The tank was lit by white lights during the day and red lights at night. The white lights were controlled by a time switch and the setting was adjusted at about six week intervals to give night lengths similar to ambient varying from 600 min in November to December to 810 min in June to July. Temperature was allowed to follow ambient levels and had a daily variation of 1° to 2° C and an annual range from 14° C in June to 26° C in February. Temperature in the tank was measured between 08.00 and 09.00 h each day. Salinity in the tank varied between 30 and 35‰.

In addition to a single *P. esculentus* at a time, the 6 m tank contained 16 spanner crabs, *Ranina ranina,* as part of a separate experiment. The crabs spent most of the time buried, emerging for an average of 1 h during the day mainly when food was put into the tank. In 18 months there was only one case of a prawn being attacked by a crab. Generally the prawns were ignored by the crabs and vice versa.

Recorded tapes were played back on a monitor with a 300 x 380mm screen. The times at which a prawn emerged and buried, as well as periods when it was stationary on the surface were noted. Because *P. esculentus* rarely emerged during the day, the analysis of emergence was limited to the night and to two hours before dusk and after dawn. To measure locomotory activity, the track of the prawns was traced on to a transparent plastic overlay on the monitor screen. At temperatures of 20° C and above, the first hour of movement was tracked, below 20° C all movement was tracked. The distance which the prawn moved in a night was calculated from the length of the track as measured on the overlay by a calibrated map measuring wheel. These data together with the time spent moving were used to calculate speed of movement. The night on which a moult occurred as well as the night preceding and the night following a moult were not included in the analysis because Wassenberg and Hill (1984) showed that emergence of *P. esculentus* is reduced during this time. Data were collected from the 6m tank on 237 nights using 48 *P. esculentus* with carapace length (CL) in the range 21 to 45mm ($\bar{x}$ 31.4mm). Most prawns were recorded for about five nights (range 2 to 10 nights).

Because short nights were in summer when temperatures were high and long nights were in winter when temperatures were low, there was a significant negative correlation (r = -0.49) between night length and temperature in the 6m tank. An independent experiment was run to separate these two effects. The effect on duration of emergence of varying night length at a constant temperature was measured in two 2m diameter tanks housed in separate light- and temperature-controlled laboratories. These tanks each contained a 50mm layer of sand and 500mm depth of water kept at 24±1° C. The tanks were monitored by closed-circuit television cameras and time-lapse recorders (National NV-8050) which incorporated a time and date generator. Duration of nocturnal emergence of individual prawns in the 2m tanks was obtained by measuring the difference between the times of emergence and burial. Experiments were repeated for four night lengths (600, 675, 720 and 780min). At each night length 10 different animals were recorded for three successive nights. At least two weeks before the experiments commenced, prawns were transferred from the outdoor holding tanks into an indoor 2m tank kept under conditions similar to the experimental ones.

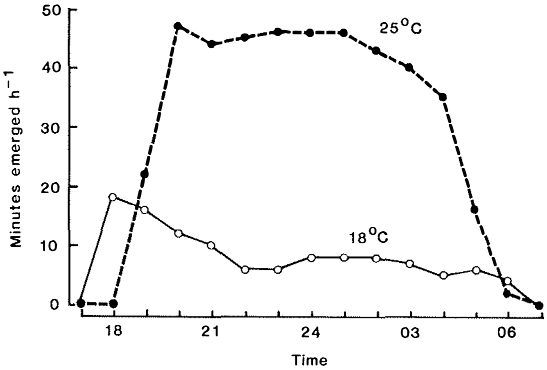

Figure 1. Mean number of minutes emerged h^{-1} by *Penaeus esculentus* between 17.00 h and 07.00h at 25° C (n = 33) and 18° C (n = 19).

Prawns in holding and experimental tanks were fed to excess each evening with pieces of greentail prawn, *Metapenaeus bennettae.* Food was provided only occasionally for prawns in the 6m tank because of the availability of pieces of fish supplied to excess three times a week to crabs in the tank.

Results

Duration of emergence

At 25° C prawns in the 6m tank spent 40 to 50min emerged each hour of the night but at 18° C they spent only 10 to 20min emerged each hour (Fig. 1). At both temperatures the pattern of emergence was skewed with more prawns emerged in the first 4h of the night than later.

Night length showed a seasonal pattern with the shortest period (600min) in December and the longest (810min) in June (Fig. 2a). Mean monthly temperature in the 6m tank ranged from 26° C in February to 14° C in June (Fig. 2b).

The mean monthly duration of nocturnal emergence in the 6m tank varied seasonally with duration of emergence less than 150min $night^{-1}$ in June and July, and longer than 300min $night^{-1}$ from December to April (Fig.2c). At temperatures above 17° C nearly all prawns emerged every night but below this temperature the proportion emerging declined sharply and only 5% emerged at 14° C (Fig. 3a). The mean duration of nocturnal emergence was directly related to temperature and varied from less than 50min $night^{-1}$ at 16° C to more than 350min $night^{-1}$ at 24 to 26° C (Fig. 3b). The regression model relating the duration of nocturnal

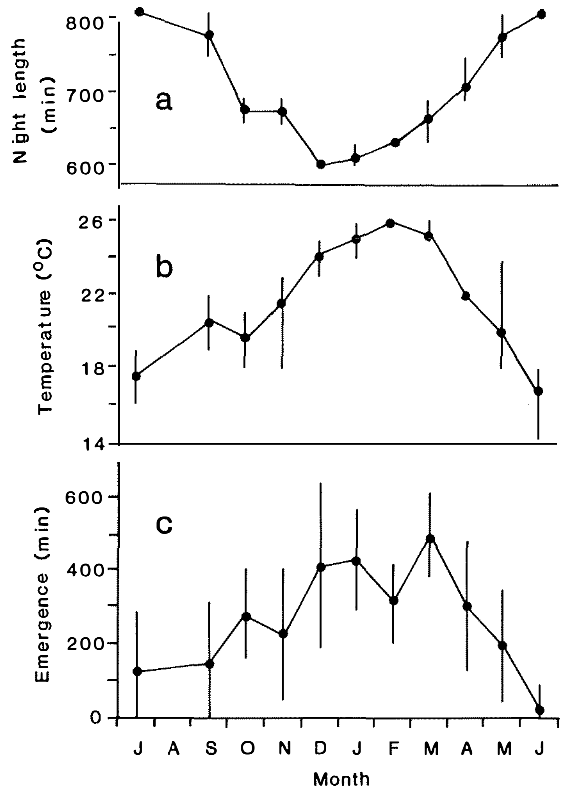

Figure 2. Conditions in a 6 m experimental tank and the behaviour of *Penaeus esculentus* under these conditions. **a.** Monthly mean and range of length of night. **b.** Monthly mean and range of temperature. **c.** Mean (±95% confidence intervals) of the duration of nocturnal emergence each month. n = 9 to 44 (mean 21.6) at each point in **a**, **b** and **c.**

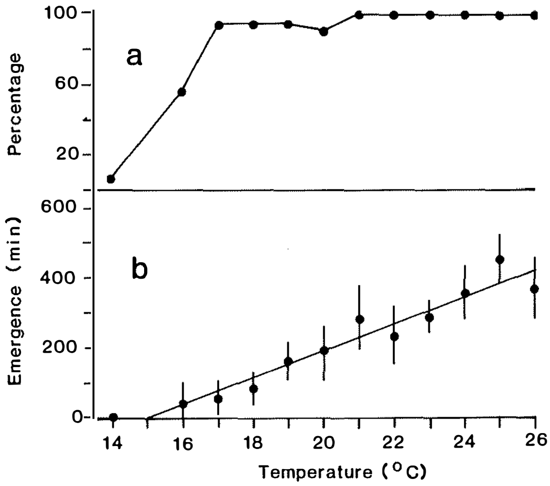

Figure 3. Behaviour of *Penaeus esculentus* at a series of temperatures. **a.** Percentage which emerged. **b.** Duration of emergence (mean ± 95% confidence intervals). n = 9 to 35 (mean 19.6) at each point in **a** and **b**. Formula for the line fitted to data given in text.

Speed of movement

Penaeus esculentus rarely swam in the tank and nearly all movement was by walking. Swimming was observed on only two occasions. On the first, a 30 mm male swam at an average speed of 143 m h^{-1} for 16 min at 22° C. On the second, a 36 mm female swam for 36 min at 116 m h^{-1} at 23° C. When walking in the 6 m tank, prawns seldom encountered the wall but changed

emergence (E) to temperature (T) was—

$E = 34.7T - 488$ ($r^2 = 0.40$, 236 df, $P<0.01$).

This model explained 40% of the variation in emergence. In the experiments in the 2 m tanks in which night length was varied at constant temperature, there was little alteration in duration of emergence with change in night length from 600 to 780 min (Fig. 4). The two variables were not significantly correlated ($r = 0.19$, df = 38, $P>0.01$) indicating that change in night length did not affect duration of emergence. This conclusion was supported by data from the 6m tank since addition of night length as a second independent variable to the emergence temperature model altered the correlation only marginally ($r = 0.65$, 235 df). An F-test indicated that the addition did not significantly improve the model ($F = 4.82$, df = 1, 235, $P>0.01$).

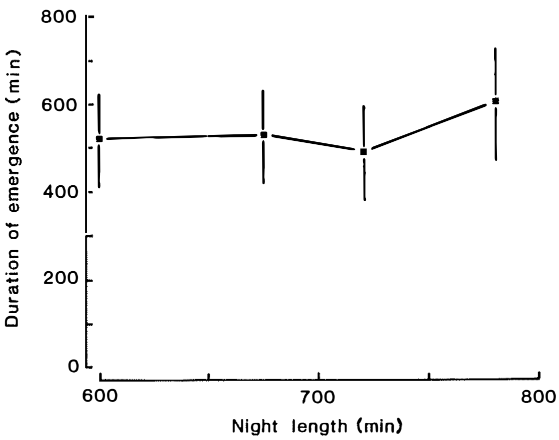

Figure 4. Duration of emergence of *Penaeus esculentus* kept in 2 m diameter tanks and exposed to different night lengths at 24±1° C. Mean and 95% confidence intervals, n = 30 at each point.

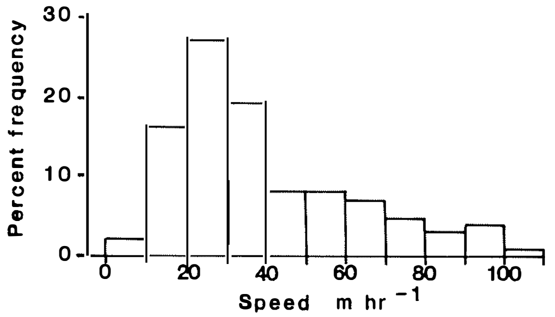

Figure 5. Frequency distribution of speeds of movement of *Penaeus esculentus* at 24±1°C (n = 59).

direction frequently giving rise to an erratic, highly convoluted track with no major directional component. The modal speed of walking at 24°C was 20 to 29 m h^{-1}, the most rapid was 109mh^{-1} (Fig. 5).

At low temperatures prawns moved almost continuously when emerged but, as temperatures rose, there was an increasing tendency to remain stationary for part of the night (Fig. 6a). There was a significant positive linear relationship between speed (S) and temperature (T) (Fig. 6b).—

$$S = 3.83T - 54 \quad (r^2 = 0.78, n = 92)$$

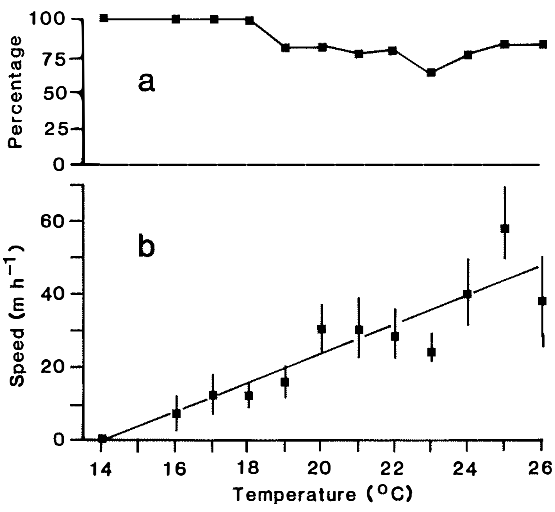

Figure 6. Movement of *Penaeus esculentus* over a range of temperatures. **a.** Percentage of emergence time during which the prawns were moving. **b.** Mean (± 95% confidence intervals) of speed of movement at different temperatures. Mean at each point in **a** and **b** is based on 9 to 35 values (mean 19.6). Formula for the line fitted to data is given in the text.

At 25 to 26°C *P. esculentus* moved at approximately 40 to 50m h^{-1} but at 16°C speed dropped below 10m h^{-1}. A t test showed a significant relationship between carapace length (CL) in mm and speed (S) in m h^{-1} at 24±1°C (t = 3.029, 184 df). The relationship was best described by a power curve of the form—

$$S = 0.71\ CL^{1.119} \quad (r^2 = 0.1122, n = 92).$$

Discussion

Seasonal changes in photoperiod affect the behaviour of many Crustacea. Kanciruk and Herrnkind (1973) for example found that the spiny lobster *Panulirus argus* moved more frequently in summer compared to winter when kept in near constant temperature. There is little evidence for similar photoperiod effects in penaeids. Moller and Jones (1975) stated that *P. semisulcatus* and *P. monodon* moved more frequently when exposed to a short night (18h light, 6h dark) than in a long night (6h light, 18h dark). The lower level of movement in the long night occurred for a longer period however and thus it is not clear whether the difference was significant. Fuss and Ogren (1966) showed that the period during which *P. duorarum* emerged seemed to be controlled primarily by photoperiod but the proportion of shrimp emerged at any one time was determined by water temperature. This situation appears to apply to *P. esculentus* since duration of emergence is unaffected by the length of the night in the range 600 to 780 min but it is a function of temperature.

At temperatures above 17°C, nearly all (90 to 100%) *P. esculentus* emerged every night but below 17°C, emergence decreased and at 14°C they emerged on only 5% of nights. Aldrich et al (1968) found that, in tanks, postlarval *P. aztecus* buried into the substrate as temperature dropped to 12 to 17°C. They suggested that this was a form of hibernation which enabled the prawns to survive cold periods until temperatures were more favourable for activity and growth. The work of Achituv and Cook (1984) on the carid *Palaeomon pacificus* provides a physiological basis for hibernation in a decapod crustacean. They showed that if *P. pacificus* was active at low temperatures, their metabolic losses exceeded their ingested ration. Thus emergence at low temperatures would result in negative growth. At high temperatures, ingested energy is directed considerably more efficiently into growth.

The reduced duration of emergence of *P. esculentus* at low temperatures could contribute to the decrease in catch per unit effort (CPUE) which occurs for this species in winter. White (1975) produced a mathematical model which attempted to explain seasonal changes in CPUE of commercial catches of *P. esculentus* in Exmouth Gulf, Western Australia. White's model included a factor to compensate for the effects of temperature on catchability. Incorporation of this temperature compensatory factor reduced the error sum of squares of the model significantly, indicating that temperature has a major effect on catchability. White (1975) also used his temperature compensatory factor to estimate the catchability of *P. esculentus* at low temperature in July as a percentage of the catchability at high temperature in February. These estimates showed that White's (1975) temperature compensatory factor could not account for all the changes in catchability. For example, the temperature drop in Exmouth Gulf from February to July in 1969 and 1971 was similar (5.0° C and 5.5° C) but in 1969 catchability in July was 70 to 80% of that in February, whereas in 1971 it was only 40%. In order to compare White's temperature compensatory factor with my experimental results, the duration of emergence of *P. esculentus* was calculated at the temperatures reported by White (1975) for February and July in each of the three years of his study (Table 1). In 1969 and 1971, the February temperature in Exmouth Gulf exceeded the upper limit of the experiments described in this paper (26° C). I have assumed however that the relationship between temperature and duration of emergence continues to be linear to 28° C. The estimated mean duration of emergence at the July temperature is 63% of that at the February temperature (Table 1). According to White (1975), the mean July catchability was 47% of the catchability in February. These two values are close considering that factors apart from temperature may be affecting the catchability of the field population. This suggests that the model relating temperature to duration of emergence derived from the experiments described in this paper could be used for standardising abundance indices derived from CPUE data for *P. esculentus*.

Table 1. Catchability of *Penaeus esculentus* in Exmouth Gulf in July expressed as a percentage of catchability in February in three years; temperatures in Exmouth Gulf in these months; estimated duration of emergence at February and July temperatures based on laboratory experiments; and the duration of emergence at the July temperature expressed as a percentage of emergence at the February temperature. Exmouth Gulf data from White (1975).

Year	Percentage catchability Exmouth Gulf	Temperature (° C) Feb	Temperature (° C) July	Estimated emergence (min) Feb	Estimated emergence (min) July	Percentage emergence laboratory
1969	70 to 80	27.5	22.0	466	275	59
1970	40 to 50	24.3	21.0	355	241	68
1971	40	28.0	23.0	483	310	64
Mean	47	26.6	22.0	435	275	63

Somers and Kirkwood (1984) undertook a tagging study of *P. esculentus* in the western Gulf of Carpentaria. They found that *P. esculentus* moved 30 to 50 km from inshore nursery areas to offshore spawning grounds over a three to five month period (February release to May and June recapture). This is an average displacement of about 10 km month^{-1} or 330 m day^{-1}. The amount which *P. esculentus* moves in a night is affected by temperature. Although Somers and Kirkwood (1984) did not report temperatures in their study area, Munro (1984) shows offshore seawater temperatures in the southeastern Gulf of Carpentaria ranging from 21 to 23° C in June to 29 to 30° C in February. At the average of these temperatures (26° C), *P. esculentus* in laboratory tanks moved about 200m day^{-1}. This movement was highly convoluted and non-directional, suggesting that even if the prawns had not been confined to a 6 m diameter enclosure, their net displacement would have been considerably less than 200 m. Thus it is unlikely that the movements reported by Somers and Kirkwood (1984) represent the summation of random nightly excursions. They are probably the result of a migration in which the movement has a strong directional component and which must involve either sustained high speeds or movement continued for longer periods than were observed in the laboratory situation. Although *P. esculentus* rarely swam in the tanks, they are capable of swimming and they may possibly use tidal currents when migrating. Rothlisberg (pers. comm.[1]) measured surface currents of 2.4 to 3.6 km hr^{-1} in the region of one of Somers and Kirkwood's (1984) release areas in March 1985. Use of strong tidal currents would enable *P. esculentus* to cover large distances fairly rapidly. The speeds and displacements found for *P. esculentus* are small compared to those

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reported for tagged *P. plebejus* which undertakes an extensive spawning migration along the east coast of Australia with six cases reported of migrations in excess of 700 km at speeds of 2.0 to 5.6 km day^{-1} (Ruello 1975).

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Moult staging the tiger prawn *Penaeus esculentus*

Abstract: Heavy pigmentation in the thin pleopods and uropods of the tiger prawn, *Penaeus esculentus,* prevents the use of established techniques for moult staging. A set of criteria has been developed that incorporates setal staging and epidermal withdrawal in the uropods and is supported with histological evidence. Using these criteria the five major moult stages and the premoult and postmoult substages as well as their relative duration may be rapidly and accurately determined. Since excision of appendages is not required, this technique is non-destructive and permits repetitive moult staging of an individual.

Introduction

The physiology, behaviour and reproduction of crustaceans is intrinsically linked to the moulting cycle. Hence in experimental studies it is necessary to be able to identify accurately the stages of the moulting cycle in order to interpret observed biochemical or biological changes. The moulting cycle was divided by Drach (1939) into five main stages which were further divided into various substages and this system has since been almost universally adopted. The main stages are A (immediate postmoult), B (postmoult), C (intermoult), D (premoult) and E (ecdysis). Two types of intermoult stage have been described (Knowles and Carlisle 1956): anecdysis, where there is a long interval between the end of postmoult and the start of premoult, and diecdysis, where there is not a clear intermoult period between the end of postmoult and the start of premoult. The natantians usually have a diecdysal moulting cycle.

Drach (1939) identified the stages of the moulting cycle of the brachyurans *Cancer* and *Maia* using criteria based on readily observable changes in the integument. These criteria have been adapted to enable moult staging of many species within the Crustacea, (reviewed and modified in Drach and Tchernigovtzeff 1967). Further studies on a variety of decapods have also produced either more precise definition of the criteria that Drach (1939) originally proposed or alternative criteria which are more widely applicable (Stevenson et al 1968; Stevenson 1972; Aiken 1973).

The methods used for moult staging generally involve observations of the degree of hardness of the exoskeleton and microscopic examination of the transparent edge of the uropods or pleopods where epidermal withdrawal and development of new setae can be observed (Passano 1960; Drach and Tchernigovtzeff 1967; Yamaoka and Scheer 1970). However only a few authors have verified their interpretation of the moult staging criteria with histological observations (Travis 1955, 1957; Skinner 1962; Stevenson 1968; Stevenson et al 1968). In species that are heavily pigmented, the development of setae is either partially or completely masked so as to be of little use as criteria (Read 1977; Lyle and MacDonald 1983). With these species new criteria need to be established. Earlier studies of the moult stages of penaeid prawns have included *Penaeus duorarum* (Schafer 1968), *P. indicus* (Read 1977), *P. californiensis* and *P. stylirostris* (Huner and Colvin 1979) and *P. merguiensis* (Longmuir 1983). The moulting behaviour of *P. esculentus* has been described by Wassenberg and Hill (1984).

Previously at our Cleveland laboratories, the stages of the moulting cycle of the tiger prawn, *P. esculentus*, have been determined for physiological investigations using criteria based on those of Drach and Tchernigovtzeff (1967). Because of the nature of the investigations and the need for repetitive moult staging of individual prawns, excision of pleopods for microscopic examination was unacceptable and so characteristics of the uropods, in vivo, were used. Owing to the high level of pigmentation in the tiger prawn, reliable identification of setal development in the uropods was not feasible so a new set of criteria for the premoult stages was developed. The new criteria were based on features of the epidermal line where the new setae were developing and were supported with both histological evidence from sections taken from the abdomen and observations of setal development in the exopodite of the pleopods.

Materials and methods

The prawns used in this study were caught by trawling in Moreton Bay (27° S, 153° E) Queensland, and maintained in 350 l tanks supplied with running seawater from the open system used at these laboratories.

The size range of animals that were used to establish the moult staging criteria was 20 mm to 35 mm carapace length (CL) or approximately 5 g to 35 g wet weight. Some of these animals were held individually for a study of the duration of each moult stage and for photomicroscopy of uropods and pleopods. These selected animals, which had a size range of 25.5 mm to 28.5 mm CL, were maintained at 25° C ± 1° C at a salinity of between 32‰ and 36‰, and were fed daily on greentail prawn, *Metapenaeus bennettae.* The duration of the moulting cycle, for animals of this size held at this temperature, is approximately 20 days. (The length of the moulting cycle varies with size and environmental conditions). When the prawns either grew out of the size range or had an appendage removed for photography, they were discarded.

For routine moult staging the edge of the inner uropod in the region adjacent to the telson tip was examined (Fig. 1). Excision of the uropod was not necessary as the prawn could be held immobile and quiescent while wrapped in a wet paper towel. Visual inspection of uropod and pleopod setae was carried out using a Wild stereomicroscope with either x50 or x100 magnification and transmitted light.

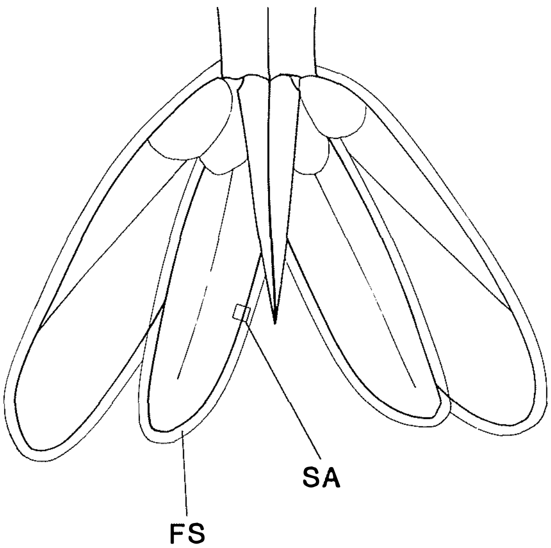


Figure 1. Uropods showing the sample area (SA) used for staging, and fringing setae (FS).

Photomicroscopy was carried out using a Wild Photoautomat automatic exposure controller fitted to a Wild M20 compound microscope and to a Wild M7 stereomicroscope. Uropods and pleopods were excised and mounted under a coverslip in filtered seawater and photographed immediately at x30 magnification on the Wild M7 and at x100 magnification with phase contrast on the Wild M20. Photographs were taken of all samples using both Ektachrome colour slide film and Kodak Technical Pan 2415 black and white film.

Animals used for histological examination were killed by severing the cephalothorax. The second abdominal segment was cut off and immediately fixed in 5% formalin in seawater. Prior to processing and embedding in paraffin wax, the segments were soaked in 5% formalin with 2% acetic acid in distilled water for 24 h to decalcify the cuticle. Sections were cut with a rotary microtome at a thickness of between 5 μm and 8 μm and stained with haematoxylin and eosin.

Results

Stage A

Stage A is divided into two substages, A_1 and A_2, which are identified by the consistency of the cuticle and the appearance of the cellular matrix within the setal lumen.

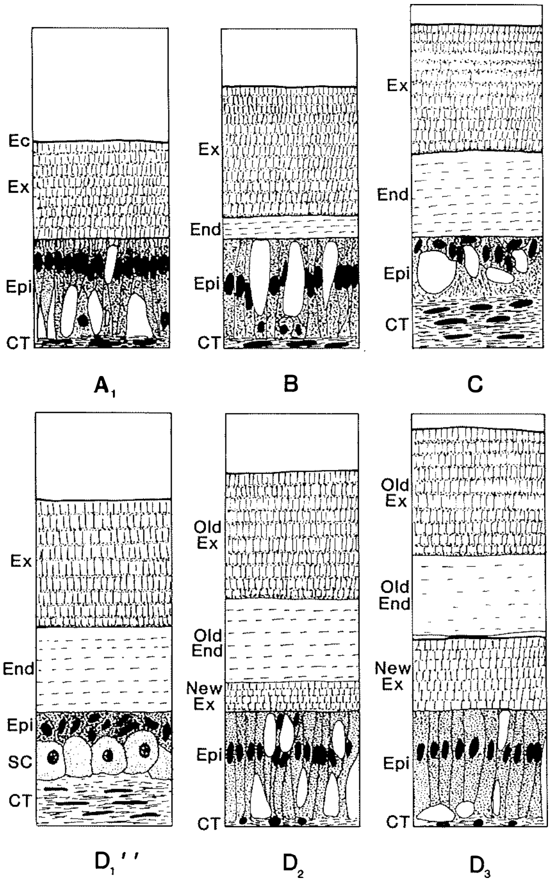


Figure 2. Semi-diagrammatic representations of sections of abdominal cuticle and epidermis. A_1, B, C, D_1'', D_2, D_3 moult stages (see text). Ec, epicuticle; Ex, exocuticle; End, endocuticle; Epi, epidermis; CT, connective tissue; SC, storage cells.

A_1: Stage A_1 begins immediately after the prawn has flicked clear of the exuviae. The cuticle is slippery and has a very soft membranous consistency. The setae and setal bases are filled with a cellular matrix. Histological sections of the abdomen show only epicuticle and exocuticle, and closely packed, tall epidermal cells (Fig. 2, A_1). The end of A_1, which occurs about one hour after moulting, is marked by the loss of the slippery feel of the cuticle and the start of retraction of the cellular matrix from the distal end of the setae.

A_2: During A_2 the cuticle, though still membranous at the start, gradually becomes firmer. The cellular matrix continues to retract from the distal end of the setae. As the retraction progresses, constrictions begin to form at the proximal end of the lumen of the setae (Fig. 3, B). This happens more rapidly in the pleopods than in the uropods. The retraction of the cellular matrix and the constriction of the setal lumen may also be seen more clearly in the pleopods than in the setae of the uropods. In histological sections, a thin layer of endocuticle is just visible three hours after moulting, quite distinct by six hours.

Stage B

Stage B starts six to nine hours after moulting. The exoskeleton which at the start has a parchment-like consistency becomes relatively hard though flexible. Epidermal cells appear less closely packed than they were immediately after moulting and the secretion of the endocuticle continues (Fig. 2, B) until it attains its maximum thickness. Formation of the setal plugs or cones continues until they are present in most setae. The setal cones are obvious in the pleopods but are sometimes difficult to identify in the uropods. The duration of stage B is approximately 10% of the moulting cycle.

Stage C

Stage C begins when the secretion and hardening of the exoskeleton has been completed and may be identified by the presence of setal cones in most of the setae. The epidermis fills the bases of the setae and has a narrow translucent border that extends round the nodes as well as the bases (Fig. 3, C). This border is the cuticular edge of the uropod or pleopod.

The end of stage C occurs when the epidermis begins to withdraw from the border. Histological sections of the abdomen indicate that the endocuticle is about 70% of the thickness of the exocuticle and the epidermis consists of a layer of irregular cells (Fig. 2, C). Stage C lasts for only 5 to 10% of the whole moulting cycle.

Stage D

By convention, premoult has been divided into five substages from D_0 through to D_4. Details of setal development which provide a precise indication of premoult substages may be observed with difficulty in the pleopods but cannot be observed clearly or consistently enough in the uropods to be used as criteria for staging. However, the degree of epidermal withdrawal and the shape of the epidermal line in the medial region of the uropod were found to be consistent. These have been correlated

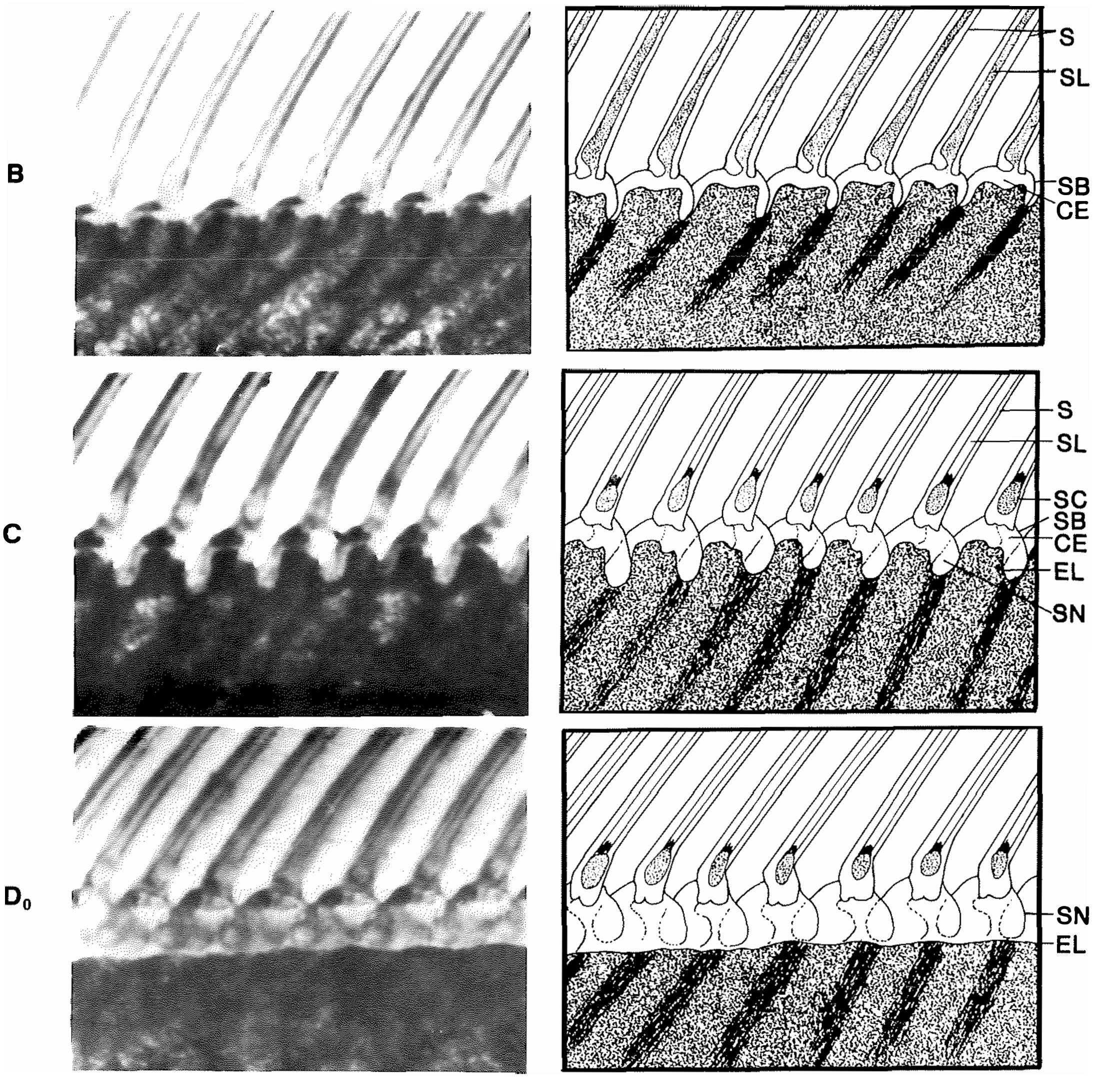
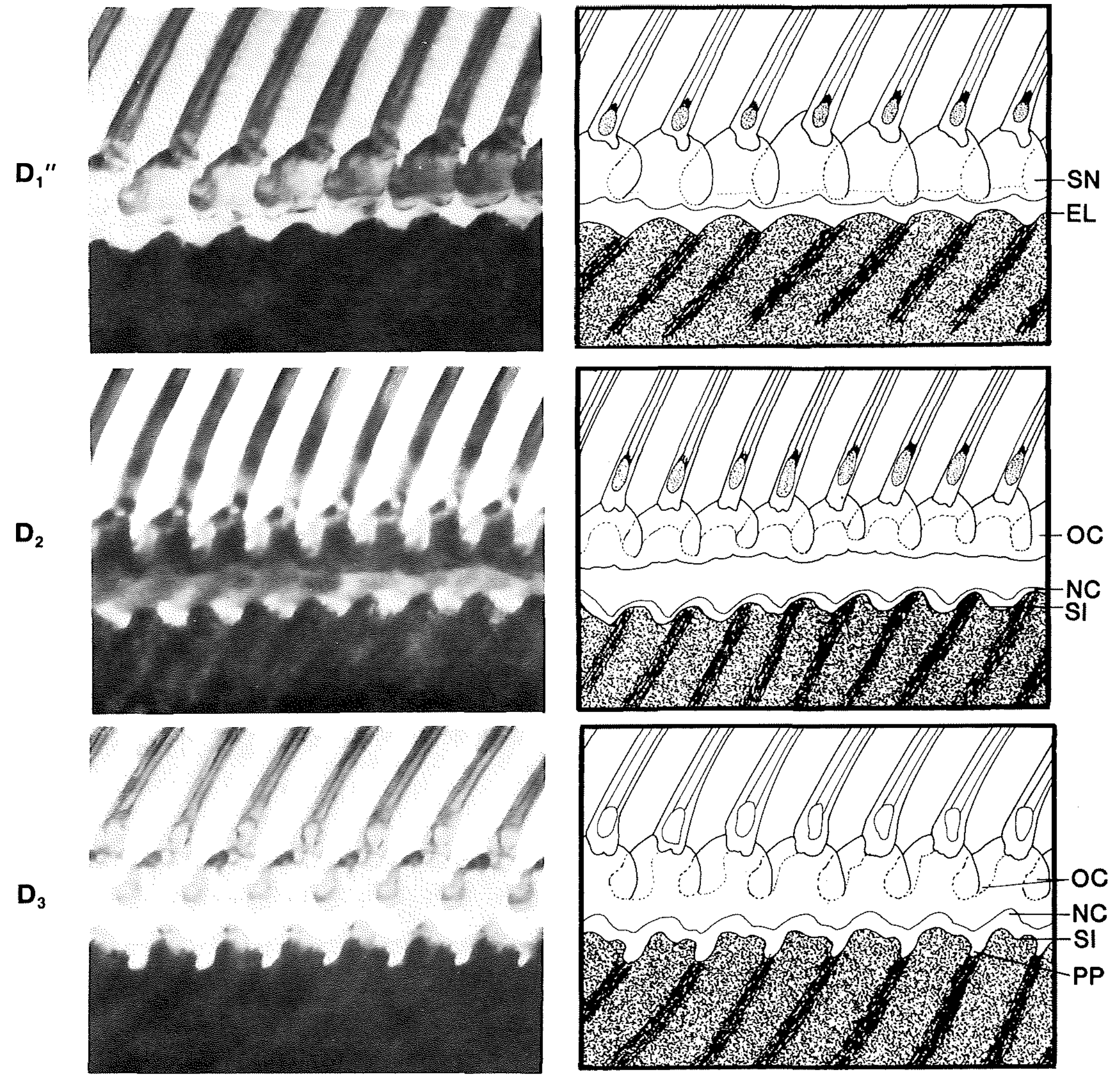


Figure 3. Photographs, using transmitted light, of the uropod edge indicated in Fig. 1. The line drawings are tracings of the photographs. B, C, D_0, D_1'', D_2, D_3 moult stages (see text). S, setal shafts; SL, setal lumen; SB, setal base; SC, setal cone; SN, setal node; CE, clear cuticular edge of uropod; EL, epidermal line; OC, old

with setogenesis in the pleopod and have been used instead. The duration of Stage D is approximately 80% of the intermoult period.

D_0: The retraction of epidermis from the exoskeleton (apolysis), defines the start of D_0. This is readily recognised in the distal end of the setal bases in the uropods. The retraction continues until the epidermis has withdrawn out of the setal bases and forms a straight line below and parallel to the setal nodes (Fig. 3, D_0). There is no obvious separation of the epidermis and endocuticle in the histological sections taken from the abdomen. The organisation of the epidermal cells is similar to that of stage C. Under optimal conditions the duration of stage D_0 is about 15% of the moulting cycle but is extended under adverse conditions.

D_1: The period of development of new setae (setogenesis) categorises this substage. It has been further divided into three subdivisions which identify the developmental stages of the new setae. The shape of the epidermal line in the medial section of the uropod can be used to identify these subdivisions. Further epidermal



cuticle; NC, new cuticle; SI, setal invagination which everts to form seta in the new cuticle at ecdysis; PP, area visible as pinpoints of light in this stage.

withdrawal occurs during stage D_1 creating a translucent zone between the epidermis and the setal bases. Epidermal cells show signs of elongation and new cells, which appear to be storage cells, are present in large numbers (Fig. 2, D_1'). Stage D_1 is by far the longest period in the moult cycle, occupying approximately 50% of the total period.

D_1': First signs of invagination of the epidermis at the site where the new setae will develop. This is indicated by a change in the epidermal line of the uropods from being straight to wavy.

D_1'': Invagination of the epidermis continues to increase. The epidermal edge of both the pleopod and the uropod is more scalloped. New setal tips are generally visible (Fig. 3, D_1'').

D_1''': This is the period when the setae reach maximum invagination and then continue to develop. The scalloping of the epidermal edge reaches a maximum and has a uniform undulating appearance.

D_2: Secretion of the pre-exuvial (epi- and exo-cuticle) layers of cuticle characterises stage D_2

(Fig. 2, D_2). These are pigmented layers and may be positively identified in the dead animal by cutting a portion of the exoskeleton and peeling it away from the tissue. In live animals the stage may be identified in the uropod by the change in the scalloped appearance of the epidermal edge where the setal shafts disrupt the smooth curves of the scalloping (Fig. 3, D_2). In the pleopod, the proximal ends of the new setal shafts may be seen to take on a definite form. Early in this stage they are bifurcate but later become blunt. The setal shafts of the uropod and pleopod in the latter half of D_2 have a distinct orange-red colour. The stage occupies 10% of the moulting cycle.

D_3: The period of maximum reabsorption of components of the old exoskeleton defines stage D_3. It starts about nine hours before moulting and may be recognised initially by the increased distinction of the new setal nodes between the bases of the new setae in the uropod. At this time, when viewed under a microscope with transmitted light, a pinpoint of light may be seen coming from one or two nodes in the mid region of the inner edge of the uropod. However, at about four hours before moulting, these pinpoints of light may be seen coming from most of the setal nodes (Fig. 3, D_3). It was observed that exocuticle was still being formed six hours before moulting. The old exoskeleton becomes obviously separated from the new pre-exuvial layers (Fig. 2, D_3). From about this time, the exoskeleton becomes increasingly brittle as a result of reabsorption of components of the old exoskeleton.

D_4: During this period the prawn loosens itself within the old exoskeleton and the ecdysial sutures open. The old exoskeleton has become so delicate that it may be broken by lightly rubbing it. This stage lasts about one hour.

Stage E

Ecdysis. This is the process during which the prawn extracts itself from the old exoskeleton and everts the setae on the new exoskeleton. Exuviation takes less than 60 seconds.

Discussion

The classification of the stages of the moulting cycle as described above and in Table 1 is in accord with the description of the stages given by Drach and Tchernigovtzeff (1967) although different criteria were used to identify some of the stages, namely, changes of the epidermis in the edge of the mid region of the uropod. In contrast, the changes in the epidermal line in the pleopods cannot be interpreted in the same way. To identify the premoult stages from the pleopods, observations of development of the new setae within the epidermal stratum must be made. Whether the pleopod or uropod is observed for moult staging will depend on the characteristics of the species being studied and the proposed use of the prawn after staging. Prawns that are lightly pigmented such as *P. merguiensis* may be moult staged using the pleopods following the technique described by Longmuir (1983) or by the technique described here using the uropods. In most cases pigmentation in the exoskeleton of *P. esculentus* makes observation of setal development difficult in the pleopods and unreliable in the uropods. If a prawn is to be studied further after moult staging, one must consider its tolerance to handling during uropod examination or the consequences of pleopod excision. Mortality as a result of handling, particularly with the stress-prone *P. merguiensis,* has been minimised by wrapping the prawn in a wet paper towel when moult staging. Little is known about the physiological or behavioural effects, if any, of the excision of one or more pleopods. If experiments are to be conducted using a prawn following moult staging, one should endeavour to avoid pleopod excision. Read (1977) reported that *P. indicus* obtained from a marine environment, in contrast to those from an estuarine environment, were pigmented to an extent that prevented precise identification of setal development in early premoult, and hence he grouped the stages D_0 and D_1 as D_{0-1}.

Stevenson (1968) proposed that the start of A_2 be defined by the beginning of the secretion of the endocuticle, whereas Drach and Tchernigovtzeff (1967) identified A_2 as starting when the contents of the setae begin to retract. These authors also stated that the beginning of the secretion of the endocuticle and the calcification of the pre-exuvial layers occur during A_2. In *P. esculentus,* the cuticle loses its slippery feel at about the same time as the endocuticle begins to be secreted and the cellular matrix begins to retract, and so provides a rapid way of determining the postmoult stage which minimises handling stress for the animal. The change in skeletal hardness from a membraneous to a parchment-like consistency in stage A, which has been reported for other species (Scheer 1960; Drach and Tchernigovtzeff 1967; Huner and Colvin 1979) does not occur in *P. esculentus* until the start of stage B. This inconsistency may be due

Table 1. Criteria for moult staging of *Penaeus esculentus*. Times are based on a 20-day moulting cycle.

Stage	Approx. duration	Criteria
A_1	1 h	Starts immediately following ecdysis Cuticle has slippery, very soft and membranous consistency Cellular matrix fills setae and setal bases
A_2	5 h to 8 h	Cuticle no longer slippery, still soft and membranous Cellular matrix begins to retract from proximal ends of setae Secretion of endocuticle starts
B	2 d	Cuticle has parchment-like consistency, becomes more rigid Constrictions in setal lumen begin and develop into plugs
C	1 d to 2 d	Exoskeleton achieves maximum rigidity Setal plugs present in most setae Epidermis fills setal base, has narrow translucent fringe
D_0	4 d	Starts at first sign of withdrawal of epidermis from setal bases, continues until epidermis forms a straight line below setal bases
D_1'	3 d	Uropod: Epidermis withdraws further from setal bases. Epidermal line becomes wavy Pleopod: First signs of invagination of epidermis
D_1''	3 d	Uropod: Epidermal line becomes moderately scalloped Pleopod: Invagination in epidermis deepens to half its final depth
D_1'''	3 d	Uropod: Scalloping of epidermal line is uniform and at maximum depth Pleopod: Invagination in epidermis deepened to maximum depth
D_2	2.5 d	Uropod: Uniform edge of scalloping disrupted by tip of new setae Setal shafts develop a distinct orange-red colour Pleopod: Proximal ends of setae are bifurcate and alter become blunt
D_3	9 h	Exoskeleton becomes increasingly brittle and delicate Uropod: Pinpoints of light may be seen in new setal nodes
D_4	1 h	Exoskeleton very delicate and easily broken

to the interpretation of "parchment-like" as a measure of the degree of hardness.

The commencement of stage B is marked by a slight hardening of the exoskeleton which occurs between six and nine hours after moulting. Wassenberg and Hill (1984) observed that tiger prawns did not bury themselves in the substrate for approximately six hours after moulting (mean time 354 min, SE=34.8, n=16). These observations included eight where the prawn had moulted after 03.00 h and these did not bury when the lights came on at 06.30 h as would normally be expected. This suggests that burying behaviour is limited by the lack of rigidity of the exoskeleton in stage A, and that by stage B it has achieved the necessary rigidity.

Natantians generally appear to exhibit a diecdysic intermoult stage where the transition from postmoult to premoult is not separated by a well defined intermoult stage or stage C (Knowles and Carlisle 1956; Scheer 1960; Longmuir 1983). The intermoult stage in *P. esculentus* is diecdysic, lasting for between one and two days. The external feature that indicates the start of stage C is defined as the completion of the formation of setal cones in most of the setae. While this feature was present in the setae of the pleopods, the setal cones may not form until early premoult in the uropods.

The start of withdrawal of the epidermis from the transparent edges of appendages has been defined as the start of premoult (Jenkin 1966). In *P. esculentus* this may be observed quite clearly and unambiguously in the mid region of the uropod (Fig. 1). The withdrawal of pigment from the setal bases of *P. indicus* was described by Read (1977) as occurring in stages B and C. In *P. esculentus* withdrawal of pigment from the setal bases was observed to be associated with epidermal withdrawal and so by definition occurs in the first stage of premoult, D_0. There is, however, no noticeable retraction of epidermis from the endocuticle in the histological sections of the abdomen until the start of the secretion of the pre-exuvial layers. The new epicuticle also adheres closely to the old endocuticle until stage D_3.

The method of describing the substages of D_1 using the shape of the epidermal line in the uropod has been correlated with the development of setae within the epidermal strata of the pleopods. Read (1977) refers to the scalloped appearance of the epidermis of *P. indicus* in stage D_{0-1} and D_2 but did not use it to define the stages. Photomicrographs by Van Herp and Bellon-Humbert (1978) of the tips of the developing setae of *Astacus leptodactylus* in premoult stages also illustrates the relationship between the shape of the epidermal line and the development of setae. Examination of the epidermal line in the uropods of *P. merguiensis*, *P. plebejus* and *Metapenaeus bennettae* indicate that this method of moult staging could also be applied to these species. This suggests that the method could be more widely used to define substages in early premoult, especially where pigmentation prevents observation of setal development.

Setule formation at the distal end of the developing setae has been used to identify stage D_1''' (Drach and Tchernigovtzeff 1967; Van Herp and Bellon-Humbert 1978; Longmuir 1983). With the methods used in the study reported here the tip of the developing setae in the translucent zone between the epidermal line and the base of the setae is generally observed from D_1 onwards. It is seen as a translucent structure and no ornamentations such as setules have been observed.

Stage D_1 occupies the longest period (about 50%) of the moulting cycle, but is perhaps the least understood. Fig. 2, D_1'', shows large cells with the appearance of storage cells (SC) which appear in the epidermis at this stage. Dall (1965) noted groups of cells and single amoeboid cells in the epidermis at this stage in *M. bennettae.* These cells were strongly positive for acid mucopolysaccharide and appeared to be discharging their contents into the epidermis, and Dall (1965) suggested that they were supplying material for cuticle formation. In our sections of *P. esculentus* the storage cells had disappeared by late stage D_1, and while the epidermis had become more hypertrophied, it was apparently not otherwise histologically different. The rapid formation of the pre-exuvial layers in stage D_2, however, suggests the accumulation of cuticular precursor material in the epidermis in late stage D_1, some or all of which could have been provided by the storage cells. While the origin of these cells is obscure, their function appears likely to be associated with cuticle formation.

Stage D_2 is defined as commencing with secretion of the pre-exuvial layers (Passano 1960; Drach and Tchernigovtzeff 1967; Stevenson 1972). The development of the setae in the pleopods and the features of the epidermis and the epidermal line in the uropods have been studied using histological sections of the abdomen of a number of samples to follow progress of secretion of the pre-exuvial layers. The pre-exuvial layers become apparent through stage D_2 as a line slightly separate and generally parallel to the epidermis within the translucent zone. A similar line though much fainter and less consistently positioned may sometimes be observed during D_0 and D_1 in the translucent zone between the epidermis and the border of the uropod. The presence of this line does not indicate an early deposition of pre-exuvial layers. Reaka (1975) described, in a stomatopod *Gonodactylus,* a similar feature that becomes apparent early in premoult and was identified as being new exocuticle. Considering our observations, this identification, which was not supported by histological evidence, may be erroneous.

The increase in definition of the setal nodes of the new exoskeleton in stage D_3 has not previously been described in the literature. We have used the appearance of the pinpoints of light in these nodes as a reliable indicator that the prawn will moult within 12 hours.

Wassenberg and Hill (1984) observed that *P. esculentus* emerged from the substrate approximately one hour before moulting and carried out movements that may be part of the process that loosens the old exoskeleton from the new. The opening of the exuvial lines are recognised as defining stage D_4 (Drach and Tchernigovtzeff 1967; Yamaoka and Scheer 1970; Stevenson 1972; Aiken 1973; Van Herp and Bellon-Humbert 1978). The behaviour reported by Wassenberg and Hill (1984) coincides with the opening of the ecdysial sutures and appears to be the mechanism by which they are opened.

In summary, the postmoult stages of a tiger prawn may be identified using both assessment of softness of the cuticle and by observation of the setae of the pleopod or uropod. Intermoult and premoult stages may be determined by observation of the epidermal line in the uropod or setogenesis in the pleopod. The criteria using features observed at the setal edge of the uropod provide a technique that does not require excision of appendages, such as is often necessary when examining the pleopods, and hence is useful for repetitive moult staging of experimental animals. Examination of three other penaeid species shows that this method may be used for a wider range of species.

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Taxonomy of the greentail prawn, *Metapenaeus bennettae,* and the western school prawn, *M. dalli*

Abstract: Although historically there has been confusion over the taxonomic status of *Metapenaeus dalli* from the west coast of Australia and *M. bennettae* from the east coast, they are currently recognised as two separate species. Starch gel electrophoresis of specimens from Brisbane and Perth revealed eight fixed allelic differences out of 44 loci surveyed. This degree of divergence is well within the range accepted to distinguish species and therefore supports the taxonomic status of *M. dalli* and *M. bennettae* as allopatric species.

However, taxonomic examination of specimens from the Gulf of Carpentaria shows male and female genitalia characteristics ranging from those typical of *M. bennettae* from the east coast to those more typical of *M. dalli* as originally described from the west coast. Computer analysis of numerical measurements of 26 attributes suggests that a geographic cline exists from *M. bennettae* to *M. dalli,* the Gulf population being intermediate.

Introduction

In Australia, *Metapenaeus bennettae* and *M. dalli* are commercially important species, commonly known as the greentail or inshore greasyback prawn and the western school prawn, respectively. The two species are unusual in that their life cycle is spent almost entirely in estuaries or coastal lakes, whereas other penaeid species move offshore to spawn (Morris and Bennett 1952). *Metapenaeus bennettae* reaches a maximum size of about 25 mm carpace length (CL) and *M. dalli* reaches about 20 mm CL.

Originally, the east coast greasyback prawn had been confused with *M. monoceros* (now *M. ensis*), and consequently could only be referred to as '*Metapenaeus* n. sp.' in a published description of its life history (Morris and Bennett 1952). Racek (1955) encompassed both the Western Australian school prawn and the east coast greasyback prawn under the one species, *M. mastersii.* Dall (1957) was the first to draw attention to some 'small but constant differences' between specimens of *M. mastersii* from Western Australia and Queensland. On this basis, the present standing of the western school prawn *M. dalli* as a separate species from *M. mastersii* was established by Racek (1957). Later, Racek and Dall (1965) renamed the east coast species *M. bennettae.*

The main differences between the two species first noted by Dall (1957) are in the genitalia of the prawn. The male petasma in *M. bennettae* bears small parallel distomedian projections of the apical portion while in *M. dalli* the distomedian projections are larger and diverging. In female *M. bennettae,* the central tubercle on the anterior margin of the median thelycal plate is prominent, while in *M. dalli* the two lateral tubercles are prominent over the central tubercle (Dall 1957, Racek 1957).

Metapenaeus bennettae is distributed on the east coast from northern Victoria to northern Queensland as far as Cooktown (Kirkegaard and Walker 1970). *Metapenaeus dalli* occurs from Peel Inlet, 70 km south of Perth to Broome in Western Australia and has been recorded from the Darwin area (Grey 1979) and from Mornington Island and Weipa in the Gulf of Carpentaria, although specimens from the Gulf resemble *M. bennettae* as well as *M. dalli* (Coles and Lee Long[1] pers. comm., D.J. Staples[2] pers. comm.).

Because of these difficulties in identifying specimens from the Gulf of Carpentaria a taxonomic study on the species complex was initiated. The aims of this study were to—

1. Determine the species status of *M. dalli* and *M. bennettae* in the east and west of Australia using both biochemical genetics and numerical taxonomy;
2. Examine variability of both species along an east:west transect following the northern coast of Australia.

Materials and methods

Samples of prawns were obtained from Brisbane, Bundaberg, Weipa, Darwin and Perth (Fig. 1). Electrophoresis was carried out on prawns from Brisbane and Perth to genetically assess their species status, the samples from Bundaberg, Weipa and Darwin were preserved in buffered 5% formalin and were not suitable for electrophoresis. The samples from Brisbane and Perth were frozen on dry ice both in the field and in transit to the laboratory and then stored at -70° C until processed. White (tail) muscle and hepatopancreas were dissected from 70 prawns from each sample and white muscle, red (walking leg) muscle and hepatopancreas were dissected from another seven prawns from each location. The latter were successfully used to resolve new enzyme stains with new buffers to increase from 33 to 44 the total number of loci examined, which contributes more to such electrophoretic studies than large sample sizes (Gorman and Renzi 1979).

The tissues were macerated in equal volumes of homogenising buffer (1×10^{-1} M Tris, 1×10^{-3} M EDTA, 5×10^{-5} M NADP+, pH 7.0) with red muscle being macerated as whole pereiopods. After centrifuging at 24000*g* at 4° C for 30 min, the clear supernatants containing the water soluble enzymes were transferred into an ultra low freezer at -70° C until electrophoresis.

Horizontal starch gel electrophoresis of tissue supernatants was carried out following the techniques described by Selander et al (1971)

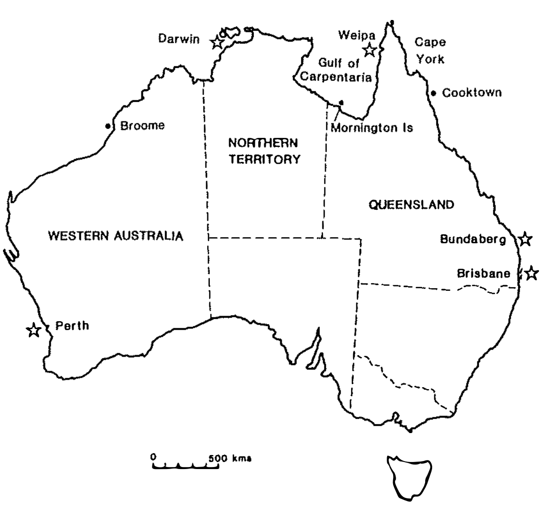

Figure 1. Collection locations ☆ of *Metapenaeus bennettae* and *M. dalli* used for genetic and numerical taxonomic comparisons.

and Redfield and Salini (1980). After electrophoresis, the gels were sliced horizontally and stained histochemically to reveal the products of specific gene loci (proteins) using stain recipes described by Shaw and Prasad (1970) and Harris and Hopkinson (1976). The slices were then incubated at 37° C in the dark until bands appeared. Each tissue was processed over a range of buffers, and the combination providing the best resolution of stain bands was used to compare the relative mobilities of the bands for the two species. Loci exhibiting genetic variation were recorded as inferred genotypes. Allele frequencies were calculated and then used to determine the average heterozygosity over all loci H, genetic identity I, and genetic distance D after the method of Nei (1972, 1975).

For the numerical taxonomy analyses, 100 prawns from each of the five locations were chosen. Only prawns between 10mm and 20mm CL were used in the analyses in order to eliminate the effects of a large size range on the results. Effects due to sex were eliminated by analysing males and females separately.

Measurements of several characters (Table 1) were made to an accuracy, depending on the magnification used, of between 0.08mm and 0.002mm. Most characters used were given as distinguishing features between *M. dalli* and *M. bennettae* by Racek (1957) and Racek and

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Table 1. Measurements from individual *Metapenaeus bennettae* and *M. dalli* used in numerical taxonomy analyses, and references which give them as distinguishing features.

	Characteristic	
1.	Carapace length	
2.	Rostrum length	
3.	Number of rostral teeth	
4.	Width of inner ramus	
5.	Telson length	
6.	Inner uropod length	
7.	Outer uropod length	—Grey et al (1983)
8.	Proportion of carapace covered by pubescence	—Racek 1957
9.	Distance from rostral tip to —rostral tooth 1	
10.	—rostral tooth 2	
11.	—rostral tooth 3	—Racek 1957
12.	Length of somite 4	
13.	Length of abdominal carina on somite 4	—Dall 1957
	Longitudinal groove on proximal section of pleopod	
14.	—length	
15.	—width	—Racek 1957

Table 2. Multistate characteristics of *Metapenaeus bennettae* and *M. dalli* used in numerical taxonomy analyses, and references which give them as distinguishing features.

	Characteristic	Possible states
1.	Pubescence bordering postrostral carina	diverging backwards parallel to carina diverging abruptly —Dall 1957, Racek 1957
	Pleonic pubescence	none present
2.	—somite 1	covering <5%
3.	—somite 3	covering 5-50%
4.	—somite 6	covering >50% —Racek 1957
	Female genitalia Median plate	
5.	—tubercle 1	almost indiscernible
6.	—tubercle 2	small
7.	—tubercle 3	large —Dall 1957, Racek 1957
8.	Margin of median plate	straight triangular —Racek 1957
9.	Lower edge of posterior plate	very rounded a little rounded rectangular —Dall 1957, Racek 1957
	Male genitalia Distomedian projections of petasma	
10.	—divergence	parallel diverging strongly diverging —Dall 1957, Racek 1957
11.	—shape	flat tubular —Dall 1957, Racek 1957

Dall (1965). Several multistate characters were also evaluated (Table 2), with integers between 0 and 3 describing different conditions. Data were analysed by stepwise discriminant analysis and the SAHN (sequential agglomerative hierarchical non-overlapping) clustering technique.

In the first approach, stepwise discriminant analysis was used on a random subset of individuals to describe the characters which best discriminate between groups from different locations. These characters are then used to generate a classification function. The subset of individuals and the remaining individuals are then classified into groups on the basis of this function. The classification of the remaining individuals acts as a check on the effectiveness of the classification function. A more detailed description of stepwise discriminant analysis is given in Jennrich and Sampson (1983).

For the SAHN analysis, a dissimilarity matrix between individuals was calculated using Gower metric, making no assumption about the existence of groups. Based on the dissimilarity matrix, groups of individuals were then sorted, using the unweighted pair group average sorting strategy (Sneath and Sokal 1973, Clifford and Stephenson 1975 and Ross 1982). The separation of the groups is output in the form of dendrograms.

Results

A total of 44 loci was resolved from the 29 specific enzyme and general protein stains using eight buffers (Table 3). The prawns from Brisbane revealed three variable loci in

Table 3. Enzymes screened and tissue and buffer combinations used for *Metapenaeus bennettae and M. dalli.* DG = digestive gland, RM = red muscle, WM = white muscle, E.C. No. = enzyme commission number.

Abbreviation	E.C. No.	Name	Tissue	Buffer
ACP	3.1.3.2	Acid phosphatase	DG	POULIK
ADA	3.5.4.4	Adenosine deaminase	WM	CAEA
AK	2.7.4.3	Adenylate kinase	WM	C
ALAT	2.6.1.2	Alanine aminotransferase	WM	CAAPM
ALD	4.1.2.13	Aldolase	WM	A
AKP	3.1.3.1	Alkaline phosphatase	DG	A
ARGK	2.7.3.3	Arginine kinase	WM	CAEA
EST	3.1.1	Esterase	DG	A
EST-D	3.1.1	Umbelliferyl esterase	RM	TC-2
FH	4.2.1.2	Fumarate hydratase	WM	TC-1
GAPDH	1.2.1.12	Glyceraldehyde-phosphate dehydrogenase	WM	A
GDH	1.4.1.3	Glutamate dehydrogenase	WM	A
G-3-PDH	1.1.1.8	Glycerol-3-phosphate dehydrogenase	WM	A
GPI	5.3.1.9	Glucosephosphate isomerase	WM	A
HK	2.7.1.1	Hexokinase	WM	A
IDDH	1.1.1.14	L-iditol dehydrogenase	WM	A
IDH	1.1.1.42	Isocitrate dehydrogenase	WM	A
LDH	1.1.1.27	Lactate dehydrogenase	WM	A
MDH	1.1.1.37	Malate dehydrogenase	WM	C
MDH (NADP+)	1.1.1.40	Malate dehydrogenase (NADP+) (= Malic enzyme)	WM	C
MPI	5.3.1.8	Mannosephosphate isomerase	WM	A
NA	3.4.11.1	B-Naphthyl amidase (= LAP)	DG	POULIK
ODH	1.1.1.1	Octanol dehydrogenase	DG	A
PEP	3.4.11	Peptidase (leucyl-leucyl-leucine)	DG	POULIK
PGDH	1.1.1.44	Phosphogluconate dehydrogenase (=6-PGDH)	DG	A
PGM	2.7.5.1	Phosphoglucomutase	WM	CAAPM
PK	2.7.1.40	Pyruvate kinase	WM	PC-2
PT		General protein	WM	A
TPI	5.3.1.1	Triosephosphate isomerase	WM	A

Metapenaeus bennettae—Gpi, Pgdh and Pgm—with apparent variation in Acp-2, Ald, Pgdh and Hk-1 being ignored as non-genetic because of uninterpretable banding patterns. *Metapenaeus dalli* from Perth also contained three variable loci—Gpi, Pgm and Idh—with non-genetic variation evident in two other loci—Pgdh and Hk-1. Genetic variation was evident in *M. bennettae* at the Odh locus but was not resolved well enough to be included for each species. Of the remaining 37 and 39 monomorphic loci found in *M. bennettae* and *M. dalli* respectively, eight loci were scored as absolute differences in relative mobilities. These loci were Acp, Alat, Na, Pep (leucyl-leucyl-leucine as substrate), Pgm, Pk, Pt-3 and Est-D. These represent 18% of the loci screened. The Pk locus difference is illustrated in Fig. 2. Heterozygosity estimates were 0.01 and 0.02 for *M. bennettae* and *M. dalli.* The estimate of genetic identity between the two species was 0.83.

In classifying the samples using the classification function derived from the discriminant analysis (Table 4), both the original subset and the remainder of the sample clearly separated into their different locations and are, therefore, readily distinguishable.

The characteristics which discriminated between locations most effectively in the discriminant analysis were—
for males: pleonic pubescence on somite 3, rostral length, telson length, length of the carina on somite 4, shape and divergence of the distomedian projections;
for females: shape of the margin of the median plate of the thelycum, pleonic pubescence on somite 3, rostral length and the distance from the tip of the rostrum to rostral tooth 2.

The F-values (Table 5) can be used to gain an indication of the relationships between the samples. For males, Weipa appears closer to Brisbane and Bundaberg than Perth and Darwin, however for females, Weipa is equidistant from Bundaberg and Perth.

The dendrograms from the SAHN analyses

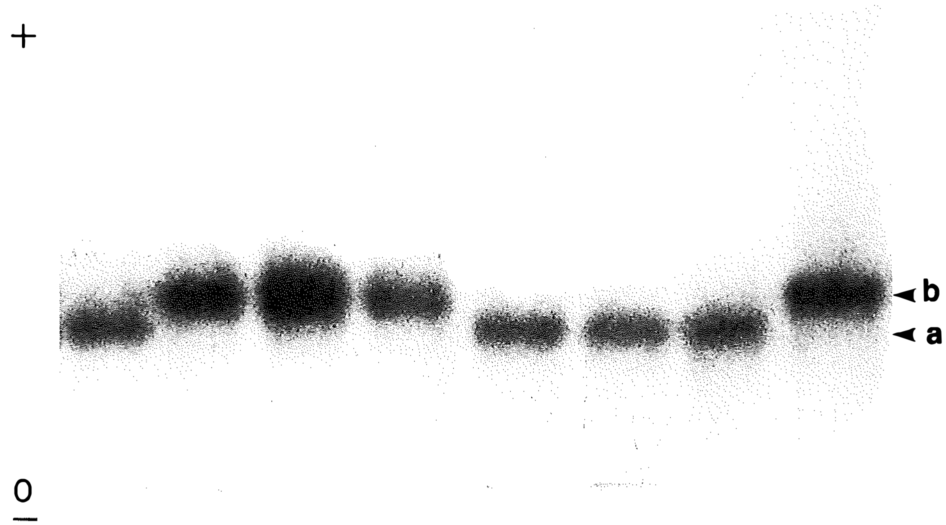

Figure 2. Fixed allelic difference at the pyruvate kinase (PK) locus between *Metapenaeus bennettae* (**a**) and *M. dalli* (**b**).

(Fig. 3) indicate two major groups for both males and females, one consisting mainly of east coast prawns (Bundaberg and Brisbane) and the other of west coast prawns (Perth and

Table 4. Discriminant analysis classification of *Metapenaeus bennettae* and *M. dalli*. Number of prawns classified according to location from a randomly selected subset from which classification function was derived and the remainder of the sample is in parentheses.

	Percent correct	Number of individuals classified into—				
		Brisbane	Bundaberg	Weipa	Darwin	Perth
Females						
Brisbane	88.9	16	2	0	0	0
	(72.2)	(13)	(4)	(1)	(0)	(0)
Bundaberg	95.8	1	23	0	0	0
	(100.0)	(0)	(2)	(0)	(0)	(0)
Weipa	100.0	0	0	5	0	0
	(80.0)	(1)	(0)	(4)	(0)	(0)
Darwin	85.0	0	0	2	17	1
	(100.0)	(0)	(0)	(0)	(8)	(0)
Perth	92.9	0	1	0	1	26
	(100.0)	(0)	(0)	(0)	(0)	(15)
Males						
Brisbane	83.8	26	4	1	0	0
	(83.3)	(15)	(3)	(0)	(0)	(0)
Bundaberg	80.0	2	16	2	0	0
	(100.0)	(0)	(11)	(0)	(0)	(0)
Weipa	100.0	0	0	13	0	0
	(100.0)	(0)	(0)	(7)	(0)	(0)
Darwin	93.8	0	0	0	15	1
	(83.3)	(0)	(0)	(0)	(5)	(1)
Perth	100.0	0	0	0	0	30
	(90.0)	(0)	(0)	(0)	(1)	(9)

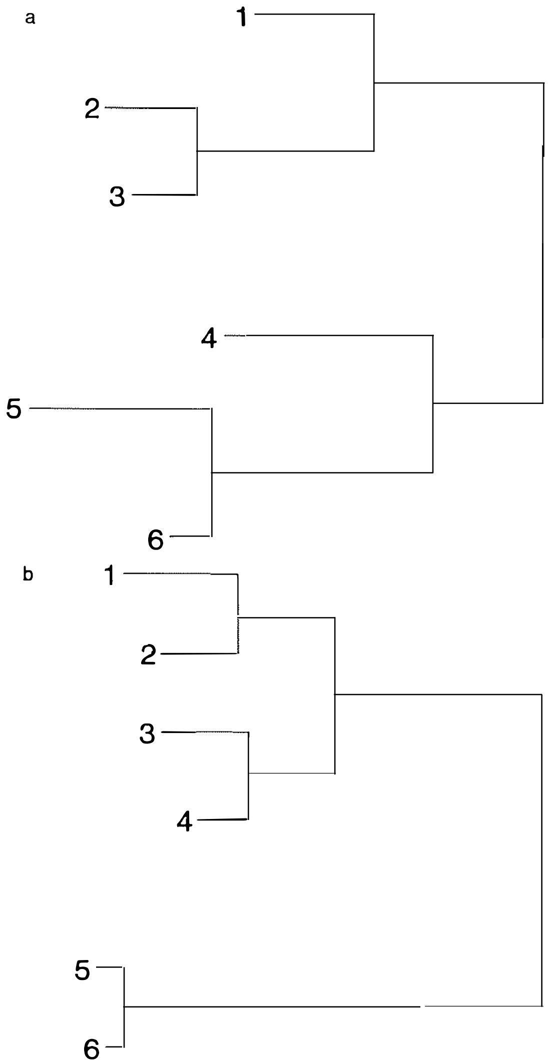

Figure 3. Dendrograms showing sequential agglomerative hierarchical non-overlapping (SAHN) classification of **a.** male, and **b.** female *Metapenaeus bennettae* and *M. dalli* collected from five locations around Australia (see Table 6).

Darwin). The Weipa males grouped with the east coast prawns (Table 6, groups 4,5 and 6) and the Weipa females grouped with the west coast prawns (Table 6, groups 1,2,3 and 4). However, overlap occurs, especially in females. For example, females group 4, which is in the major division containing all of the west coast prawns, contains 7.8% of the Brisbane sample and 17.3% of the Bundaberg prawns as well as 77.8% of the Weipa prawns.

Table 5. Discriminant analysis F-matrix for *Metapenaeus bennettae* and *M. dalli* of 10 to 20 mm carapace length. Critical values for F at P = 0.05 are 2.21 (males) and 2.45 (females).

	Brisbane	B'berg	Weipa	Darwin
Males				
Bundaberg	8.36			
Weipa	9.10	5.16		
Darwin	58.19	63.76	15.46	
Perth	88.71	81.71	19.81	14.44
Females				
Bundaberg	13.94			
Weipa	75.87	40.41		
Darwin	99.94	63.28	12.63	
Perth	218.73	121.92	41.91	24.83

Discussion

The eight loci representing absolute differences between *M. bennettae* and *M. dalli* represent about 18% of the 44 loci resolved. Avise (1975) found similar levels of genetic differences between closely related species of vertebrates and invertebrates (mostly *Drosophila*) with between 20 and 50% of the resolved loci showing absolute differences.

The genetic identity between the two species, 0.83, is within the published values for species comparisons in fishes (Shaklee and Tamaru 1981) and other invertebrates (Avise 1975). Within the Decapoda, published values for closely related species appear consistently uniform. Hedgecock et al (1977) obtained I = 0.90 over 37 loci between the European lobster *Homarus gammarus* and the American lobster *H. americanus.* Mulley and Latter (1980) in a study of the phylogenetic relationships of 13 penaeid prawn species reported similar values with 37 loci. The more closely related species of *Metapenaeus* analysed (*M. bennettae, M. eboracensis* and *M. insolitus*) have genetic identities of between 0.82 and 0.85 (Table 7), which compares well with I = 0.83 for *M. bennettae* and *M. dalli.* Therefore, within their documented distributions on the east and west coast, *M. dalli* and *M. bennettae* are sufficiently different electrophoretically to be considered as two separate species. This is supported by taxonomic evidence—*M. dalli* from Perth and *M. bennettae* from Brisbane are distinguishable by Racek's (1957) classical taxonomic criteria, and in our numerical analyses, Perth and Brisbane individuals were separated with a 100% success rate.

Table 6. Percentge of the samples of *Metapenaeus bennettae* and *M. dalli* classified to each group of the dendrogram in the sequential agglomerative hierarchical non-overlapping (SAHN) classification (see Fig.3).

Males	Brisbane	Bundaberg	Weipa	Darwin	Perth
1	0	0	0	0	32.0
2	0	2.3	9.1	88.5	62.0
3	0	0	0	3.8	2.0
4	75.0	52.3	0	0	4.0
5	2.8	0	81.8	7.7	0
6	22.2	45.5	9.1	0	0
Females	Brisbane	Bundaberg	Weipa	Darwin	Perth
1	0	0	5.6	9.7	0
2	0	0	0	74.2	97.6
3	0	1.9	16.7	16.1	2.4
4	7.8	17.3	77.8	0	0
5	5.9	1.9	0	0	0
6	86.3	78.8	0	0	0

In view of the results of the genetic work, there are four possible hypotheses regarding the identity of the Gulf of Carpentaria prawns—

1. Two species exist in Australia, with the Gulf of Carpentaria population belonging to either *M. bennettae* or *M. dalli*;
2. Two species exist, and their distributions overlap in the Gulf of Carpentaria;
3. A third species exists in the Gulf of Carpentaria;
4. A geographic cline from *M. bennettae* to *M. dalli* exists, the Gulf populations being intermediate.

If the first hypothesis were supported, it would be expected that both males and females would clearly separate into east and west coast groups and that the Gulf of Carpentaria prawns would consistently group with one or the other. For males, the existence of east and west coast groups is suggested by the results of both the SAHN and discriminant analysis techniques, with the Gulf population belonging to the east coast group. The SAHN analysis of females, however, suggested the Gulf of Carpentaria prawns belong to the west coast group, although this result was inconclusive as the east and west coast groups showed a significant amount of overlap. A gradual change from east to west rather than two distinct groups was suggested by the discriminant analysis on females. Since the numerical analyses were not consistently separating east and west coast groups and identifying the Weipa prawns as members of a particular one, the first hypothesis is not well supported.

Table 7. Estimates of genetic identity within the genus *Metapenaeus* (Mulley and Latter 1980)
(M. mac = *Metapenaeus macleayi*, M. ben = *M. bennettae*, M. end = *M. endeavouri*, M. ens = *M. enis*, M. ins = *M. insolitus*, M. ebo = *M. eboracensis*.

	M. mac	M. ben	M. end	M. ens	M. ins
M. ben	0.76				
M. end	0.63	0.63			
M. ens	0.63	0.66	0.69		
M. ins	0.68	0.82	0.63	0.59	
M. ebo	0.70	0.85	0.60	0.60	0.82

If the second hypothesis were true and there were east and west coast species inhabiting the Gulf of Carpentaria, it would be expected that the Gulf sample would split into two distinct groups, one similar to the east coast population and the other to the west coast population. The discriminant analysis classification and the SAHN grouping showed the Weipa population did not divide into two groups, showing no more heterogeneity than at any other location, and do not support the second hypothesis.

The SAHN analysis would be expected to show three major groups with little overlap between groups if the Gulf population were a third species. In fact it showed two major groups with overlap, in females especially, therefore the third hypothesis is not supported.

If a cline from *M. bennettae* to *M. dalli* existed, each population would be different from its neighbours, and the difference would increase with distance. This cline hypothesis is supported by the discriminant analysis which showed that the populations are readily distinguishable from each other with the only classification errors occuring between neighbouring locations, and that the difference between locations increases with distance. It is not supported by the males SAHN analysis, which indicated two major groups, although the degree of overlap between groups in the female SAHN analysis supports the cline argument.

In general, the results of the numerical taxonomy analyses, except for the male SAHN analysis, support the cline hypothesis so it is suggested that a cline exists in females and that clinal variation is occurring to a lesser extent in males because they are evolving at a slower rate. The biology of the species is conducive to clinal variation, as they are estuarine species, and little interbreeding or larval exchange would occur between populations from different estuaries, resulting in population heterogeneity. There is genetic evidence that population heterogeneity exists in populations of *M. bennettae* on the east coast (Mulley and Latter 1981), and, in view of the similarity of the life cycle of *M. dalli* to that of *M. bennettae,* it is likely that population heterogeneity also exists in *M. dalli.* It is suggested that population heterogeneity becomes greater between more distant populations of *M. bennettae* and *M. dalli,* until at the extremes of their distribution, it is great enough for them to be considered two separate species. However, this conclusion is based on the assumption that the species complex is distributed continuously between northern Victoria and Peel Inlet, Western Australia, when little is known of its distribution in northern Australia, particularly the northern part of Cape York.

Further investigation of the extent of their distribution, and genetic studies on fresh samples from northern Australia are needed so that this conclusion can be fully tested, and the status of *M. bennettae* and *M. dalli* in northern Australia resolved. Suitable samples for electrophoresis (frozen samples, not preserved) from at least Darwin, Mornington Island and Weipa would help to substantially clarify the genetic status of the species complex. A gradual change in the number of absolute allele differences across the north with genetic variation at these loci would support the species cline argument favoured by the numerical taxonomy data to date. If the cline argument is supported by genetic evidence, a further electrophoretic study is recommended to investigate the relationship between the *M. bennettae* and *M. dalli* complex and its close relative, *M. moyebi* (Kishinouye 1900) (also known as *M. burkenroadi* (Kubo 1954), which occurs in estuarine waters of the Indo-Pacific region (Racek 1957). If it is found that it is a clinal relationship, *M. moyebi* representing an extension of the *M. bennettae* and *M. dalli* complex, then *M. bennettae, M. dalli* and *M. moyebi* should be known under one name. *Metapenaeus moyebi* is recommended, as it is the original species name. If there is no evidence to support a clinal relationship, then *M. moyebi* should remain as a valid species.

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The biology of bopyrid isopods parasitic on commercial penaeid prawns in northern Australia

Abstract: A survey for bopyrid isopod parasites of commercial penaeid prawns from northern Australia was undertaken using samples taken at a processing plant. A step-down maximum likelihood linear model fitted to the data accounted for 96% of the variability in bopyrid load. The factors: prawn species, bopyrid species, season and locality accounted for 37, 21, 15 and 12% of the variability, respectively. No interactions were significant. *Penaeus semisulcatus* carried more than 90% of the population of *Epipenaeon ingens*. Of the infected animals, prawns were either lightly parasitised with *Parapeneaon expansus* or heavily infected with *E.ingens*. There was an increase in infection during autumn (April-May) with lowest levels during spring (September to November). Areas west of Mornington Island (Gulf of Carpentaria) and east of the Vanderlin Islands had no infected prawns whereas heavy infections occurred in Napier Broome Bay and Blue Mud Bay (Gulf of Carpentaria). Neither female nor male prawns, and neither the left nor right side of the prawns were preferred by the bopyrids. The size of the bopyrid was correlated to the size of the prawn host but was independent of sex of the prawn. Reproduction of bopyrids occurred year-round with depressed activity in winter and was positively correlated with water temperature. Light appeared to be important to the infection process. A liriopsid hyperparasite was found on bopyrids on the east coast of Queensland.

Introduction

Prawns constitute a $160 million export industry in Australia and contribute to the domestic market as well (Anon. 1984). Bopyrid isopods (Epicaridea) sterilise their decapod hosts (Reinhard 1956). In northern Australia, high levels of bopyrid infection on prawns occur in certain localities leading to concern about regeneration of stock in those areas. During processing, parasites have to be removed manually and automatic graders sort infected prawns to a larger size category as a result of the increase in carapace width from the bopyrid. Misgraded prawns have to be re-sorted by hand and consequently bopyrid isopods are a concern and a nuisance to the prawn industry. This study was undertaken to examine the threat posed to the prawn fishing industry by bopyrid isopods and to find the factors that cause the observed distribution of bopyrids on prawn species including host selection by bopyrids.

The generalised life cycle of bopyrid isopods has been described by Beck (1980). The female bopyrid lays fertilised eggs into her marsupium. The eggs develop into epicaridium larvae which are released into the water column when the prawn host moults. The epicaridia survive about 7 to 10 days without feeding while they search for a calanoid copepod intermediate host. After attaching, they feed, grow and moult into the microniscus and finally the cryptoniscus stage after 10 to 21 days. The cryptoniscus detaches and searches for postlarvae of the definitive host. The planktonic phase takes approximately one month to complete (Nearhos 1980). Therefore, Australian prawns are probably infected in their nursery area or prior to the settlement of the postlarvae and carry the infection to the commercial grounds.

Materials and methods

Whole cartons of prawns were selected from commercially caught prawns to give a wide geographic coverage comprising 48 localities (see Fig. 2b). Prawns were individually identified to species, counted and examined for bopyrids. Prevalance of bopyrids on prawns from northeastern Queensland was based on weights not counts. The cephalothoraxes of grossly infected prawns were removed for microscopic laboratory examination and preserved in 10% buffered neutral formalin. In the laboratory, carapace length (CL), sex, identity and location on right or left of the prawn were recorded. The identity of bopyrid, length of male and female bopyrids, reproductive state (virginal, ovigerous, with epicaridia, spent), the presence of eyespots and host-to-parasite reactions were determined using a stereo dissection microscope. Spawning activity was assessed by the percentage of spent females as compared with other stages. Histological sections, including histochemical testing for melanin (Schmorl's reaction), were made using standard techniques (Culling 1974).

Analysis of data was done using standard statistical programs. A maximum likelihood model was used to identify the important factors contributing to the variability in the data, then Student-Newman-Keuls analysis of variance and cluster analysis were used to identify the significant components in the factors. Analyses were performed on arc-sine transformed percent prevalence data. Slopes of regressions were tested for similarity using the method in Zar (1974). The bopyrid data where plotted were presented as two-point running means. Water temperature data were obtained from Staples (1983).

Results

Prawn and bopyrid interactions

During a 16-month period, 180000 prawns in 452 samples were examined from northern Australia and data collected on parasite species and abundance, and host species and abundance from the 48 different localities. The minimum mean sample size of prawns from a locality was 193; the maximum mean sample size of prawns from a single locality was 830. The mean sample size for the whole study was 393, SD = 220 with a range from 74 to 1801. The step-down linear model which was fitted to the data matrix showed that 96% of the variability could be accounted for by four factors: prawn species, bopyrid species, season and locality (Table 1). The largest interaction, prawn by season, accounted for less than 1% of the variability and was not significant ($P > 0.05$).

Prawn species

Prawn species were divided into three major groups on the basis of their parasite load by Student-Newman-Keuls analysis of variance, the heavily infected *Penaeus semisulcatus,* the lightly infected *P. merguiensis, P. indicus, P. longistylus* and *Metapenaeus ensis,* and the rarely or non-infected *P. esculentus, P. monodon, P. latisulcatus* and *M. endeavouri* (Table 2). *Penaeus semisulcatus* carried 90% of the population of *Epipenaeon ingens.* The prawns *P. indicus, P. merguiensis* and *P. esculentus,* carried 7.1, 2.6 and 0.1%, respectively (calculated from data adjusted for sample size). *Penaeus indicus, P. merguiensis* and *P. longistylus* supported 56.8, 28.4 and 14.5% of the bopyrid *Parapenaeon expansus,* respectively. *Metapenaeus ensis* carried some *Orbione halipori* and *Parapenaeonella lamellata,* but the prevalences of these bopyrids on other *Metapenaeus* species are unknown.

Bopyrid species

Epipenaeon ingens was found in 84% of infections, and *Parapenaeon expansus* in 15%. Within the Gulf of Carpentaria, 98% of all infections were *E. ingens.* Although the overall prevalence was low (Table 2) some areas had infection levels around 30% (see later). In this study, *Parapenaeon expansus* was found only where *P. indicus* occurred, namely west of

Table 1. Variability of bopyrid infection accounted for by maximum likelihood linear analyses. Factors given in order of decreasing importance and order of fit.

Factors	Multiple correlation coefficient	% variance for each added factor	Independent correlation coefficient	% variance for independent factors	Partial correlation coefficient	% variance for partial effects	F value	Probability
Prawn species	0.701	49.14	0.540	29.16	7.48	36.64	18.31	.001
Bopyrid species	0.897	31.26	0.456	20.83	0.0	20.83	8.33	.001
Season	0.954	10.63	0.361	13.03	1.49	14.52	5.38	.01
Location	0.981	5.23	0.300	8.99	2.60	11.59	4.15	.05
Total		96.24		72.01	11.57	83.58	810.53	.001

Table 2. The percentage occurrence of five bopyrid species parasitic on seven species of *Penaeus* and two species of *Metapenaeus* and groupings of prawn species by Student-Newman-Keuls analysis of variance ($P < 0.05$). N shows number of specimens.

Prawn species	Sample size	Bopyrid species: *Epipenaeon ingens*	*Parapenaeon expansus*	*Orbione halipori*	*Parapenaeonella lamellata*	*Parapenaeon* spp.	Student-Newman-Keuls grouping
Penaeus							
semisulcatus	31 474	2.9	0	0	0	0	1
esculentus	43 737	0.0007	0	0	0	0	3
merguiensis	70 520	0.2	0.2	0	0	0	2
indicus	8 218	0.4	0.4	0	0	0	2
monodon	120	0	0	0	0	0	3
latisulcatus	1 010	0	0	0	0	0	3
longistylus	507	0	0.4	0	0	0.4	2
Metapenaeus							
endeavouri	6 923	0	0	0	0	0	3
ensis	15 193	0	0	0.02	0.04	0	2
N	177 702	1,090	195	3	6	2	

Vanderlin Island to Admiralty Gulf. In contrast, on the coast of eastern Queensland, where *P. indicus* does not occur, king prawns, *P. longistylus* and *P. plebejus* are carriers.

Season

The occurrence of *E. ingens* on *P. semisulcatus* peaked from April to June (Fig. 1). There was a sharp decline during July with a further decline until November. Data from other species of prawns were not available.

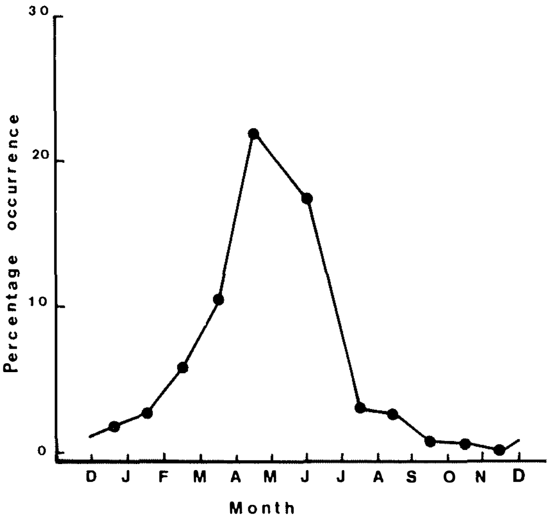

Figure 1. Seasonal occurrence of the bopyrid parasite, *Epipenaeon ingens*, on the penaeid prawn, *Penaeus semisulcatus*.

Locality

The distribution of *E. ingens* was patchy. In areas like Napier Broome Bay, Stevens Island and Blue Mud Bay the prevalence of *E. ingens* on *P. semisulcatus* was high. Infection was not present in areas west of Mornington Island (Fig. 2a). High prevalence of *E. ingens* on *P. semisulcatus* was also found in Albatross Bay. Cluster analysis showed Torres Strait to be more similar, in terms of its bopyrid infections, to the Great Barrier Reef and the northeastern Queensland coast regions, than to the Gulf of Carpentaria including the adjacent Merkara Shoal area. Admiralty Gulf was the major focus of infection of bopyrids on all prawn species other than *P. semisulcatus*. Where *P. semisulcatus* and *P. merguiensis* co-occur only *P. semisulcatus* became infected with *E. ingens*, eg Albatross Bay and around Groote Eylandt. Where no *P. semisulcatus* occurred *P. merguiensis* became infected with *E. ingens*, eg the southeastern corner of the Gulf (Fig. 2b). Preliminary studies of *E. ingens* in coastal areas of northeastern Queensland showed *P. esculentus* to be a major host there. Estimates of prevalence based on catch weights suggest 0.1 to 0.2% of *P. esculentus* were infected, which contrasts to the very low prevalence in the Gulf.

Effects of bopyrid infection

Sexual sterilisation of hosts by bopyrids is well known (Reinhard 1956) and will not be dealt with here. Squashing of the gills occurred in all infected prawns but gill erosion was rare and confined to the distal ends of the gill filaments. Deposition of pigment (histochemically positive

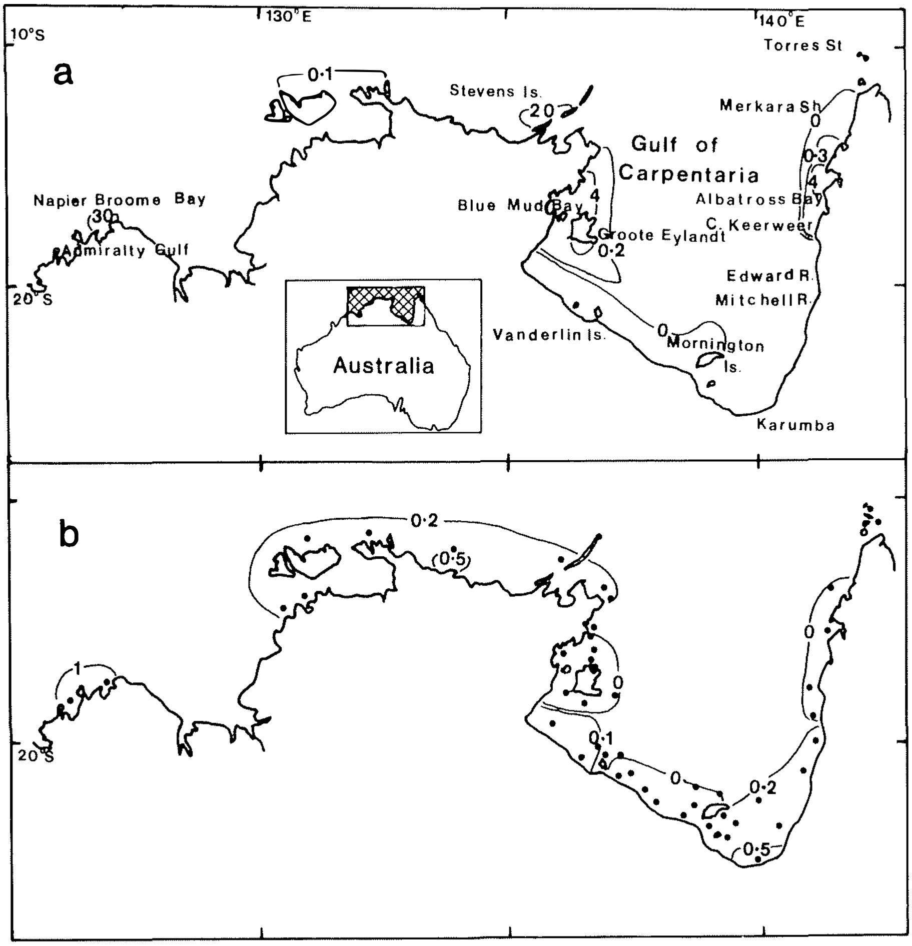

Figure 2. Geographical distribution and contours of prevalence of parasitic bopyrids on two species of *Penaeus* **a.** Areas of prevalence of *Epipenaeon ingens* on *Penaeus semisulcatus* showing localities mentioned in text **b.** Areas of prevalence of bopyrids on *Penaeus merguiensis*. Sample locations shown •.

for melanin) occurred primarily in the oostegites of the bopyrid which faced upwards. *Epipenaeon ingens* showed a strong pigmentation response, and 14% on *P. semisulcatus*, 55% on *P. esculentus*, 86% on *P. indicus* and 97% on *P. merguiensis* had abnormal pigmentation. Regardless of hosts, *Parapenaeon expansus* contained no pigment. In only two of 820 infected prawns was pigmentation of the gills noticed as small, discrete foci but this was not believed to be a response to the bopyrid.

Biology of bopyrids

Growth of bopyrids

The lengths of both *E. ingens* and *Parapenaeon expansus* were positively correlated with carapace length (CL) of all prawn host species (Table 3). Of the t tests carried out on the slopes of the regression lines, only *E. ingens* on *P. semisulcatus* and on *P. merguiensis* were not significantly different ($t=1.53$, $DF=331$, $P>0.05$) from each other (Table 4). The size of *E. ingens* on the combined *P. semisulcatus* and *P. merguiensis* is given by the equation $y=0.843x - 9.41$ ($r=0.92$, $n=335$, $P<0.001$). The largest *E. ingens* were found on large *P. indicus*. Those on *P. merguiensis* and *P. semisulcatus* were intermediate in length and those on *P. esculentus* were the smallest. *Parapenaeon expansus* was generally larger than *E. ingens* on the same hosts up to 39mm CL. On larger hosts *E. ingens* was the larger species. The sex of

Table 3. Slopes, intercepts, and correlation coefficients of regression lines relating carapace length of four species of *Penaeus* to the size of the bopyrids *Epipenaeon ingens* and *Parapenaeon expansus*.

Bopyrids:	*Epipenaeon ingens*				*Parapenaeon expansus*	
Hosts: *Penaeus*	*semisulcatus*	*esculentus*	*merguiensis*	*indicus*	*merguiensis*	*indicus*
slope of regression line	0.82	0.54	0.93	1.18	0.68	0.41
intercept	-8.63	0.78	-12.22	-19.94	-2.31	7.32
correlation coefficient	0.92	0.76	0.91	0.77	0.83	0.46

host had no significant effect on the size of *E. ingens* on *P. semisulcatus* (t=0.077, DF=240, P>0.05). Neither female nor male prawns, and neither the left nor right side of the prawns were preferred by the bopyrids (P>0.05). The size of the hyperparasitic male correlated with both the size of the female bopyrid (y=0.211x+0.938, r=0.81, n=486, P<0.001) and the size of the prawn host (y=0.182x -0.831, r=0.86, n=486, P<0.001). The slope of the relationship between size of *E. ingens* and the size of *P. merguiensis* from this study was not significantly different (t=0.66, DF=112, P>0.05) from the slope published by Owens (1983) based primarily on juvenile banana prawns caught in the estuaries.

Longevity of bopyrids

Ten percent of *P. semisulcatus* and 8.6% of *P. merguiensis* had swollen cephalothoraxes without the bopyrid. The percentage of prawns having empty bopyrid pockets increased with age after 26.5mm CL, for both *P. semisulcatus* (r=0.83, n=327, P<0.05) and *P. merguiensis* (r=0.95, n=117, P<0.05) (Fig.3). The pocket reduced in size over successive moults but was visible for an estimated two moults after the loss of the parasite (based on the reduction of the size of the pocket compared with the normal size for a prawn of that CL). Survival analysis suggested that the median age for *E. ingens* was greater than the expected longevity of the hosts, *P. semisulcatus* and *P. merguiensis* (Lucas et al 1979, Kirkwood and Somers 1984). Therefore the majority of bopyrids lived as long as the prawn host but increasing numbers were lost as the prawns approached their asymptotic CL.

Breeding of bopyrids

Epipenaeon ingens spawned all year round with depressed activity from June to August (Fig.4). The maximum levels of spawning activity at 25 to 30% occurred between December and April. Although numbers of *Parapenaeon expansus* were too small for an accurate year-round picture, where numbers were sufficient (sample size >10, in December, March and June), it followed the same trend as *E. ingens*. Spawning activity was positively correlated with water temperature (r=0.845, n=12, P<0.05). All embryos in the marsupium of the bopyrids were at the same stage of development in each bopyrid (synchronous development) for all bopyrids found in this study. Epicaridium larvae are shed as the prawn moults (Overstreet 1983). In two cases out of the 815 examined, soft-shelled, freshly moulted prawns had bopyrids with not yet fully developed eggs in their marsupia. This suggests that in a small percentage of cases release of epicaridia might not occur at every moult of all prawns.

Table 4. T-test values on slopes of regression lines relating carapace length of four species of *Penaeus* to the size of the bopyrids, *Epipenaeon ingens* and *Parapenaeon expansus*.

		Bopyrids					
		Epipenaeon ingens				*Parapenaeon expansus*	
Bopyrids	*Penaeus*	*semisulcatus*	*esculentus*	*merguiensis*	*indicus*	*merguiensis*	*indicus*
Epipenaeon ingens	*esculentus*	3.28*					
	merguiensis	1.53NS	6.42*				
	indicus	2.68*	4.96*	2.05*			
Parapenaeon expansus	*merguiensis*	ND	ND	5.23*	ND		
	indicus	ND	ND	ND	4.80*	1.98*	

NS P > 0.05   * P < 0.05   ND not done

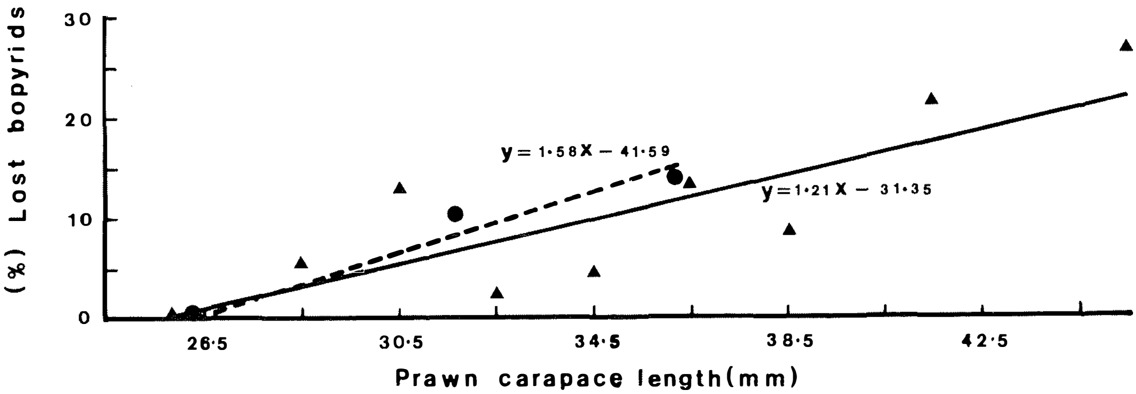

Figure 3. The relationship between carapace length of prawn and empty bopyrid pockets (lost bopyrids). Solid line for *Penaeus semisulcatus* (▲). Dotted line for *Penaeus merguiensis* (●).

Eyespots

Epicaridium larvae of *E. ingens* and *Parapenaeon expansus* released from the marsupium had no eyespots. Cryptonisci of *E. ingens* and *Parapenaeon expansus* had prominent, compound eyes. After metamorphosis, both the bopyridium females and the adult males retained their eyespots. By 5 to 7mm the eyespots of female *E. ingens* were vestigial and sunken below the surface of the cephalon, and by 9mm females had no eyespots. The majority of males of *E. ingens* had no visible eyespots at 7mm when their female partner was approximately 28mm. Most *Parapenaeon expansus* males lost their eyespots at 5 to 6mm, slightly before *E. ingens* males. Cryptonisci had functional eyes but stages in the life cycle preceding and following the cryptonisci have not. This suggests sight, and hence light, are important in the infection of postlarval prawns by cryptonisci.

Parasites of bopyrids

Eighteen of 48 *E. ingens* collected on the northeastern coast of Queensland had adult females and cryptoniscid male liriopsids (Epicaridea : Isopoda) in the marsupium of the bopyrid. Cryptoniscid males were attached to the females which consisted of a segmented sac filled with epicaridia. The hyperparasites

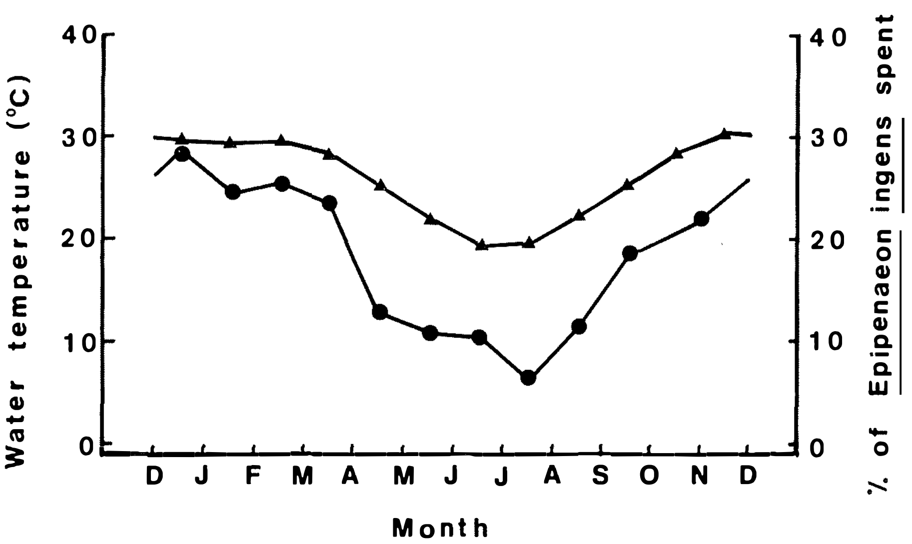

Figure 4. The spawning activity of *Epipenaeon ingens* (●) shown together with water temperature (▲).

were classified as Liriopsidae (=Cryptoniscidae) from descriptions in Schultz (1969). Up to three liriopsid females and four males were recovered from one bopyrid. Infected bopyrids were thinner and their ovaries much reduced. None of 615 *E. ingens* west of Cape York had liriopsids or evidence of their previous presence. No infected *Parapenaeon expansus* were detected anywhere. Some bopyrids had a whitish coloration to the pereiopods but whether or not this is a microsporidian infection was not ascertained.

Discussion

Biology of bopyrids

Owens (1983) argued that banana prawns, *P. merguiensis*, <6mm CL became infected with *E. ingens*. No small bopyrids were found on large prawns in this study, again suggesting initial infection is limited to juvenile or younger stages. This supports the claim in Beck (1980) that cryptonisci most frequently attach to the larvae or early postlarval hosts.

Concurrent growth of the hosts and the bopyrids is usual, for this parasite-to-host relationship, and has been adequately reviewed by Beck (1980). As most parasites die when the host dies the life span of the host and parasite are similar in most bopyrids (Beck 1980), as was also the case in this study. Breeding of bopyrids occurs throughout the year but with a seasonal peak. The onset of winter and cooler temperatures reduces egglaying activity. Beck (1980) suggests photoperiod might be the cue for breeding activity, but the lack of eyespots, their migration into the tissue of the cephalon when they are present and the orientation of the eyespots of the female towards the gills of the host suggests this is unlikely. Furthermore Sadoglu (1969) found no nerve connection between the eyes and brain of the females of *Gyge branchiatis* (Bopyridae). The male, whose eyes remain longer, might stimulate the female as photoperiod changes but we suggest that changes in breeding activity probably result from the effect of temperature on the bopyrid.

Host specificity of bopyrids

Host specificity of bopyrids on prawns is not controlled solely by genetics of the prawns. Congeneric neighbours often have different levels of parasitism. *Penaeus semisulcatus* is heavily infected while its closest genetic relatives, *P. monodon* and *P. esculentus* (Mulley and Latter 1980), may be unparasitised or rarely parasitised. The same trend occurs in the king and endeavour prawn groups ie *P. plebejus* and *P. longistylus* are infected while *P. latisulcatus* is not, and *M. ensis* is infected while *M. endeavouri* is not. Although a genetically controlled reaction to the bopyrids differs between the prawns, there is no evidence of the response killing bopyrids.

Differences in postlarval and juvenile prawn habitat does not appear responsible for differences in prevalence rates between prawn species. *Penaeus semisulcatus*, *P. esculentus* and *M. endeavouri* all cohabit in seagrass beds as juveniles (Staples et al 1985) and *P. merguiensis*, *P. indicus* (Le Reste 1971) and *M. ensis* all are found on the mangrove littoral zone and extend upstream to freshwater (D.J. Staples[1] pers. comm.). Juvenile *P. latisulcatus* (Penn 1975), *P. plebejus* (Young and Carpenter 1977) and *P. longistylus* are all found on sand substrates. All these prawns vary markedly in their infection rates to the various bopyrids, with prawns in one habitat no more heavily infected than those in other habitats.

Penaeus semisulcatus, which carries 90% of the adult population of *E. ingens*, has the highest prevalence rates, and *E. ingens* on *P. semisulcatus* has the least amount of pigment deposition. In most areas where *P. semisulcatus* and *P. merguiensis* co-occur, *P. merguiensis* appears not to be parasitised. *Penaeus semisulcatus* is the host for *E. ingens* throughout the Indo-west Pacific and into the Mediterranean Sea (Bourdon 1979). *Epipenaeon ingens* has a larger host specificity rating (0.89) than *Parapenaeon expansus* (0.79) (calculated using the formula of Rhode 1980). These facts all suggest *P. semisulcatus* is the primary and reservoir host for *E. ingens*, the other species being infected only when *P. semisulcatus* is not available to be infected. We suggest that cryptonisci of *E. ingens* must selectively search for *P. semisulcatus* and only accept other prawns if *P. semisulcatus* cannot be found within a reasonable period. On the other hand *Parapenaeon expansus* has a lower host specificity index (0.79) and more hosts share the burden of the parasite population. *Parapenaeon expansus* does seem to be primarily restricted to those areas where *P. indicus* occurs and when *P. indicus* cannot be found the bopyrid readily accepts other hosts. King prawns, *P. longistylus* and *P. plebejus* appear particularly favoured but the matter is

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complicated as other *Parapenaeon* spp. are found on *P. longistylus.*

Basically the bopyrids are found commonly on prawns with Indo-west Pacific distributions and not on prawns endemic to Australia. It appears that prawns migrating to Australia as the continent approached Asia (in geological time) have brought their bopyrids with them and the bopyrids have not adapted to fill the vacant niche offered by endemic prawns. However, *E. ingens* on the northeastern coast of Queensland infects *P. esculentus* much more heavily than anywhere west of Cape York Peninsula. This suggests subpopulations of either the bopyrid or the prawn or both. Using electrophoresis, Mulley and Latter (1981) found no evidence for subpopulations of *P. esculentus* from either side of Cape York Peninsula. Furthermore, liriopsids are restricted to *E. ingens* on *P. esculentus* and *P. semisulcatus* on the northeastern coast of Queensland, also suggesting a distinct population of *E. ingens* east of Torres Strait. Therefore it seems *E. ingens* is adapting to the endemic *P. esculentus.*

Geographical distribution of bopyrids

Nearhos and Lester (1984) using prawn landings at Karumba in the southeastern Gulf, have recorded *E. ingens* and *Parapenaeon expansus* on various prawns. The reference to Karumba is misleading as our data show that species of some prawns and parasites are not found in the vicinity of Karumba. The opportunity to correct these records is taken. The nearest infected *P. semisulcatus* to Karumba (Queensland Museum W10438, QM W10445) are those found southwest of Groote Eylandt and north of Vanderlin Island. Although infected *P. semisulcatus* occur in Albatross Bay and Cape Keerweer, those prawns are more likely to be landed at Weipa (Albatross Bay) than Karumba. *Parapenaeon expansus* (QM W10451) is found only in the western Gulf on *P. merguiensis* or *P. indicus* with the closest locality likely to be Vanderlin Island. *Epipenaeon ingens* was found at a prevalence of 0.2% on *P. merguiensis* offshore from both the Mitchell and Edward Rivers, an area shown as having zero prevalence by Owens (1983). To be 95% confident of an area having zero bopyrids when prevalence is actually 0.2%, a sample of 430 prawns must be examined (Cannon and Roe 1982). This sample size is much greater than the 200 prawns sampled by Owens (1983).

Economics and control

Annually about $1.5 to $2 million worth of prawns are infected with bopyrids (estimated using prevalence of the bopyrids on the different prawn species). Because of specialised processing, these prawns are not lost to the industry but the loss of reproductive potential is difficult to estimate. *Epipenaeon ingens* breeds for the first time when the prawn host is 20 to 22 mm CL and before the prawn breeds (Owens 1983). Fishing for prawns smaller than this size to remove the parasite from the environment before it breeds is not practical. The liriopsid parasite is at present restricted to the east coast of Queensland and achieves a prevalence of 40%. It might be possible to introduce this parasite into heavily infected foci as a biological control agent. Before this could be done, the biology of the liriopsid would need to be investigated, especially to determine whether its intermediate host is present in the Gulf.

Acknowledgements

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Importance of estuarine overwintering in the life cycle of the banana prawn, *Penaeus merguiensis*

Abstract: Abundance, size composition and gonad development in the banana prawn, *Penaeus merguiensis,* populations from the central Queensland coast were examined. Tagging experiments demonstrated that, although most adult banana prawns dispersed north and south after moving to offshore waters, a small number returned to estuarine areas. It is hypothesised that the species has two peaks of spawning activity, one in February to May and the other from August to December, giving rise to two generations of banana prawns each year. These generations are separated by geographic distribution as well as time. With a generation time of six months an overwintering generation apparently spawns in estuarine areas and contributes to an offshore spring spawning peak.

Introduction

The banana prawn, *Penaeus merguiensis,* supports valuable fisheries in the Indian Ocean and the western Pacific region. In Australia, fisheries for the species occur north of 29° S in waters adjacent to Western Australia, the Northern Territory, and along most of the Queensland coast. The fishery on the central and south Queensland coast is of particular interest both because it occurs near the southeastern limits of the species' fished distribution, and because it is exploited heavily.

The fishery between 22° S and 26° S on the central Queensland coast has two components. In estuarine areas, small (5 to 8 m) dinghies and dories are permitted to tow trawl gear of unlimited headrope length, but spread by a beam of no more than 5 m length. Their catch is a mixture of banana prawns, *P. merguiensis,* and greasyback and endeavour prawns, *Metapenaeus* spp. The fishery is controlled by a number of management measures, including regulation of mesh size, a limit on entry, and controls on the areas in which individual fishermen may work. This last regulation has effectively confined some 25 beam trawl operators into estuaries between 24° S and 25° 20′ S.

Banana prawns are also taken in the open sea between 24° S and 25° 30′S by a fleet of more than 50 otter trawlers. Banana prawns are rarely found more than 20 km from the coast, although there is sufficient fishing effort outside this area to locate them if they did occur further offshore (Dredge in press). In the Gulf of Carpentaria, Lucas et al (1979) estimated that the annual exploitation rate of the banana prawn stock exceeded 75%. Fewer than 300 trawlers fish for banana prawns along 1200 km of the Gulf's perimeter up to 30 km offshore. With more than 50 boats in a much smaller area in central Queensland waters, the density of boats per unit area of banana prawn trawling ground is considerably greater than in the Gulf and the exploitation rate although not quantified, is believed to be high.

Data on the biology and dynamics of banana prawn stocks have been published by a number of authors. Munro (1975) gave an outline of the species' life cycle in the Gulf of Carpentaria and described four phases. These were (1) a larval stage, in which transport from offshore spawning grounds to estuarine nursery areas occurred, (2) a juvenile phase in which the small prawns grew rapidly while in estuarine areas, (3) an adolescent phase when prawns left the estuaries and moved to shallow coastal flats, and (4) an adult phase during which banana prawns attained sexual maturity as they moved into deeper water away from the coastline. The four phases were closely linked to distinct geographic distributions and the life cycle model follows the general pattern described by Kutkuhn (1966). Tuma (1967) described the reproductive physiology of banana prawns and Crocos and Kerr (1983) described the reproductive potential of the species in a number of areas within the Gulf of Carpentaria by combining data on population levels of gravid females with estimates of their individual fecundity. Data on gonad development of females in different areas within the Gulf collected over a 12-month period suggested that there were two or three major peaks of spawning activity in the year. These spawning peaks had variable outputs of larvae according to area. Thus in the southeastern Gulf the major periods for spawning activity were in spring (September-October), and autumn (March-April) whereas in Albatross Bay, near Weipa, the corresponding peaks in reproductive activity were in August-September and March.

Staples (1980a,b) has described the ecology of the estuarine phase of banana prawns in the southeastern Gulf of Carpentaria. His work suggested that although there were two peaks of larval immigration to estuaries over the annual cycle, only postlarvae which recruited in the spring and early summer period were significant contributors to the pulse fishery on aggregations of prawns in March-April (Lucas et al 1979).

Gwyther (1982) estimated von Bertalanffy growth parameters and population parameters, and gave a description of the fishery for *P. merguiensis* in the Gulf of Papua. He suggested that recruitment into the fishery was continuous and the growth parameters he gave varied considerably from those of Lucas et al (1979), with given values for K and L_{∞} being about 0.126 week and 32.3mm, as opposed to the Lucas et al (1979) values of 0.08 week and 38.0mm respectively. The fishery, unlike that in the Gulf of Carpentaria, is based on a dispersed stock. Thus the life cycle of the banana prawn appears to vary depending on local environmental conditions.

In central and southeastern Queensland, the presence of estuarine and offshore fisheries, gives the opportunity of studying the estuarine phase of the animal's life cycle in detail.

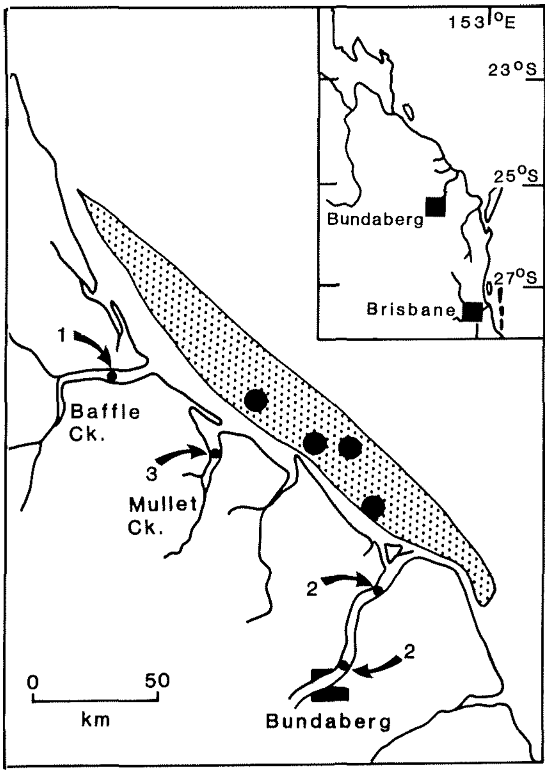

Figure 1. Release sites (•), offshore recapture area and estuarine recapture sites (arrows plus number of recaptures) for *Penaeus merguiensis* tagged in April 1981 and March 1983.

Methods

Offshore study

Catch and effort data collection

In the period between March 1977 and December 1980 offshore otter trawler operators based between Yeppoon (23° 10'S) and Tin Can Bay (26° S) were issued with logbooks. Data collected from these books were aimed primarily at describing catch rates and effort distribution for the Queensland scallop, *Amusium japonicum balloti,* fishery. There was, however, also provision for recording shot-by-shot catch and effort for banana prawns in 10 minute square grids from 22° 50'S to 26° 10'S.

Data on catch rates and distribution of effort in the estuarine beam trawl fishery were available from about five fishermen who kept catch and effort records (usually in the form of weight of banana prawns and greasyback prawns taken for each day fished) and who made these records available for this study.

Tagging

A study of the dispersal and stock composition of banana prawns on the central Queensland coast was undertaken by tagging. In April 1981, 700 banana prawns in the size range 21 to 35 mm carapace length (CL) were caught on the commercial fishing grounds, tagged with Petersen disc tags and released in three sites 5 to 15 km north of the Burnett River mouth in 4 to 10 m depth (Fig. 1).

In March 1983, 1150 banana prawns in the size range 22 to 38 mm CL were tagged with Floy streamer tags and released on a fourth area in the commercial fishing grounds between 10 and 50 km north of the Burnett River mouth, in depths of 4 to 6 m (Fig. 1).

Tagged prawns were recaptured by both otter and beam trawling, and data on recapture date and location were collected from individual fishermen at their landing wharves, or from processors who had bought tagged prawns. Tag data on recapture location from the latter source were considered unreliable and discarded.

Estuarine study

A series of nine sample sites was established in the Burnett River estuary. The sites, all of which were on commercially fished grounds, were selected to give as wide a range of habitat types as possible (Fig. 2). Fortnightly samples were taken at each site during daylight hours within one hour of low tide (see Staples and Vance 1979) from January 1982 until March 1983. Sampling of the five stations near the river mouth was continued until November 1983. Samples were taken with a 7.3m headrope Yankee Doodle trawl (28 mm stretched mesh) towed from a 5 m outboard powered dinghy for 15 minutes. Bottom water temperature and salinity were measured during each trawl.

At each site, prawns were sorted from the remainder of the catch and stored on ice. In the laboratory, banana prawns were separated and weighed and the CL of a subsample, of at least 120 prawns were measured to the nearest mm. Subsamples of female prawns with CL>25 mm were retained for classification of gonad development using criteria of Tuma (1967). A further subsample of gonads were fixed, stained and sectioned for confirmation of macroscopic gonad examination and classification.

Size of offshore prawns

In the period 19 February to 7 May, 1981 fortnightly collections of banana prawns were made from commercially fished grounds 5 to 40 km north of the Burnett River mouth, in depths of 5 to 10 m, using twin 7.4m headrope otter trawls (41 mm mesh) towed from a 13m trawler. A total of 30 half- to one-hour trawl shots was completed in this program. Banana prawns were sorted, weighed and the CL of subsamples of 2.5kg of prawns from each shot was measured.

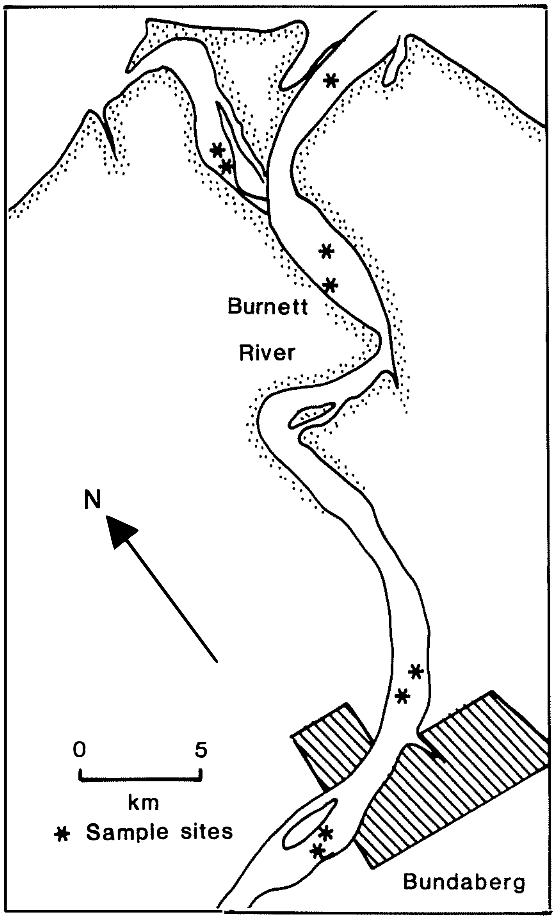

Figure 2. Sample sites used to study the estuarine phase of *Penaeus merguiensis* in the Burnett River estuary.

Results

Offshore study

Catch and effort data

During the three years in which logbook data on banana prawn catches were collected,

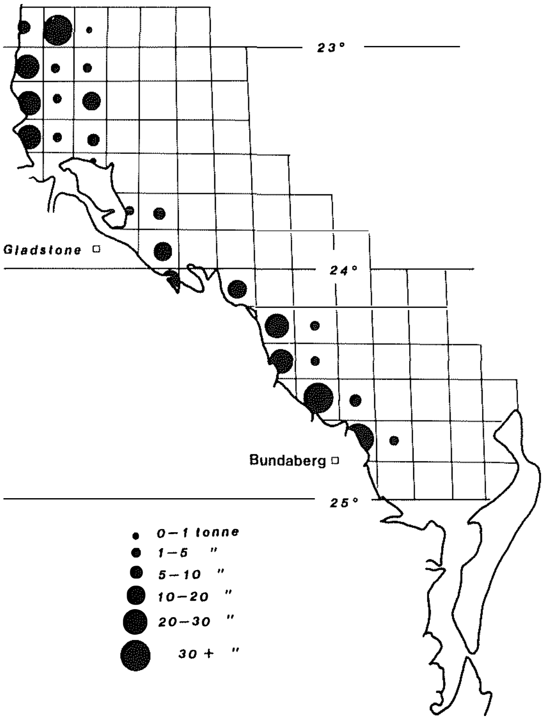

Figure 3. Distribution of offshore *Penaeus merguiensis* catch between 22° 50′S and 25° S (1978 to 1980) from logbook data.

10600h of otter trawling effort aimed at this species, was monitored for distribution and catch rate. The logbook catch of banana prawns (about 300t), was approximately 20% of the total landed by otter trawlers in that period. Banana prawns were rarely taken more than 15km from the shore south of about 23° 30′S, and more than 20km from the shores between 22° 50′S and 23° 30′S (Fig.3). Field observations made when logbook data were being collected suggest that trawling for banana prawns occurred in a body of discoloured water found between the shore and oceanic waters during summer and autumn (February to May).

In the three years of study (1977 to 1980) the offshore banana prawn fishery was always restricted to a four-month season between February and May. Both effort and catch per unit effort attained maximum values in March-April and declined rapidly thereafter (Fig.4). The mean CL ranged from 24.6mm to 28.4mm during 1981 (Table 1).

Table 1. Mean carapace length (CL) (± standard error) of *Penaeus merguiensis* taken in otter trawl grounds during 1981. n = number measured.

Sample date 1981	Mean CL (mm)	Standard error	n
17 Feb.	27.6	0.17	389
3 Mar.	26.8	0.12	867
18 Mar.	24.6	0.15	309
2 Apr.	27.5	0.16	613
21 Apr.	26.7	0.14	416
6 May	28.4	0.24	146
Total			2740

Catch and effort data on estuarine beam trawling covered 349 boat days of trawling in the period from 1981 to 1983. The temporal distribution of estuarine beam trawling for banana prawns differs markedly from the offshore fishery in that it continued more or less year-round (Fig.4). Catch rate data, which reflect weight taken, showed a prolonged summer maximum, with an irregular winter and spring fishery.

Tagging

Of the 700 tagged prawns released in April 1981 there were 83 reported recaptures (Table2). The maximum period between release and recapture was 54 days, and the maximum distance moved by a tagged prawn was 60km north of the release site. No tagged banana prawns were taken more than 10km offshore despite the presence of trawl fisheries in the area between the shore and the continental slope, 80 to 90km offshore. Movement of prawns represented dispersal rather than migration. Three tagged prawns were recaptured by estuarine beam trawlers, two 2km upstream from the Burnett River mouth and the other, 3km upstream of the mouth of Baffle Creek (Fig.1)

A total of 150 of the 1150 banana prawns tagged in March 1983 were returned, and the distribution of recaptures was essentially the same as for the 1981 release (Table 2). The longest period between release and recapture was 73 days, and the maximum recorded net movement, 50km to the north. Five were recaptured in estuaries. Of these, two were taken 8km upstream of the Burnett River mouth, and three were taken 5km upstream from the mouth of Mullet Creek (Fig.1).

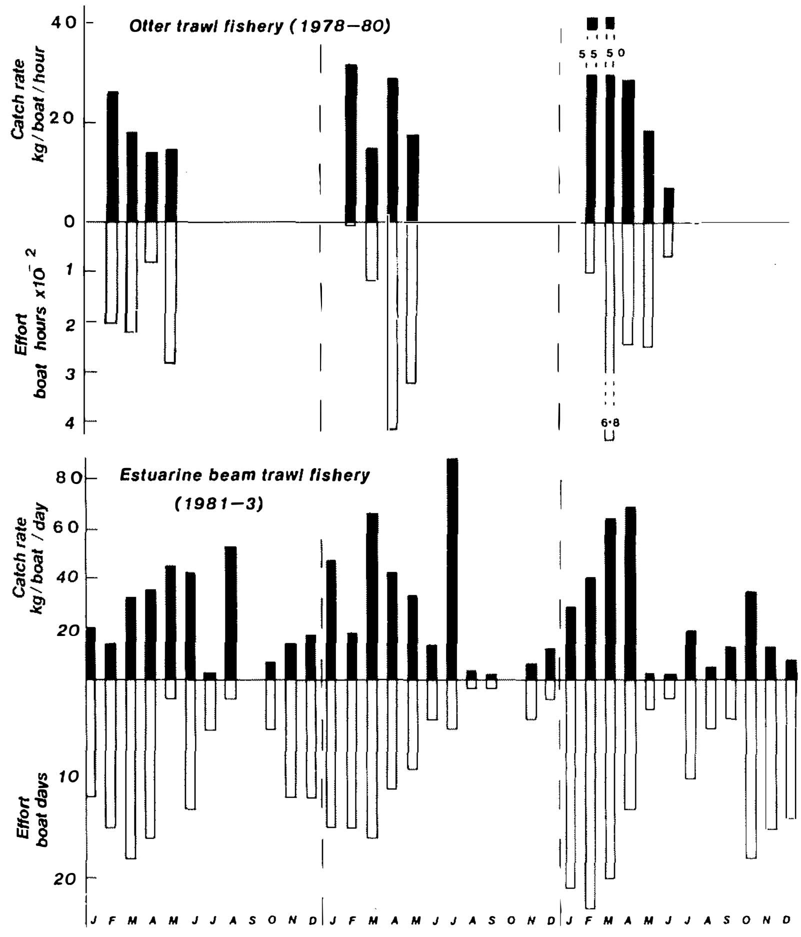

Figure 4. Catch and effort data from two fisheries for a common stock of *Penaeus merguiensis.*

Table 2. Number and direction of movement of tagged *Penaeus merguiensis* during 1981 and 1983.

	Distance moved (km)					Direction moved			
1981	0-9	10-19	20-29	30-39	>40	N	S	W	Nil
Time (weeks)									
0—1.9	3	4	1	1	—	4	—	2	3
2—3.9	45	9	8	1	1	18	4	—	42
4—5.9	4	—	—	—	—	1	—	—	3
6—7.9	5	—	1	—	—	1	3	—	2
Totals	57	13	10	2	1	24	7	2	50
1983									
0—1.9	88	—	1	—	—	4	—	3	82
2—3.9	44	2	1	2	—	7	1	2	39
4—5.9	5	—	—	—	1	1	1	—	4
6—7.9	—	3	—	—	1	3	1	—	—
>8	2	—	—	—	—	—	—	—	2
Totals	139	5	2	2	2	15	3	5	127

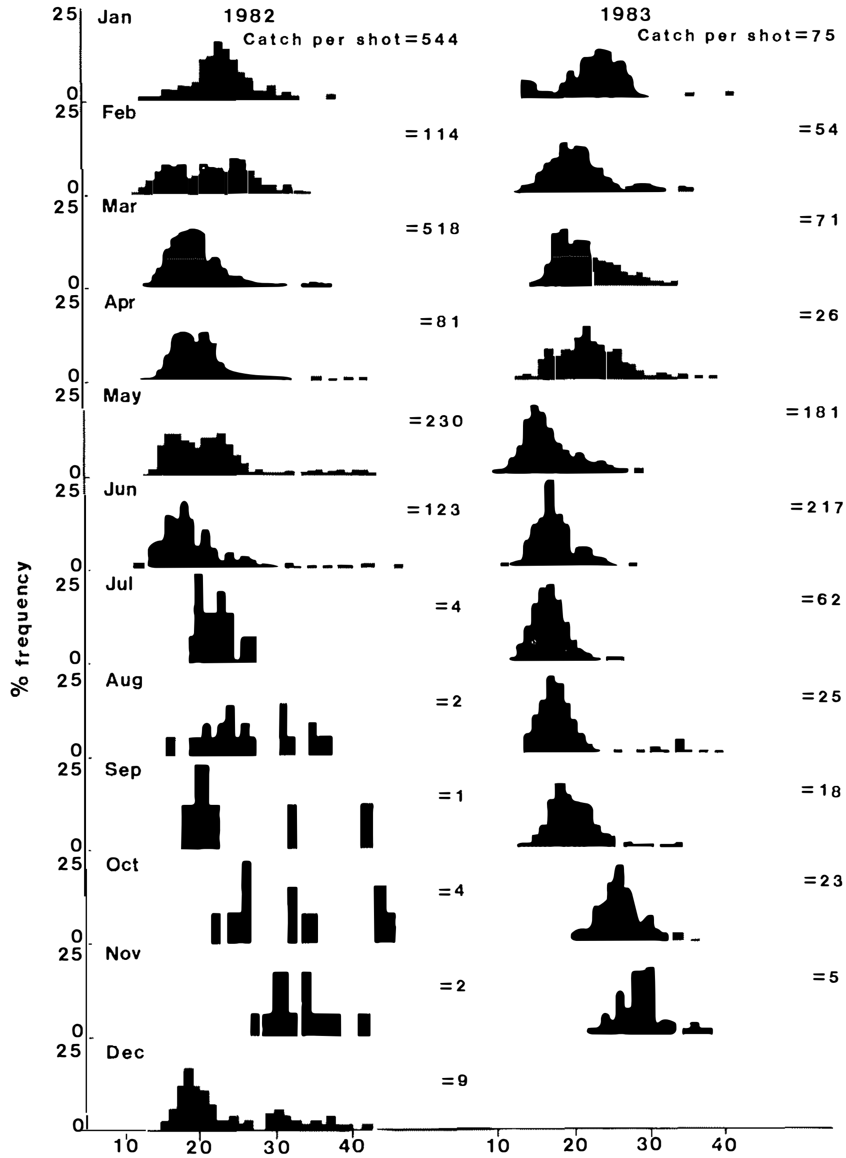

Figure 5. Size frequency and relative abundance (catch per trawl) of *Penaeus merguiensis* in the lower Burnett River estuary.

Estuarine study

Abundance and size

Size composition and relative abundance of prawns taken in the five stations near the river mouth were examined over 23 months (Fig. 5). The 28 mm mesh used for sampling had a 50% retention size of 12 mm CL (unpublished data).

Whereas absolute abundance varied considerably between 1982 and 1983, within-year size composition and trends in abundance were more consistent in the two years' data. Commercial fishing at the sampling sites may have masked peaks of abundance in periods when fishing pressure was heavy.

Two phases of recruitment into the estuarine population were identified each year. The first occurred in May-June in both years (Fig.5). This autumn group of prawns could be followed through until November and December, by which time individuals were in the size range of 18 to 36mm CL. The progressive increments in size and decrement in numbers of these prawns from month to month support the concept of an overwintering cohort. The second recruitment phase occurred in a series of pulses from December to March. Because fishing of small prawns occurs offshore in February, it would appear that the offshore fishery is based mainly on these cohorts.

A wide size range of prawns was taken in the lower Burnett River estuary during late summer and autumn, particularly in March and April. The presence of small numbers of large (>30mm CL) banana prawns observed in these months was consistent with tagging results which showed a small proportion of the population returned from coastal waters to estuarine areas.

Gonad development

Tuma (1967) and Crocos and Kerr (1983) suggested that female banana prawns commenced gonad development when in the size range 23 to 27mm CL. Gonad development of female *P. merguiensis* >25mm CL collected from the Burnett River are related to time of year in Table 3. Of 306 female prawns examined, 128 were classified as being at stage 3 (maturing) or stage 4 (mature), and 29 were classified as being at stage 5 (spent). Sexually developed and spent females were taken in the period February to May and August to December. Few prawns >25mm CL were present in either January or June to July. A combination of these changes in maturity and relative abundance of larger females suggest a six monthly pattern of spawning activity.

There was no evidence of the larger prawns which had returned from offshore waters to the estuary mouth in March and April either surviving or remaining in the estuary during winter. Size frequency data (Fig.5) from this period show an abrupt truncation below 30mm CL in June or July, when the larger prawns taken in earlier samples did not appear. Sexually developing females found in the period August to December were therefore apparently derived from the overwintering generation of autumn recruited juveniles.

Table 3. Frequency of occurrence of five gonad developmental stages in female *Penaeus merguiensis* (>25mm carapace length) taken from the Burnett River estuary.

	Gonad developmental stage				
	Immature (1-2)	Maturing (3)	Mature (4)	Spent (5)	Total Sampled
Month					
Jan.	3	0	0	0	3
Feb.	25	13	3	1	42
Mar.	38	19	10	1	68
Apr.	9	6	0	0	15
May	4	8	0	0	12
Jun.	0	0	0	0	0
Jul.	0	0	0	0	0
Aug.	7	1	0	0	8
Sep.	1	2	1	2	6
Oct.	44	17	11	10	82
Nov.	16	17	11	10	54
Dec.	2	7	2	5	16
	149	90	38	29	306

Temperature and salinity

The seasonal temperature cycle in the Burnett estuary is consistent with the normal summer-winter cycle (Fig.6) but changes in salinity levels over time are more complex. While individual stations had salinity levels of 35 to 36‰ throughout the winter months, average salinities were below that of normal seawater in all but one month of data collection. Low salinity conditions were recorded in March 1982 and May to June 1983. Salinity regimes in the estuary are affected by irregular overflow from the Burnett River barrage as well as irregular summer (monsoon) and winter rains.

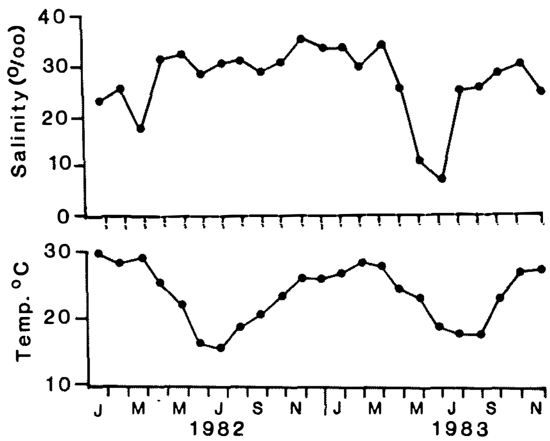

Figure 6. Mean monthly salinity and temperature for the lower Burnett River estuary from January 1982 to November 1983.

Discussion

Work published by Gwyther (1982) suggested that in the Gulf of Papua the recruitment of banana prawns to the offshore fishery from estuarine nurseries was not greatly affected by time of year. In the Gulf of Carpentaria, offshore spawning activity was pulsed into two or three major peaks during the year (Crocos and Kerr 1983). Immigration of banana prawn postlarvae to estuaries peaked in September to November (spring) in the southeast of the Gulf of Carpentaria but in the northeastern estuaries postlarval recruitment was normally greatest in March to April (autumn). On the basis of these findings Staples (1979) offered the hypothesis that banana prawns in the Gulf of Carpentaria undergo a 6-month generation period, but a 12-month lifespan. Recruitment to the offshore fishery was synchronised by summer monsoon rain. Therefore prawns taken in the southern Gulf during the late summer and autumn fishery were approximately six months old whereas prawns taken in the northeastern Gulf were either taken at approximately six months of age in spring, or recruited to the late summer fishery at an age of approximately one year.

Near the southeastern limit of their distribution, a further variation of the species' life cycle pattern, represented schematically in Fig. 7, appears to take place. In this cycle, two generations are also observed each year. Spawning appears to take place in autumn (March to June) and spring (September to December). In the period between March and June adult prawns, distributed both offshore and in estuaries, spawn and give rise to a generation which overwinters in estuaries. These prawns reach sexual maturity at an age of approximately six months while still in the estuary and spawn to repopulate the estuaries with juveniles throughout summer.

September to December spawned juveniles apparently recruit into an offshore, late February to May, otter trawl fishery after being subjected to an estuarine beam trawl fishery. These banana prawns attain sexual maturity offshore during autumn, spawn and complete the two generation per year life cycle by repopulating the estuaries with postlarvae.

Contrary to the typical penaeid life cycle, the distribution of the autumn adult stock in coastal or offshore waters did not appear obligatory; tag returns showed that some individuals returned from the open sea to estuaries. Such

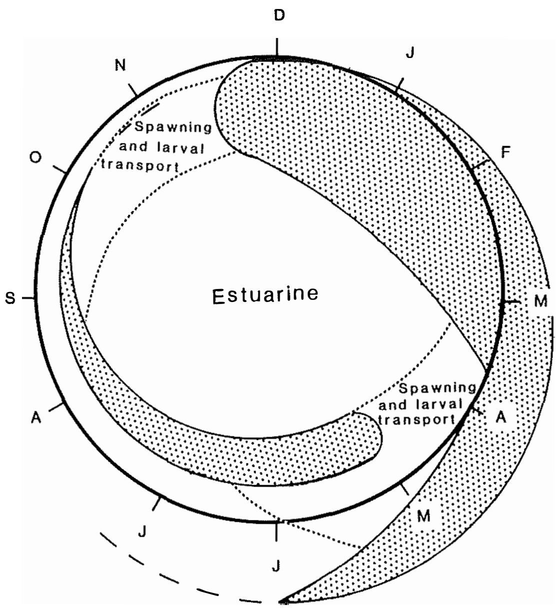

Figure 7. Schematic impression of the life cycle of *Penaeus merguiensis* in the central Queensland coast. Stippled areas represent relative abundance of prawns in estuarine (inside circle) and coastal and offshore (outside circle) environments over twelve months.

an occurrence has also been suggested by Neal (1975) for the white shrimp, *Penaeus setiferus*. Litchatowich et al (1978) have also suggested that banana prawns could spawn and larvae survive in open earthen ponds in which salinity varied between 33 and 44‰. For banana prawn larvae and juveniles to survive the salinity observed in the Burnett River during this study an even greater tolerance of hyposaline conditions would be necessary.

The major difference between the present proposed life cycle schema and that given by Rothlisberg et al (1985) for banana prawns in the Gulf of Carpentaria is the significance of the estuarine winter generation. In the southeastern Gulf of Carpentaria, the spring peak of estuarine postlarval recruitment is thought to be derived from large female prawns spawned in the previous spring. Although there is an autumn spawning phase, it is normally of little significance in terms of recruitment to the fishable stock or re-establishing an estuarine population of juveniles. In the northeastern Gulf, Rothlisberg et al (1985) argued that the autumn generation becomes more important but never to the extent of spawning in the estuary and being the major source of the spring generation as observed in this study.

The relative importance of the contribution of estuarine and offshore banana prawns to the next generation is worth considering. Given that a substantial population of adults exists offshore in autumn, with only a small proportion returning to estuarine areas, it seems likely that the majority of autumn spawning activity takes place offshore. Survival of prawns from this spring and early summer generation, however, through to the following winter appears to be low as both offshore and estuarine fisheries exploit the stock intensively over its restricted distribution. Logbook data show that banana prawns are not a component of commercial offshore and coastal otter trawl catches in winter and spring between 23° S and 26° S. I suggest that the autumn spawned generation which overwinters in central Queensland estuaries supply an appreciable component of recruits into the spring-summer generation. Such an alternation of two generations per year was suggested by Le Reste (1978) for *P. indicus.* Garcia (1985) noted that many penaeids have six-monthly spawning behaviour, with a predominant spring peak. He also commented on the importance of the autumn spawning for a stock whose spring spawned population was subject to heavy fishing pressure.

The existence of a year-round estuarine fishery for banana prawns may pose a threat to the continuity of commercial fisheries for the species at their present levels. Existing fisheries statistics are inadequate to determine if a long-term downward trend in landings is taking place, but given the life cycle timing and the intensity and nature of the fishery, the possibility of recruitment overfishing should be monitored closely in the future.

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A review of the life history of the banana prawn, *Penaeus merguiensis*, in the Gulf of Carpentaria

Abstract: Seasonal cycles of egg production, larval, postlarval, juvenile and adult abundance have all been determined for the banana prawn, *Penaeus merguiensis*, in two areas of the eastern Gulf of Carpentaria. Spawning shows two peaks of activity each year; one in the spring (August to October) and another in autumn (March). The generation time of *P. merguiensis* is basically six months, although some prawns survive and contribute to the second spawning at the age of 9 to 12 months. Because of different size and abundance of spawning females, total egg production is higher during the spring in the north and higher during autumn in the south. In contrast, the larger and more consistent peak of postlarval immigration and settlement occurs following the smaller of the two peaks in egg production in both areas. Studies on tidal currents and larval behaviour have shown that the anomalies between major spawning and postlarval recruitment periods can be explained by seasonal changes in the advection of larvae from spawning areas to the nursery grounds, combined with seasonal differences in the settlement success of postlarvae. Superimposed on this bimodal pattern of spawning and larval recruitment, is a unimodal pattern of juvenile emigration from the nursery grounds during the summer wet season. Therefore, the six-monthly pattern of spawning and larval abundance results in only one main period of offshore recruitment and commercial abundance each year in both areas, although the size structure of the adult populations differs due to differences in the contribution of the spring and autumn generations.

Introduction

The banana prawn, *Penaeus merguiensis*, is widespread in the Indo-West Pacific region and ranges from the Persian Gulf, through Pakistan, India, Malaysia, Thailand, southern China, Indonesia, Papua New Guinea, the Philippines, New Caledonia and Australia (Holthuis 1980; Grey et al 1983). Throughout this range it is of considerable commercial importance, and even with some allowance for confusion with *P. indicus* in commercial catches, *P. merguiensis* is one of the most important commercial species of prawn in the world (FAO 1984, calculations from Table B-45).

Like several other species within the genus *Penaeus*, *P. merguiensis* spawns offshore and uses estuarine nursery areas for postlarval and juvenile growth (for review see Garcia and Le Reste 1981). The species is also characterised by large fluctuations in population size which are caused by mortalities induced by a variety of biotic and abiotic factors at each of the life history stages. In spite of its large commercial importance and apparent wide fluctuations in recruitment and catches, there have been few comprehensive studies on the life history of the banana prawn.

The first attempt to describe the life history of *P. merguiensis* in northern Australia was carried out by Munro (1975). Munro's study was restricted almost entirely to the southeastern Gulf of Carpentaria, and in this region he concluded that *P. merguiensis* had a life span of approximately 15 months and a one year generation time (the time taken to complete the cycle from egg to egg). He suggested that prawns mated in March-April (autumn) but delayed spawning until the following

September-October (spring). These conclusions were drawn largely from the interpretation of size frequency distributions of juveniles in the Norman River and adults offshore. Reproductive activity was inferred from the percent occurrence of ripe and spent ovarian stages in the population. Movements of larvae, juveniles and adults were also inferred because of the lack of adequate tools to identify larvae and monitor migrations. In spite of these severe limitations the study provided a large amount of information about the life history, which formed the basis of later biological research on the species in the Gulf and throughout the Indo-West Pacific.

Following Munro's study, a large-scale sampling program for juvenile *P. merguiensis* was undertaken across northern Australia in an attempt to predict offshore catches on the basis of juvenile prawn abundance in the estuaries (Hynd 1974). The attempt failed because it was wrongly assumed that the number of prawns recruiting into the fishery was directly related to the number of juveniles in the estuary several months earlier. This however, was not the case (see Staples 1985). Hynd did note that juvenile prawn abundance was highest in summer in the southern Gulf and highest in winter in the northern Gulf, an observation which did not fit with Munro's simple annual life cycle hypothesis. A more detailed analysis of these seasonal patterns was made by Staples (1979), who suggested that *P. merguiensis* in the Gulf had a six month generation time and also demonstrated that the Gulf could be divided into four main areas, each characterised by its own seasonal pattern of postlarval immigration and juvenile abundance.

In 1974, in response to concern about the growth of fishing effort and continued wide fluctuations in catch, the Commonwealth Scientific and Industrial Research Organization (CSIRO) began the Tropical Prawn Research Project. This was a broadly based program aimed at providing ecological, physiological and behavioural information that would ultimately allow accurate stock assessments and predictions of catches of the major fisheries in the Gulf (Dall in press). Because of the importance of *P. merguiensis* in the Gulf at the commencement of the program, more information was collected for this species. The present paper synthesises the basic life history findings from the program on larval ecology, juvenile ecology, and reproductive dynamics of *P. merguiensis* in two regions of the eastern Gulf. It draws on previously published accounts and also puts forward an overview and explanation of the dynamic mechanisms that maintain *P. merguiensis* stock structure in northeastern waters (Albatross Bay) compared with the southeastern Gulf. The different studies obtained samples in different habitats, appropriate to each life history stage, but at different times, different frequencies and different spatial scales. The lack of sampling synchrony and possible confounding effects of year-to-year variation must be kept in mind when interpreting the results.

Methods

Larval ecology

Larval sampling was carried out over the whole Gulf of Carpentaria with towed nets as described by Rothlisberg and Jackson (1982). For this paper a subset of stations, off Weipa and in the southeastern corner of the Gulf (solid circles, Fig. 1), was considered for the abundance of zoeal stages of *P. merguiensis* as an indication of recent spawning. Larvae were identified using techniques developed by Rothlisberg, Jackson and Pendrey (1983, 1985). Larval vertical migratory studies, using a plankton pump (Rothlisberg 1982), were also done within the southeastern Gulf (ringed circle, Fig. 1) to assess the role of larval behaviour and currents in affecting the distance and direction of larval advection. Gulf-wide, seasonal models of currents and larval advection have also been developed (Rothlisberg, Church and Forbes 1983). A total of five spawning locations around the Gulf were included in the model to determine the directions of advection in different regions and seasons in the Gulf. Two of these spawning locations, one off Weipa, one in the southeastern corner of the Gulf (stars, Fig. 1), are of particular relevance to this paper.

Juvenile ecology

One river in the northeastern Gulf (Embley River) and one river in the southeastern Gulf (Norman River) were chosen for this paper to describe the seasonal cycles of postlarval immigration, juvenile abundance and juvenile emigration back to offshore waters (Fig. 1). Details of sampling of the different stages in the nursery areas are given by Staples and Vance (1985, in press). Briefly, sampling at the estuary mouth involved monitoring postlarval ingress during the peak flow of the flood tide and juvenile emigration over the whole ebb tide period. This was done at least weekly for four

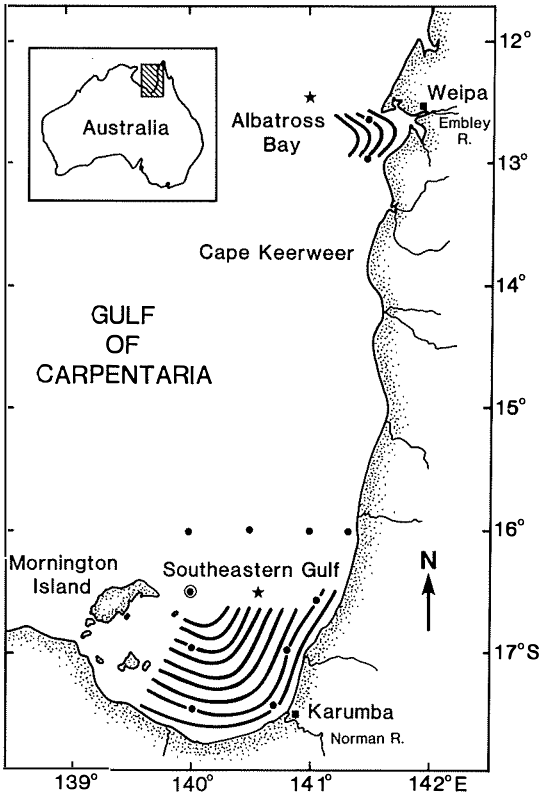

Figure 1. Gulf of Carpentaria study area. • CSIRO plankton sampling sites used in present analysis; ◉ plankton pumping station. ★ larval release sites in advection model (see text). Lines are trawling transects used for adult sampling.

years, using set nets suspended from a buoy in the middle of the river channel. The mean catch of postlarvae (no. 10 m^{-3}), taken over three depths, was used to describe postlarval immigration dynamics. The number of juveniles caught while emigrating in the surface waters was used to monitor the emigration rate.

Benthic postlarvae ($\leq$ 3 mm carapace length (CL)) and juveniles (>3 mm CL) were sampled by towing a 1 m beam trawl parallel to the shore along a 200 m station near the estuary mouth. Results were expressed as mean abundances (no. m^{-2}). Seasonal differences in the upstream distribution of the population were taken into account by multiplying the no. m^{-2} near the estuary mouth by the proportion of the upstream section of the estuary found to be inhabited by *P. merguiensis*. Sampling techniques in the two rivers were the same, but sample sizes of emigrants from the Embley estuary were too small to be reliable and were dropped from the analyses.

Adult ecology

Trawl sampling of adult *P. merguiensis* was carried out in three areas along the eastern side of the Gulf of Carpentaria (Crocos and Kerr 1983). Approximately 2500 trawls were carried out over 13 sampling cruises, each of 20 days duration, from August 1977 to August 1978. Four transects covering 37 stations in Albatross Bay and nine transects covering 135 stations in the southeastern Gulf (solid lines, Fig. 1) are considered in this paper. Sampling was standardised about the lunar month, with each cruise commencing 10 days prior to the new moon. All stations were sampled for 30 min at night using twin, 7 m headrope otter trawls. All *P. merguiensis* in the catch were sexed, CL measured to the nearest mm and details of the moult stage were recorded. Up to 50 female *P. merguiensis* were collected from each sample to ascertain reproductive condition, spermatophore implantation and ovarian development, the latter by histological examination of ovary tissue in the laboratory. An index of egg production was formulated based on the abundance of spawners, their size and relative fecundity (Crocos and Kerr 1983). This index was calculated for each month and each area, and used to ascertain temporal and spatial spawning dynamics. Commercial catch of adult prawns in each region was obtained from the Northern Prawn Logbook database (Commonwealth Department of Primary Industry, Canberra).

The results and interpretation that follow are a composite of the three studies carried out on different temporal scales. The Gulf-wide larval cruises were carried out in alternate months, over a 22 month period from August 1975 to May 1977. Where the same month was sampled in successive years the mean of the two samples is used. Postlarval and juvenile abundances in the southeastern Gulf, were based on monthly means, over four years (1975-76 to 1978-79) in the Norman River, and the sampling in the Embley River was every three weeks for one year, from September 1981 to September 1982. Earlier results for this northeastern region were obtained from Staples (1979). The adult sampling cruises were monthly from August 1977 to August 1978, and the commercial catch data are monthly averages taken over the period 1970 to 1983.

Results

Southeastern Gulf of Carpentaria

In the southeastern Gulf egg production by *P. merguiensis* had two peaks, one in September-October (spring), the other in March (autumn) (Fig. 2a). The spring peak in egg production was produced by a small number of large females, and the autumn peak came from the large number of females during the commercial season (cf Fig. 2e). Larval abundance follows a similar pattern but the spring numbers were much lower than those in the autumn (Fig. 2a). On average, over the four years of study, the mean planktonic postlarval abundance observed at the estuary entrance was also bimodal with peaks in spring (November) and autumn (March) (Fig. 2b). On a year-to-year basis however, the spring peak was much more consistent and the autumn peak was observed only once during the four years (Staples and Vance 1985). Thus, the main spring period of postlarval immigration occurred at a time of relatively low numbers of both offshore females and larvae. Superimposed on this disproportionate survival of larvae is the differential settlement of postlarvae in spring and autumn. Postlarvae that arrived in the estuary in autumn, after the wet season, had a relatively low settlement success compared with the spring immigrants; a smaller proportion thus survived through to the juvenile stage (Fig. 2b and 2c). Juveniles from the spring generation remained in the estuary for one to four months and began emigrating during the wet season which occurred from December to March (Fig. 2d). The relatively few survivors from the autumn generation appeared to overwinter in the estuary and emigrate the following spring (October-November), prior to the wet season. The main wave of recruits to the commercial fishery therefore, appeared in the catches in March and April (Fig. 2e) when the majority of them were six to seven months old. The modal size of the ripe female prawns during this time was 33 mm CL and a high proportion (between 80 and 90%) of the group were larger than the minimum size of first spawning (25mm CL). These prawns produced the large autumn spawning peak, but, as shown above only a small proportion of this spawning survived through to adults. This result, plus the large size of the spawning females during the September-October spawning season suggests that the spawning stock was made up mainly of adult prawns which had escaped from the autumn fishing season. Females in this group have a very high fecundity due to their large size (Crocos and Kerr 1983), so spawning of relatively small numbers of individuals produces a large number of eggs. This low number of spring spawners was apparent in both commercial catches and CSIRO survey samples during the period (Fig. 2e). As a result of seasonal differences in the mortality of the spring and summer generations, coupled with a very restricted single wet season each year, the bimodal pattern of spawning resulted in a unimodal pattern of offshore recruitment and commercial abundance each year.

Albatross Bay

In Albatross Bay there were also two peaks of spawning activity (Fig. 3a). The relative magnitude of the two peaks of egg production, as indicated by the egg production index, however, was opposite to that of the southeastern Gulf; the spring peak in September was larger than the autumn peak in March. From the limited number of stations sampled for larvae in 1975 and 1976 only the autumn peak in larval abundance was apparent. Planktonic postlarvae arrived in the Embley River adjacent to Albatross Bay in three pulses over a prolonged period from November through to July (Fig. 3b). Benthic postlarvae showed a marked trimodal pattern in 1981-82 with peaks in December, March and May. Staples (1979) noted that over the period 1970 to 1974 the autumn influx of postlarvae into the estuaries of several northern rivers was more consistent from year to year and larger than the pre wet season influx. No direct emigration data are available for the Embley River, but on the basis of the timing of peaks of juvenile prawns in relation to the timing of the wet season, we suggest that some juveniles overwintered in the estuary and emigrated in spring (broken line, Fig. 3c). Offshore sampling also showed that, unlike the southeastern Gulf, some small prawns recruited offshore during the winter (broken line, Fig. 3d). Their relative abundance, however, is hard to assess because of seasonal catchability differences. Therefore, although the density of adults in Albatross Bay appeared

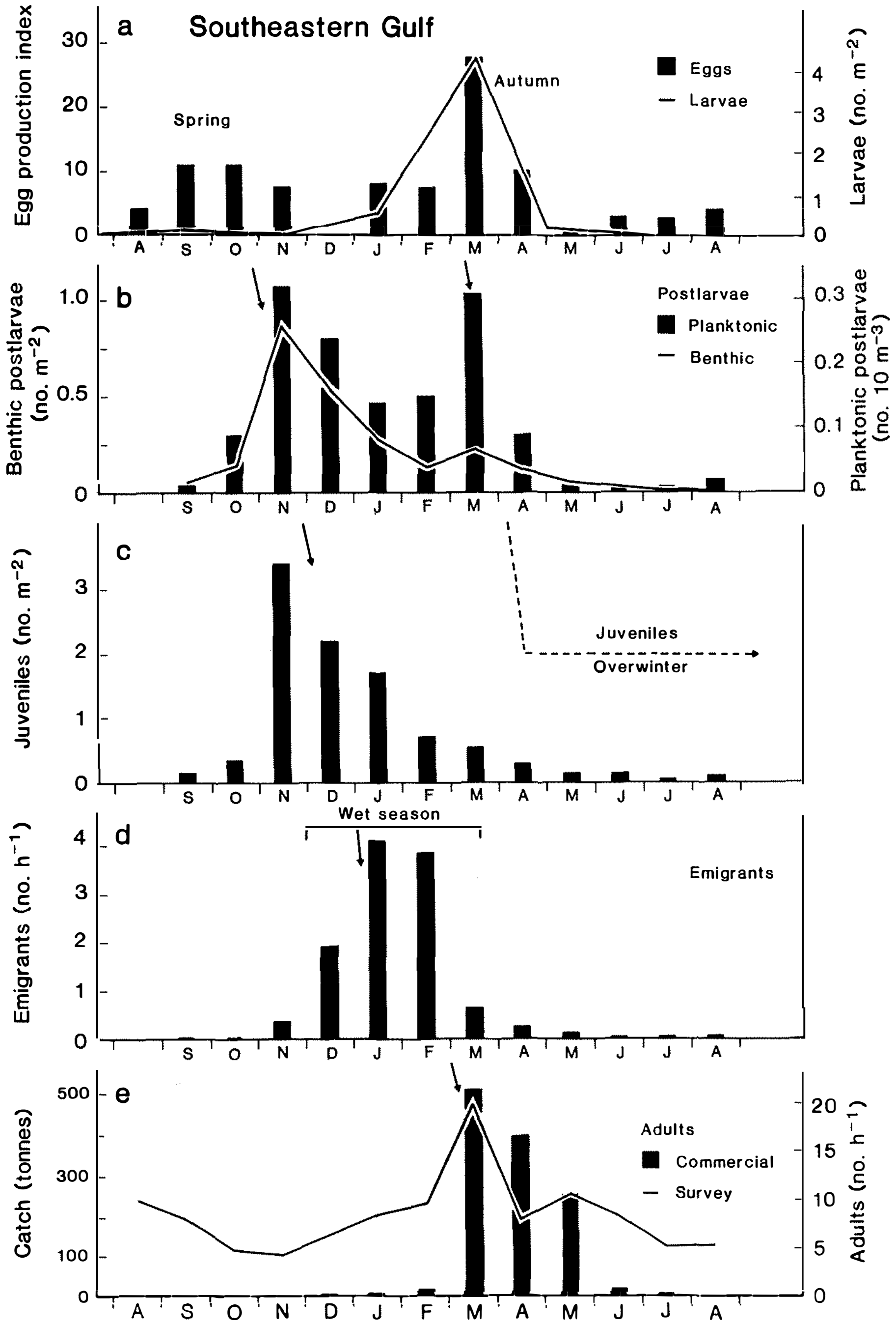

Figure 2. Seasonal abundance of *Penaeus merguiensis* in the southeastern Gulf of Carpentaria: **a.** eggs and larvae; **b.** postlarvae; **c., d.** juveniles and **e.** adults. Solid arrows indicate main cohorts.

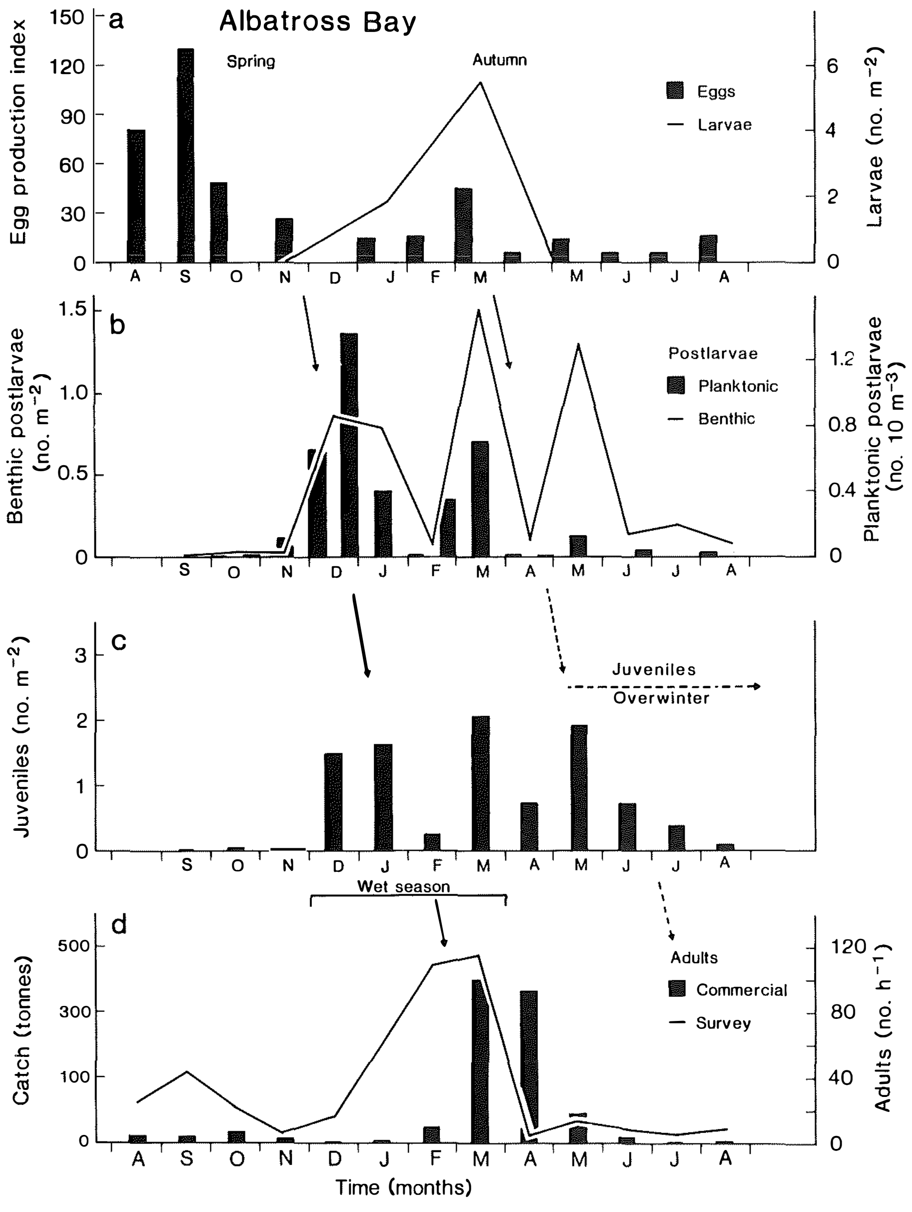

Figure 3. Seasonal abundance of *Penaeus merguiensis* in Albatross Bay, northeastern Gulf of Carpentaria: **a.** eggs and larvae; **b.** postlarvae; **c.** juveniles and **d.** adults. Solid arrows indicate main cohorts.

to be low in September-October (Fig. 3d), it was higher than in the southeastern Gulf at the same time of year (Fig. 2e). Numbers of adults increased in February and March as a result of summer emigration of juveniles and formed the basis of the commercial fishery.

Discussion

The life history of *P. merguiensis,* in the Gulf of Carpentaria, is not a simple annual cycle as first proposed by Munro (1975). We suggest that the basic life history is one of a six month generation time, modified by complex hydro-meteorological events. Only by studying each of the life history stages in detail and understanding the dynamic interactions between stages can the complexity of the variations on this basic, two generations per year, scheme be understood.

The use of an index of population fecundity in this study provides a more meaningful account of reproductive output than a simple measurement of the percentage of ovigerous females in *P. merguiensis* populations as was done by Munro (1975), Thubthimsang (1976) and Chong (1980). Their method gives a biased measure of population reproduction. Munro suggested, on the basis of the percentage of ripe and spent females observed, that most of the spawning of *P. merguiensis* in the southeastern Gulf occurred in spring and early summer. In the current study we confirmed that the percentage of ripe females was highest during spring, but the major peak of egg release occurred in March. This is because the very large adult population during March requires only a relatively small proportion to spawn to produce a relatively large number of eggs. Chong (1980) made no assessment of the contribution of a small population of ripe *P. merguiensis* females observed between February and July in the Straits of Malacca and may have overlooked an important component of the seasonal spawning cycle.

By combining the population fecundity index with a measure of larval abundance the most rigorous method of demonstrating reproductive output is attained. This can be done only if the early larvae can be identified to the species level. The tools to identify the first three zoeal stages of four species (*P. merguiensis, P. latisulcatus, P. esculentus, P. semisulcatus*) in the Gulf of Carpentaria, have been developed (Rothlisberg, Jackson and Pendrey 1983, 1985). The identification technique, together with a systematic sampling of the plankton of the Gulf, has shed light on the large-scale temporal and spatial reproductive dynamics of the four species (Rothlisberg, Jackson and Pendrey 1985). The analysis of two geographic subsets (Albatross Bay and the southeastern Gulf) of the Gulf-wide data set, in this study, shows that the timing of peaks of *P. merguiensis* larval abundance are in general agreement with the peaks of egg production except for the September-October reproductive activity in Albatross Bay. No early larvae were found in samples from Albatross Bay in August to September in either year. The relatively broad peak of larval abundance in autumn coincides with the peak of postlarval immigration. It is interesting to note that the timing of postlarval immigration in this region of the Gulf coincides more closely with the timing of larval abundance than with the pattern of egg production. There are many possible reasons for the apparent enigma, one of which might be the unsuccessful hatching of early spring eggs, but more work is required in this area.

Although the general timing of egg production, larval and juvenile abundance in both regions agree in most cases, there are large seasonal differences in the relative proportions of the different stages. The main population in the southeastern region is derived from a small spring spawning, whereas in the north it is the large autumn juvenile population which arises from the smaller spawning peak. Seasonal differences in the survival of all early life history stages appear to be involved. Rothlisberg, Church and Forbes (1983) have demonstrated seasonal differences in larval advection, due to phase changes in tidal residual currents, with respect to the diel cycle of larval vertical migratory behaviour. During September-October when there are lower numbers of eggs and larvae in the southeastern Gulf, the larvae are moved in a southerly direction, toward the major nursery grounds. In March, when there is a peak of egg and larval abundance, the majority of larvae are moved offshore, hence the inconsistency and low numbers of postlarvae arriving at the adjacent nursery grounds. In Albatross Bay the seasons of peak egg production and postlarval immigration are reversed with respect to the southeastern Gulf. The patterns are not as clear as in the south possibly because of the relationship between coastal orientation and seasonal advection directions off Albatross Bay. After reaching the estuaries, disproportionate survival of the spring and autumn generations in the two areas of the Gulf is further increased by the large seasonal differences in the relative success of settlement of postlarvae in the estuaries. In the southeastern Gulf settlement of the spring generation appears more successful than for the autumn generation, whereas in the northeastern Gulf the reverse is the case. The combined effects of larval advection and postlarval mortality result in timing differences of juvenile abundances in the northern and southern regions of the Gulf first observed by Hynd (1974).

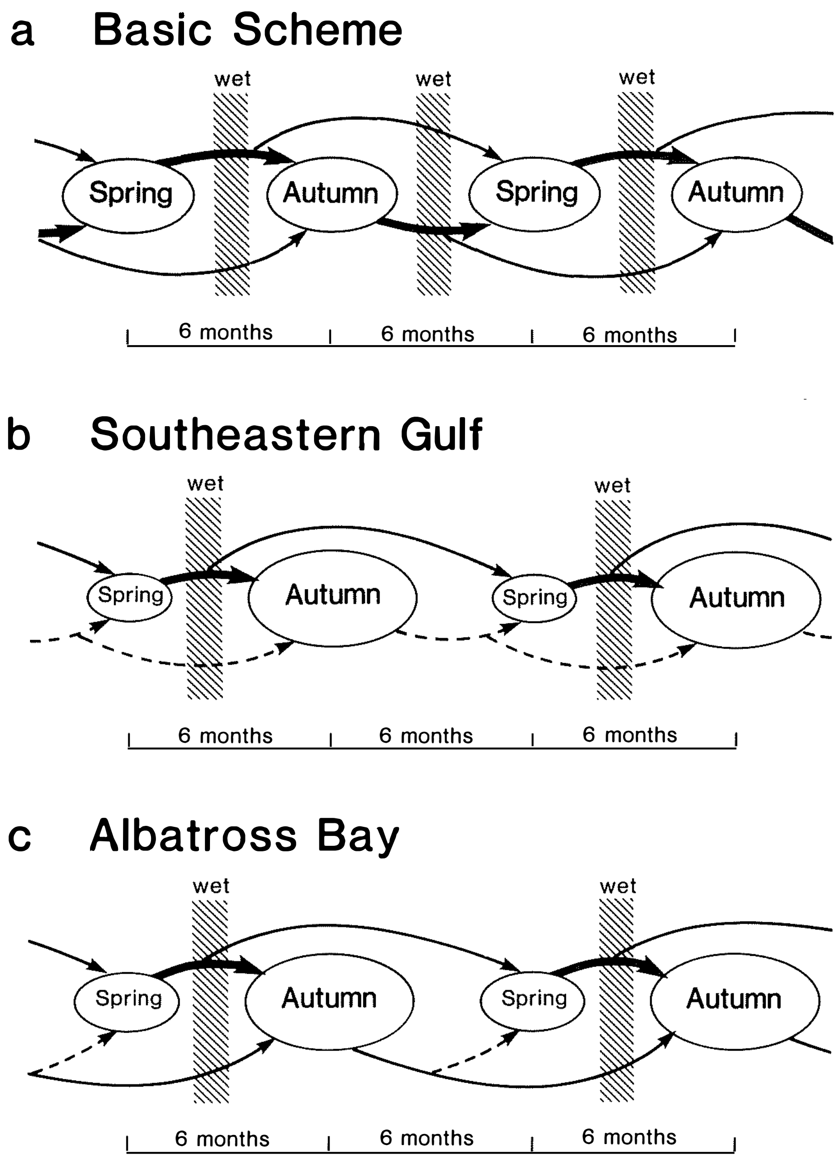

Figure 4. Schematic representation of the postulated *Penaeus merguiensis* life cycle: **a.** Basic pattern for the Indo-West Pacific; **b.** Pattern in the southeastern Gulf of Carpentaria; **c.** Pattern in Albatross Bay, northeastern Gulf of Carpentaria. See text for explanation of various line types.

The emigration of juvenile *P. merguiensis* from nursery grounds in the Gulf of Carpentaria is clearly associated with rainfall (Munro 1975; Staples 1980; Staples and Vance in press; Vance et al in press). Because there is only one short wet season each year in the Gulf, the main period of emigration is also very seasonal. Chong (1979) found that emigration of *P. merguiensis* in the Straits of Malacca was also closely related to rainfall but in this area both recruitment and rainfall were more protracted than in the Gulf of Carpentaria. Increased recruitment into the offshore fishery in the Straits did occur following increased rainfall in October-November. Gwyther (1982) found continuous recruitment into the offshore *P. merguiensis* fishery in the Gulf of Papua, an area which experiences little seasonality in rainfall and runoff (McAlpine and Keig 1983).

As a result of regional differences in the timing and strength of migrations of the different life history stages, the offshore population structure also varies in different parts of the Gulf of Carpentaria. In the southeastern Gulf during January to March, when the main wave of recruits is entering the offshore area, the size composition of both sexes is essentially unimodal. The modal size of spawning females at this time is about 33 mm CL. This main recruitment group can be followed throughout the winter period, finally disappearing from the population in December-January. In contrast, the size composition of both sexes during the main summer recruitment period in the Albatross Bay area is bimodal. In January, the modes lie at about 34mm and 43mm CL for spawning females (Crocos and Kerr 1983). We suggest that the smaller mode represents the new recruits of the spring generation and that the larger mode is composed mainly of autumn spawned prawns which have overwintered either in the estuaries or offshore. However, it is very difficult to follow these groups by means of modal progressions and other interpretations are possible. For example, it could be argued that the group of large prawns simply represents the remnants of the previous spring generation (ie 18 month old prawns) implying that longevity of prawns is greater in the north than in the south. To provide firmer interpretations we need to know more precisely the relative importance of the input from the autumn generation. Only low numbers of *P. merguiensis* are caught in winter in the Gulf but in the Albatross Bay area a large proportion of these are small prawns (<25 mm CL). The significance of this recruitment is difficult to determine because of confounding catchability factors. It is possible that after allowing for temperature differences between winter and summer, this apparently small group of prawns represent a major recruitment, but more work on factors affecting catchability is needed before this can be resolved.

We propose the following basic life history scheme for *P. merguiensis* (Fig. 4a) anywhere in its range. In our basic scheme both the spring and autumn populations are about equal in size and each contributes significantly through spawning, juveniles and offshore migration to the subsequent population six months later (thick arrows, Fig. 4a). Some survivors from each population provide a lesser contribution in 9 to 12 months (thin arrows, Fig. 4a). With two monsoonal wet seasons each year, juveniles of both populations contribute directly to a year-round offshore fishery, and overwintering of juveniles through a dry season does not play an important part.

The Gulf of Carpentaria has only one short wet season each year. The life cycle of *P. merguiensis* in the Gulf, therefore, is quite different from the basic cycle proposed in our model. In all regions of the Gulf, prawns migrate from the estuaries to the offshore area mainly during the summer wet season. The spring and autumn populations are therefore unequal in size and the autumn (post wet season) population is the only one large enough to support a commercial fishery.

In the southeastern Gulf (Fig. 4b) the large autumn population contributes little and only sporadically to either the subsequent spring or autumn populations (broken lines, Fig. 4b). The small spring population, made up mainly of survivors from the autumn fishery (thin solid lines, Fig. 4b), therefore, is the only significant source of the autumn fishery.

In Albatross Bay the picture differs slightly (Fig. 4c). Here too the populations are of unequal size with the autumn population forming the main commercial fishery. The population is made up mainly of prawns originating from the spring population, growing up as juveniles in the estuaries during the spring and summer and migrating offshore during the summer wet season. However, in this region there is also a significant and consistent contribution of postlarvae and juveniles from the spawning of the autumn population. These juveniles can move directly into the spring population by leaving the rivers in winter (broken lines, Fig. 4c), or overwinter in estuaries and contribute to the autumn population 9 to 12 months later (thin solid line Fig. 4c).

In contrast to our scheme, Garcia (1985) argues that the normal generation time for the whole genus *Penaeus* is one year. He defines generation time as the period between the massive reproduction of the parent generation to massive reproduction of the progeny generation. His general scheme (Garcia 1985, his Fig. 3), based on observations of *P. semisulcatus* in Kuwait and *P. notialis* in the Ivory Coast, includes two generations each year but does not allow for a major spawning within the first six months. According to Garcia the first spawning occurs at 12 months and subsequent spawnings occur at 18 and 24 months. This scheme is the same as the 'Equatorial Alternation of Populations' put forward for *Metapenaeus* spp. in Singapore by Hall (1962). Hall also suggested that the spring generation is derived mainly from the previous spring generation and that the autumn generation is derived mainly from the autumn generation with a one year generation time. It is interesting to note that in all these schemes, twice yearly spawning and postlarval immigration will be observed. The main difference is whether or not the six month old prawns contribute significantly to the total population egg production. Garcia invokes evolutionary fine tuning to place the most important (massive) egg production in spring when phytoplankton abundance is at a maximum and argues that shorter generation times would be inefficient. Different seasonal patterns of phytoplankton blooms including spring and autumn maxima, however, have been observed in different locations around the world and would appear to depend on the degree of water mixing, as well as, seasonality of physical factors (Sinclair and Tremblay 1984).

With *P. merguiensis*, in the Gulf of Carpentaria, maximum spawning output occurs six months out of phase between southeastern Gulf and Albatross Bay and the highest egg production does not coincide with the highest postlarval immigration. It could be argued that 15 years of fishing pressure in the southeastern Gulf have reduced the number of spring spawners down to such a level whereby the relative importance of the spring and autumn peaks have become reversed. However, to invoke this hypothesis in one part of the Gulf but not another without firm data is premature. Staples (1979, 1980 and 1985), has suggested that the timing and relative abundance of juvenile prawns in one estuary of the southeastern Gulf has not declined since 1970. Further evidence for a twice yearly spawning pattern for *P. merguiensis* can be inferred from a number of observations of one or more stages in the life history elsewhere in the species' range. Chong (1980) found bimodal seasonal changes in the frequency of occurrence of ripe females in Malaysia, as did Thubthimsang (1976) in the Gulf of Thailand. Bimodal postlarval immigration patterns have been seen in India (Selvakumar et al 1977; Goswami and George 1978), the Philippines (Motoh 1981) and Singapore (Hall 1962). In the Gulf of Carpentaria there are also two peaks of early larval abundance in *P. latisulcatus* and *P. semisulcatus* (Rothlisberg, Jackson and Pendrey 1985) and two peaks of postlarval *P. semisulcatus* and *P. esculentus* immigration in Albatross Bay (Staples 1984), although we do not know yet whether the first main spawning occurs at 6 or 12 months for these species. Further evidence for a six month generation time comes from Hall (1962), who showed growth rates of juveniles and adults, assessed from size frequency progressions, that would allow attainment of reproductive size within six to seven months. Le Reste (1978; cited in Garcia and Le Reste 1981) also suggested a six month generation time for *P. indicus* in Madagascar, as did Dredge (1985) for *P. merguiensis* in southeastern Queensland.

It appears that in the Gulf of Carpentaria, an entire generation can be lost if prevailing currents and hydrological conditions are not suitable for larval advection and postlarval settlement and the output from the massive spawnings of *P. merguiensis* are not finely tuned with their environment. The apparently robust reproductive strategy of *P. merguiensis* is therefore, a combination of both a six month and 12 month cycle with a six month generation time and a second spawning at an age of 9 to 12 months. In the Gulf, it is the 12 month cycle that is in fact the main link between generations. This strategy has obviously allowed the species to invade new territory when it became available (eg the Gulf of Carpentaria within the last 6000 years) and has allowed the species to persist in diverse and variable hydro-meteorological environments. As we have shown with *P. merguiensis* in the Gulf of Carpentaria the importance of cohorts cannot be measured by their absolute or even relative size. The timing of the reproductive events and recruitment through the various stages in the life cycle and habitats is more important and needs further examination with most of the world's penaeids. With this understanding, more accurate and sophisticated population, yield and predictive models and management regimes can be formulated.

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Population dynamics

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Reproduction, stock assessment models and population parameters in exploited penaeid shrimp populations

Abstract: During the last few years, penaeid shrimp stocks have been intensively studied over the tropical regions of the world and a wealth of knowledge has accumulated. Some difficulties, however, still remain. The paper summarises the main developments in the understanding of the nature of shrimp fisheries and underlines some of the fields where more research is needed. In order to provide a basis for discussion, a general schema describing the seasonal cycles of reproduction, recruitment and life cycle of the genus *Penaeus* is presented. It is tentatively concluded that the generation time from birth to massive spawning of these shrimp is essentially one year and the advantages of such a strategy for population maintenance in a seasonally oscillating environment are discussed. The various models used for stock assessment are briefly reviewed and some of their limitations or particular properties when applied to shrimp are discussed. These include production models, stock recruitment relationships, yield per recruit models, forecasting models and De Lury-Leslie estimators. Some emphasis is put on the use of analysis of length frequency data and commercial size categories as well as the potential usefulness of comparative population analysis in a situation of data shortage.

Introduction

Coastal penaeid shrimp stocks have become more intensely studied in the intertropical region during the last three decades as their importance in tropical fisheries has increased. Much progress in biological research has been accomplished since the FAO World Science Conference on biology and culture of shrimps and prawns held in Mexico in June 1967. The scientific work on population dynamics and stock assessment has greatly developed in Australia, as shown by the First Australian National Prawn Seminar held in Maroochydore (Queensland) in November 1973 (Young 1975). Similar developments have also occurred in Latin America, North America, West Africa, Madagascar, Persian Gulf, eastern Indian Ocean and South East Asia. More recently the progress in biological understanding and management of shrimp has been reviewed at the Workshop on the Scientific Basis for the Management of Penaeid Shrimp, Key West, Florida, November 1981 (Gulland and Rothschild 1984).

Critical review of available knowledge is always important and a first attempt was made by Garcia and Le Reste (1981) who examined in detail the most important aspects of the shrimp life cycle (including abundance, variability and sampling methodology, exploitation systems, collection of fishery data, tagging, growth, mortality, changes in catchability, modelling, selection, recruitment, stock assessment and management, using literature up to 1979. The present paper tackles particular issues that received little attention in the above review.

The limiting factor in shrimp stock assessment and management at present does not appear to be a shortage of methodologies, at least for single species, but rather in the scarce knowledge of the mechanisms of shrimp production as well as superficial knowledge of the fleet dynamics. For these reasons, the first part of this paper is focused on life cycles especially for the genus *Penaeus* and presents some speculations about reproduction strategies. Unless these mechanisms are understood, it will not be possible to determine the most appropriate of the available methodologies and the need for new ones.

The paper recalls first the differences between brown and white shrimp. It then presents a schema for a typical *Penaeus* life cycle including a review of seasonal spawning and recruitment cycles and discussion on the generation time. I am perfectly aware that this may be an oversimplification but it should offer a basis for future comparison between species and regions especially with respect to the consequences of the shrimp life history strategy on the fishery and on our stock assessment concepts. It is intended to stimulate more analysis along similar lines for as many stocks and as many genera as possible in the future.

The paper also examines some typical characteristics of shrimp fisheries. It reviews the main assessment methodologies and deals briefly with the problems of using length frequency data and commercial categories for stock assessment. The conclusion presents some thoughts about specific research needs for the future.

Brown and white shrimp

To facilitate comparison within the group *Penaeus* it may be useful to distinguish between white and brown shrimp. Boddeke and Kat (1979) have shown that basic differences exist between the subgenera *Litopenaeus* and *Farfantepenaeus (Melicertus)*. This division of the genus *Penaeus* into subgenera is taken from Holthuis (1980). The *Litopenaeus* group, which includes *P. setiferus, P. vannamei, P. schmitti, P. stylirostris, P. occidentalis* consists of white shrimp which generally fetch higher prices in the market. They are active in daylight and therefore fished during the day. They live in more coastal areas as adults and they seem less sensitive to salinity fluctuations than brown shrimp. They are essentially grazers of benthic micro-organisms.

In contrast, the *Farfantepenaeus* species which include *P. duorarum, P. notialis, P. aztecus, P. brasiliensis, P. californiensis, P. subtilis, P. paulensis* tend to be active at night when they are normally fished. Apparent exceptions to this rule, like *P. notalis* in Ivory Coast, are due to peculiar local conditions of very high turbidity (Garcia 1977a). They are more predatory than white shrimp in both the field and aquaculture situations (Pedini[1], pers. comm.).

[1] M. Pedini, FAO Fisheries Department, Via delle termi di Caracalla, 00100 Rome Italy.

Penn (1984) added to this separation between white and brown shrimp by indicating that *P. (Fenneropenaeus) merguiensis* (a white shrimp) in Australia is active during the day, and tends to school, while *P. (Melicertus) latisulcatus* and *P. (Penaeus) esculentus*, two brown shrimp, tend to be active at night and do not school. This difference in behaviour could, according to Penn, affect their catchability and resilience to fishing. As *P. (Fenneropenaeus) indicus* tend to behave like *P. (Fenneropenaeus) merguiensis*, one could be tempted to consider together the subgenera groups *P. (Farfantepenaeus)* and *P. (Melicertus)* as brown and separate them from the subgenera *P. (Litopenaeus)* and *P. (Fenneropenaeus)* as white.

In many countries, when both groups are present, historically the offshore fishery has started in shallow coastal waters on whites, exploited only during the day and has developed later on browns, fishing day and night and expanding into deeper waters.

The group of brown shrimp, as previously defined, contains the striped or tiger shrimp. Usually the latter are separated commercially but it seems difficult with the information available to distinguish them clearly from other brown shrimp on the basis of their population characteristics or fishery related behaviour.

Seasonal patterns

In shrimp stocks, seasonal patterns should not be concealed by the averaging effect of using annual time intervals as is done for many long lived fish in traditional fishery science. The patterns of seasonal recruitment, growth, behaviour and catchability, fishing mortality, age structure of the exploited population, reproductive potential, biomass, etc have important consequences to the outcome of specific management measures (Garcia 1977a; Garcia and LeReste 1981).

Spawning cycle

Spawning is the base of the resource renewal mechanism and stock conservation. More work is still needed before we really understand the mechanisms of reproduction in shrimp at the population level. Most studies available on the subject are far from satisfactory. For instance, the widely used percentage of mature females is a biased index of population reproduction and must be combined with an index of adult abundance and with fecundity at size data (Garcia 1977a; LeReste 1978; Penn 1980). Furthermore, studies on monitoring of larvae or postlarvae abundance are often too short for a good average annual cycle to be obtained. Short time sampling variability is sometimes as high as the annual signal to be observed (see Garcia and LeReste 1981 for a review of sampling problems). These problems affect large parts of the literature available and complicate any attempt to generalise on penaeid life cycles. The shape and chronology of the potential fecundity seasonal cycle is largely governed by the shape and chronology of the recruitment cycle of juveniles in the sea. The recruitment cycle of these juveniles depends itself on the larval abundance cycle (and therefore on the preceding year class spawning and environmental cycle) as affected by environmental conditions during the estuarine phase.

Under these circumstances, attempts to correlate seasonal spawning indicators with seasonal environmental parameters are likely to produce spurious relationships. The long term evolutionary adaptation of the population to the oscillating environment is often wrongly interpreted as a short term cause and effect relationship. Garcia (1977a), for instance, showed that, by simulating the seasonal changes in population structure of *P. notialis* in Ivory Coast, the calculated theoretical maximum fecundity was coincident with the observed abundance of larvae and with the seasonal maximum abundance of phytoplankton (Fig. 1). He suggested that this coincidence was in accordance with the match/mismatch theory of Cushing (1975) which hypothesised that, in north temperate waters, fish populations are adapted to spawn in relation to phytoplankton blooms.

Individual shrimp are partial spawners and can lay several batches of eggs every year. At the population level, however, spawning appears to be more or less continuous, but very often seasonal, showing at least one peak, and sometimes two per year. These frequently occur during the transition periods which separate cool and warm seasons and are characterised by particular hydrological and climatological features such as rising or falling temperatures, low current velocity and wind speed, peaks in primary productivity, as well as high rainfall and severe drops in salinity. Examples can be found in Penn (1980) (*P. latisulcatus*, Australia), Garcia (1977a)

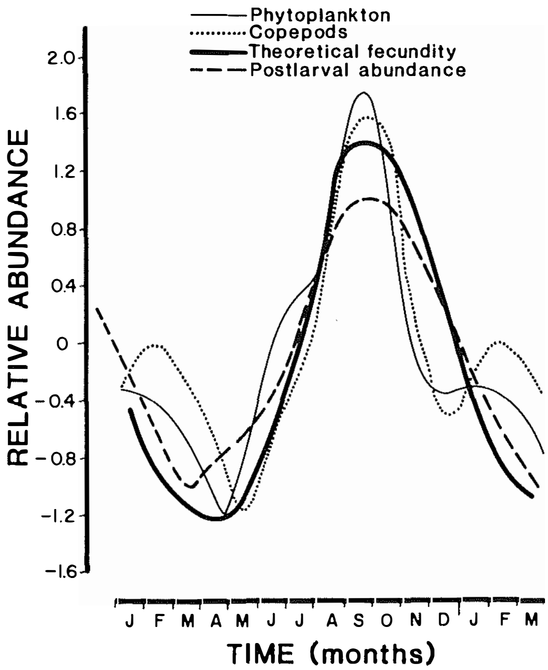

Figure 1. Comparison between observed seasonal patterns of primary production, copepod abundance and postlarval abundance and the calculated seasonal change in fecundity in *Penaeus notialis*, Ivory Coast (from Garcia 1977a). The data have been smoothed by a running mean on three values and reduced to a relative scale by subtracting the mean and dividing by the standard deviation. Postlarval data are lagged by one month.

(*P. notialis*, Ivory Coast), Berry and Baxter (1969) (*P. aztecus*, Gulf of Mexico), FAO (1982) (*P. semisulcatus*, Kuwait), Lhomme and Garcia (1984) (*P. notialis*, North Senegal), LeReste (1978) (*P. indicus*, Madagascar), Motoh (1981) (*P. monodon*, Philippines). Garcia (1977a) reviewed briefly the various types of spawning seasonal patterns and in spite of the shortcomings of the methods used for quantifying spawning activity, it seems that the double peaked pattern is the most frequent. By analogy with temperate waters we may consider the existence of a spring spawning (it occurs when seawater temperature increases and may extend somewhat into early summer) and an autumn spawning period, these two giving rise to two generations (consisting of many cohorts) per year. When two peaks occur, the spring spawning is usually the more regular in timing and amplitude. The importance of the autumn spawning varies from year to year and place to place, as well as in time of occurrence (Garcia

1977a) for *P. notialis;* LeReste (1978) for *P. indicus*). This double maximum spawning cycle seems to be very general for many marine species in the tropics and it has also been found in most coastal fish stocks in the Gulf of Guinea (ISRA/ORSTOM 1979) and in many other tropical areas (Johannes 1978). As a consequence it will be considered in this paper as the typical pattern although it is likely that shifts from this pattern may occur with latitude, or particular local conditions.

The larvae produced during the spawning cycle enter the inshore waters to grow. It has been shown (Ford and St. Amant 1971) that the survival and growth of a cohort in the estuaries is strongly affected by the inshore environment (offshore transport, tidal currents, date of entry in the estuaries, temperature during the estuarine phase). The duration of the estuarine period as well as the size (age) at migration towards the sea are affected by hydrological or climatic events (see Garcia and LeReste 1981 for a review). The seasonal cycle of recruitment is therefore expected to be an image of the spawning cycle lagged by about four months but distorted by the conditions met during the inshore phase.

Migration and recruitment

The number of shrimp leaving the estuary at any time depends on both the abundance of juveniles in the nursery area and their age structure. Both factors are directly linked to the spawning cycle and external factors which trigger emigration (like salinity, temperature, current speed, etc). It should therefore be expected that the seasonal migration oscillation mimics the spawning cycle but is also distorted by the interference with the seasonal oscillation of the environmental conditions inshore. In examples where migration has been carefully analysed it is generally observed that a main migration period occurs in summer through autumn and follows the spawning peak in spring by about four months. Secondary peaks may occur during main flooding or rainy periods, once or twice a year, in spring and again in autumn. Juveniles coming from the secondary spawning in autumn overwinter in estuaries and migrate in spring. When the temperature signal is of low amplitude, and spawning more or less continuous, the migration cycle may show one or both of these secondary peaks and the time lag (age at migration) between spawning and migration may be quite difficult to establish unless intensive sampling of the various cohorts is undertaken in the inshore waters. Double peaked recruitment patterns in shrimp seem to be common (for example Garcia 1977a, in Ivory Coast; Lhomme and Garcia 1984 in Senegal; Pauly et al 1984 in various regions; LeReste 1978 in Madagascar). These patterns are also frequent in cephalopods (Pauly 1984a, FAO/CECAF 1982).

Migration generally results in massive recruitment into the small scale inshore fishery and is followed rapidly by recruitment in the offshore trawl fishery. In most cases the shrimp appear in offshore catches in less than a month or so after migration. The more coastal the trawl fishery the shorter the time lag is. The rate of recruitment in the offshore catches depends on the availability of juveniles inshore and therefore on the migration cycle, but also on their vulnerability to trawling. The latter depends on the average depth fished by the fleet at any time. Experience shows that the main generation is generally highly vulnerable because the fleet is waiting for it close inshore, and the main depth fished increases during the fishing season as the fleet tends to follow the main generation as it grows and migrates to deeper waters (Fig. 2). As a consequence, the young pre-recruits of the secondary cohorts will probably be less vulnerable.

The recruitment cycle will, therefore, mimic the migration cycle with a possible distortion due to the behaviour of the fleet. In stock assessment, this implies that the age specific fishing pattern may vary from one cohort to another and that the seasonality in recruitment might be exaggerated when determined from abundance of small sizes in catches of professional trawlers. Another distortion may be introduced by water temperature offshore. If it is low at the moment of recruitment (of the winter cohorts for instance) and below, say 16-17° C, growth is nearly stopped and will start again only in spring. In this case, apparent recruitment can be largely delayed until spring. It should be remembered that because size and age at migration varies seasonally, size and age at recruitment could vary as well. Measuring recruitment by the abundance of small shrimp below a given fixed size in the catches could, in some cases, lead to biased results.

Despite the difficulties foreseen above, it might be said that most *Penaeus* stocks have a seasonally oscillating recruitment pattern with a main generation recruited offshore during

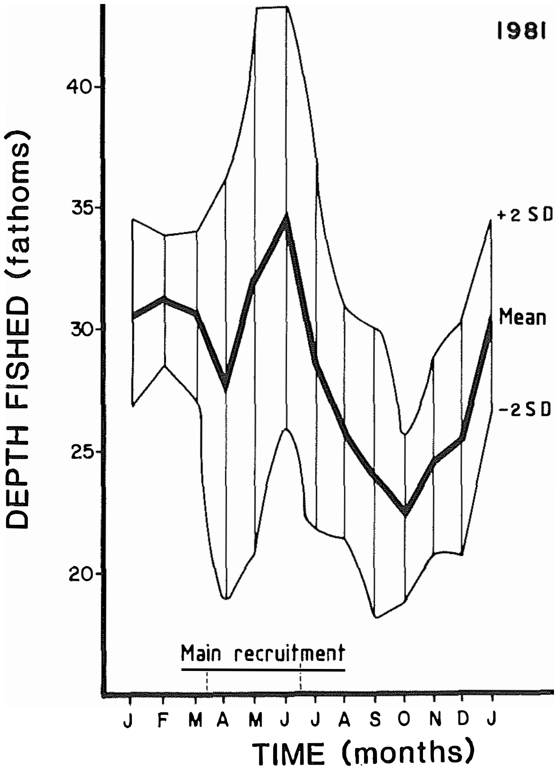

Figure 2. Seasonal variation of average depth (±2 standard deviations) in French Guiana (from Garcia et al 1984). Fathom = 1.85m.

summer and autumn and a secondary generation recruited in spring.

There are some variants to this pattern depending on the latitude for the same species (Staples 1979; Penn 1980; Lhomme and Garcia 1984) or on the species concerned when many *Penaeus* species share the same inshore areas. In this latter case, slight differences in timing seem to exist which combined with slightly different biota requirements apparently result in reducing the competition between closely related species (Young and Carpenter 1977).

In the cases where the main spawning peak is in summer, eg for *P. latisulcatus,* in Australia (Penn 1980) or *P. setiferus* in the Gulf of Mexico (Lindner and Cook 1970) the main recruitment is in autumn. When the main spawning occurs in autumn the growth can be low in inshore waters leading to recruitment in the following spring—*P. notialis* in North Senegal (Lhomme and Garcia 1984), *P. semisulcatus* in Kuwait (FAO 1982).

Life cycle and generation time

There seems to be fair homogeneity in the timing of the life cycles of shrimp and it is tempting, albeit risky, to try and describe the life cycle of a typical *Penaeus.* There certainly are deviations from the typical model from place to place and especially at the extreme geographical limits of distribution of the family. There are also obvious deviations from one cohort to another in highly seasonal environments but the following sketch could probably be considered as the most typical.

The typical *Penaeus* is spawned at sea and enters the inshore waters at an age of about three weeks to one month as a postlarva. It grows there for about three months before migrating back to sea where maturation of females can start (maturation of males can apparently start in the inshore waters). It is then about four months old and measures 80 to 100mm (total length). This migration is more clear cut for brown shrimp than for white shrimp and in lagoon systems than in estuaries or open mangroves where the phenomenon can start earlier and is more progressive.

Penaeus continues maturing as it grows and spreads on the fishing grounds in deeper and deeper waters and will spawn after reaching the minimum size for maturation and when environmental conditions are adequate. The size at first spawning, when the very first individuals of a cohort can lay some eggs, is reached at about 6-7 months but the massive maturation, ie the age at which the bulk of a cohort spawns, is closer to one year (10 to 12 months). It is very important to distinguish between the individual size at which first maturation can take place and the average individual size in the population when massive reproduction occurs. This second parameter is more important for stock renewal and therefore the definition of the generation time is from birth to the first massive spawning of that generation.

This average life cycle can of course be modified by environmental factors like currents, which may delay the recruitment of larvae in lagoons, unusual floods and cold strikes or droughts in estuaries that may shorten or protract the duration of the inshore phase and therefore modify, seasonally or from year to year, the size and age at migration, recruitment or spawning. Good information is necessary to reach some understanding of the stock and

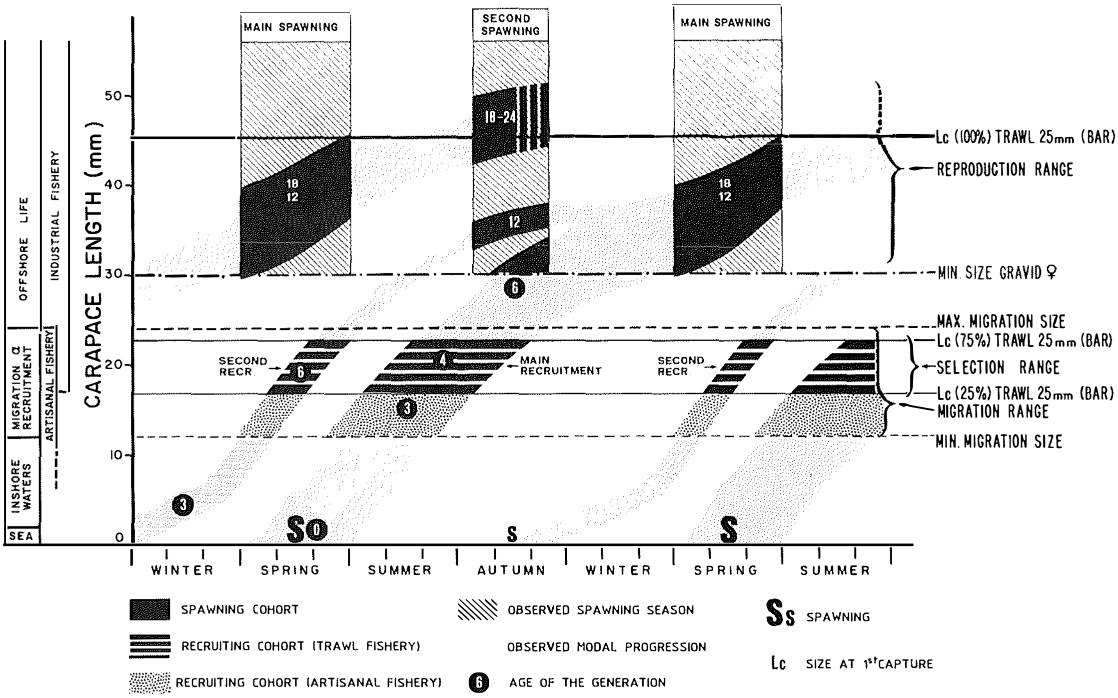

Figure 3. Theoretical model of the essential features of the life cycle and fishery of *Penaeus*.

recruitment relationship at the cohort, generation and population level. It is therefore important to find the link between the seasonal pattern of recruitment and the subsequent seasonal spawning cycle or in other words the link between the recruits at a given time and spawning stock at a subsequent time. It is also necessary to determine the basic time frame of stock reproduction and renewal or generation time.

In order to do this it is necessary to combine information collected on—

(a) seasonal patterns of spawning, inshore abundance, migration, recruitment and average size by sex in the offshore stock;

(b) population parameters: size at migration, size at 50% retention by the trawl and selection range, size at first maturation, age and size specific fecundity;

(c) growth, and in particular, seasonal changes of growth and observed modal progression;

(d) natural and fishing mortality.

A theoretical example of a graphic integration of this information is given in Fig. 3. Other examples can be found in Staples (1979), FAO (1982), Garcia et al (1984).

If, as represented in Fig. 3 and as implied from previous sections, the generation time is one year (this seems to be the case for *P. semisulcatus* in Kuwait (FAO 1982) or *P. notialis* in Ivory Coast and North Senegal) then the main spring generation would reproduce itself one year later as would also the autumn generation. Both generations would meet with different environmental conditions and would have different survival rates, especially before recruitment, and hence would have different stock recruitment relationships (Fig. 7). Some genetical mixing between generations could still occur as there might be limited spawning by each generation out of its main spawning period (for instance a limited first spawning in autumn for the spring generation in Fig. 3). Oscillating on the basic annual cycle of the environment the population appears to be placing its most important egg output during the most favourable time window and being more opportunistic during the rest of the year with the other cohorts (for instance, the irregular autumn generation).

The other important consequence of the existence of a one year generation time is that, because fishing concentrates on the main generation and drastically decreases its abundance before the main spawning can occur, there is a high risk that the capacity of the main generation to reproduce itself is impaired. This can easily be deduced from simple spawning potential per recruit calculations (Garcia 1977a; Garcia and LeReste 1981; FAO 1982) and according to Penn[2] (pers. comm.) this may have already happened for a stock of *P. latisulcatus* in Australia.

As it is not yet proved that all *Penaeus* stocks have a generation time of one year, it may be interesting to speculate about the potential value of a shorter generation time. I suggest that the population would then oscillate in asynchrony with the environment. If the generation time was six months (the first spawning just after recruitment would also be the massive one) the important spring generation would give birth to an autumn generation and vice versa. Such a scheme was proposed by Staples (1979) for *P. merguiensis* in the Gulf of Carpentaria and also by LeReste (1978) for *P. indicus* in Madagascar but the evidence given in this last case for seasonal spawning success is not entirely convincing and might be interpreted differently. This strategy would imply a high cost for the stock but might be considered the best one if a high potential fecundity was necessary to bridge over an unfavourable season as assumed by LeReste (1978). The risk of extinction of the stock would, however, be very high because the autumn secondary generation is very irregular and often disappears totally for a few successive years. If this generation would have to bear the responsibility of ensuring permanence of the stock by giving birth to the main spring generation then the system would appear to be very unstable.

Any other generation time longer than six months but shorter than a year would induce an oscillation in the population perpetually out of phase with the environment. The clear and stable seasonal spawning patterns actually observed in the population would then have to be purely the result of the environmental oscillation, with no relationship whatsoever to the size and fecundity of the cohort. The loss of energy for the stock would be even higher than with a six month generation time and one can speculate that a better adapted group of species would have replaced the genus *Penaeus*.

In conclusion, it is suggested that an annual generation time seems to have more virtues for thriving in a seasonal environment than any other and that the case for *P. notialis* in Ivory Coast and Senegal or *P. semisulcatus* in Kuwait might be a general case. More detailed analysis and simulations on other species are needed to confirm this point.

Exploitation sector

Exploitation of adults by trawl fisheries

The seasonality of recruitment has very important consequences for the fishery. It will be responsible for the seasonal variations of catch per unit effort and abundance, of average size of the stock, of spawning potential, etc. Combined with the progressive migration of the various generations towards greater depth, it will also be responsible for the great spatio-temporal heterogeneity of shrimp stocks.

Industrial penaeid shrimp fisheries around the world are very similar. The shrimpers tend to exploit the spatio-temporal heterogeneity in the best possible way, concentrating their effort (and hence fishing mortality) on the most profitable space and time allocations(Fig.4). In multispecies fisheries, the elements of choice will be multidimensional (species, space and time). During the day, they may allocate effort to white shrimp on coastal areas whereas at night they may fish deeper for browns. During the year, they concentrate effort in the months where the expected financial returns are higher. In French Guiana for instance, because of market differences, the Japanese fleet fish mainly for big *P. brasiliensis* offshore while the US fleet fishes more for small or average size *P. subtilis* closer inshore. The consequence of this is that many undetected changes occur in fishing strategy and in the relationship between effort and fishing mortality during the development of a fishery (see Garcia and LeReste 1981 for a review). This in turn affects the reliability of the results obtained through surplus production modelling using catch and effort data.

The more seasonal the pattern of recruitment the higher the time space heterogeneity and the

[2] J.W. Penn, Department of Fisheries and Wildlife, North Beach, Western Australia.

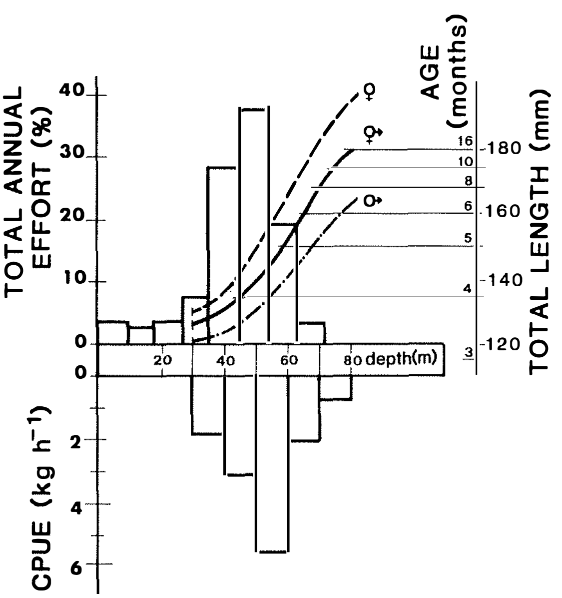

Figure 4. Bathymetric distribution of effort (upper histogram), abundance (lower histogram), average sizes for females (---), males (-·-·-) and combined sexes (——) and ages (combined sexes only) for *Penaeus subtilis* in French Guiana from Garcia et al (1984). Ages have been calculated using growth parameters for *P. aztecus* from Parrack (1979).

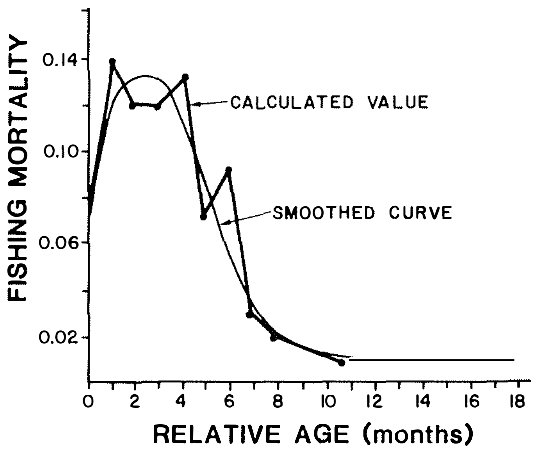

Figure 5. Age specific fishing mortality vector for *Penaeus notialis* in Ivory Coast (from Garcia 1977a).

more seasonal the fishery behaviour. The consequence of this extremely well aimed fishing strategy is that the catches may give a biased image of the stock, underestimating for instance the spawning potential available in deep waters during the recruitment months or underestimating the importance of the second recruitment peak when the first one is abundant.

The complex combination of spatio temporal heterogeneity of the resource with the economic motivations of fishing results in a particular fishing pattern or age specific fishing mortality vector. Fishing effort is distributed on the bottom (and on the stock) proportionally to abundance or, more exactly, proportionally to value. Figs. 4 and 5 show a pattern that might be considered general. This fundamental and well known aspect of shrimp fisheries seems to have received little attention when modelling the exploitation, particularly in yield per recruit (Y/R) calculations where fishing mortality (F) is usually assumed to be constant with age.

Artisanal fisheries

A review of artisanal fisheries with an emphasis on stake net fisheries is given in Garcia and LeReste (1981). Detailed analyses of these fisheries are still scarce. Artisanal fisheries for juveniles have a direct effect on trawl fisheries for adults but these effects in biological or economical terms are still largely unstudied in most areas. Garcia (1977a, 1978) provided a first analysis of yield and value as a function of exploitation rate in the lagoons, and fishing effort at sea, in the Ivory Coast. Griffin and Grant (1982) completed this analysis using economic parameters. These types of studies remain scarce despite their importance, probably because of the difficulty of obtaining accurate socio economic data on the artisanal fishery and the complexity of the artisanal exploitation sector in some countries (multigear, multispecies fisheries, links with the wider rural sector). In general, it does not seem to pay to catch small shrimp as stated already by Lindner (1966), Lucas (1975) and more recently, by Willmann and Garcia (in press). The relative benefits for each sector and for the nation as a whole, however, have to be estimated case by case and include not only financial, but also aggregated social benefits.

Assessment methods and models

A review of the methodologies used for penaeid shrimp stock assessment was given by Garcia and LeReste (1981). An analysis of stock recruitment relationships in shrimp (Garcia 1983) followed. It is easily seen that traditional temperate waters fishery science has largely been applied to date, despite the tropical character of the animals concerned. Most of the so-called new methods (either elaborate or quick and dirty) proposed in recent years for tropical populations have their roots in the very first steps of this classical fishery science and Ursin (1984) has recently pointed out some of the similarities between temperate and tropical environments and resources. The basic concepts will therefore, still be used for some time but minor adjustments have to be made by using shorter time scales, and paying more attention to seasonal patterns and environmental variables.

Production models

In the context of high spatio temporal heterogeneity of the resource exploited by a well aimed fishery, it is obviously dangerous to summarise a fishery as a set of catches and nominal efforts plotted on a bivariate graph to produce a production model and generate information on catch potentials and some sort of optimal fishing level. Many sources of drift in effort or fishing pattern can distort the model and lead to biased conclusions. Garcia and LeReste (1981) give a review of the problem in the case of shrimp. A description of this sort of change in fishing power is also given by Lucas et al (1979) for the Gulf of Carpentaria fishery.

However, in a single year class fishery, despite the lack of dependence of the biomass in one year to the biomass and fishing mortality in the preceding year, the production model approach can still provide an empirical knowledge on the apparent reaction of the stock to exploitation.

Because of the strong influence of the environment on annual shrimp production, the potential errors when this influence is not taken into account is serious, especially when the data series is short. More use should be made of multivariate models of the form—

Catch = g (effort, rainfall, temperature, etc.)

as used by Griffin et al (1976). A preliminary correlation of the residuals from the relationship between catch and effort with environmental variables known to affect recruitment or catchability could also be useful as a first step (see for instance Lhomme and Garcia 1984 for *P. notialis* in Senegal). The comparison of time series of such residuals for neighbouring stocks may also show the wide scale effect of some environmental factor (an example is given for Kuwait by Garcia and Van Zalinge 1982). A short analysis of the effect of environmental variability on production modelling is given in Garcia (1984b) and it is pointed out that the fishery trajectory across a catch, effort and environment multidimensional

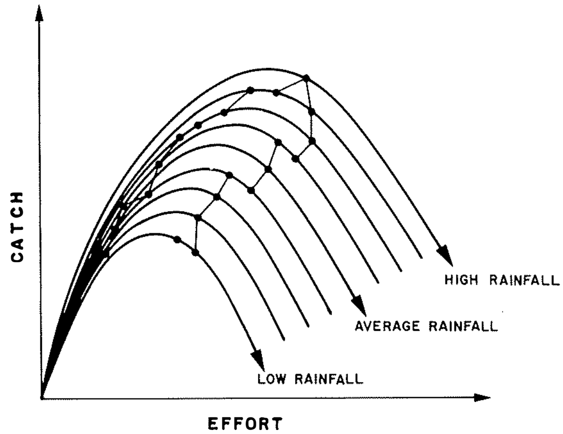

Figure 6. Theoretical example of the trajectory of a fishery (dots) across a catch, effort and rainfall production model.

space could be wrongly taken as a production model on the catch effort plane while all the basic properties of this model have, in fact, been lost. Above all, the possibility of reversing the observed evolution of the fishery stock along the same observed trajectory by reducing the amount of effort (Fig. 6) is often not feasible.

Stock and recruitment models

Despite the fact that it is relatively easy in many instances to measure the spawning stock size and the recruitment index in *Penaeus* populations, stock and recruitment relationships (SRR) have been studied only since the beginning of the 1980s. In a review of the available literature, Garcia (1983) has indicated the various types of recruitment indexes that could be used and stressed the following—

(a) annual shrimp catches have been shown to be strongly related to environmental factors. The cohort survival in lagoons and estuaries and therefore the level of recruitment are largely dependent on local climatic conditions;

(b) environmentally driven changes of stock size in short-lived species are likely to be serially correlated and therefore very likely to produce artefactual linear stock recruitment relationships (SRR) which in fact are an approximation of the opposite recruitment stock relationship (RSR) or replacement line;

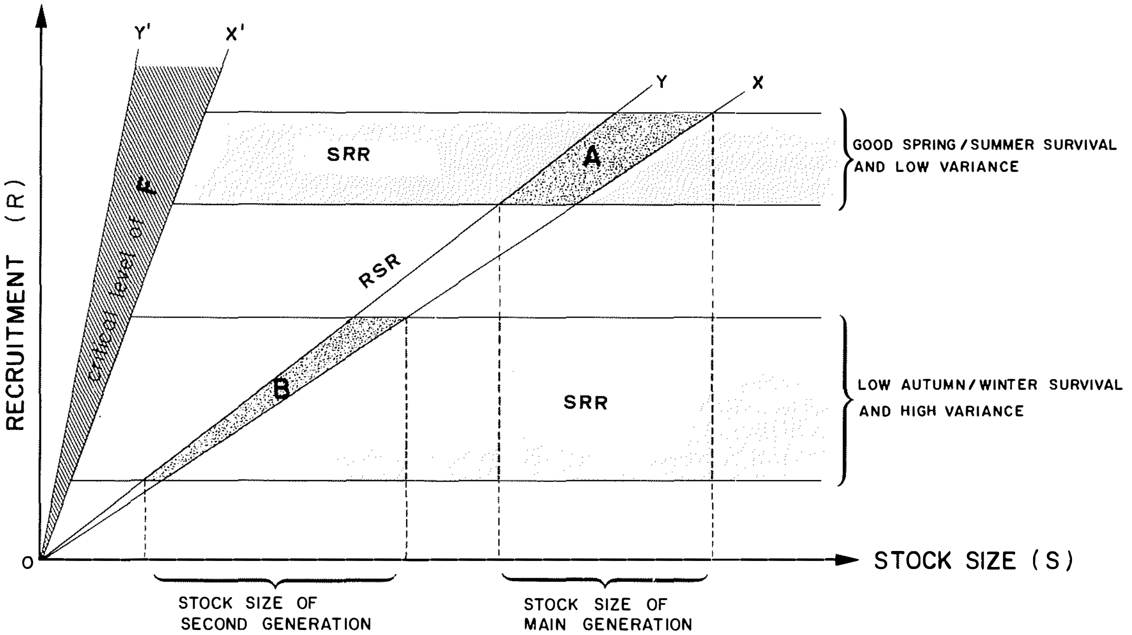

Figure 7. Theoretical example of stock recruitment for the spring and autumn generation of shrimp. A and B indicate the respective areas of equilibrium of the two generations when fished with the same intensity. Two levels of the stock recruitment relationship (SRR) are shown, corresponding to good and low survival of pre-recruits. Recruitment stock relationship (RSR) or replacement lines shown as sector XOY to allow for natural variations of catchability for a fixed fleet size. X'OY' is the replacement sector when F, the fishing mortality, reaches the critical level.

(c) there are probably many stock recruitment relationships (SRR), or more strictly many pre-recruit mortality levels depending on the birthdate of the various cohorts. In other words pre-recruit mortality is likely to vary seasonally from one cohort to another. For example, a different pre-recruit survival range for the spring and autumn generations can be expected (Fig. 7).

Under a given fishing regime (as well as in a virgin stock) one would therefore have to consider under the classical theory, two equilibrium SRR areas (A and B in Fig. 7) corresponding to the two generations. In Fig. 7 it is assumed that the RSR or replacement line is the same for both generations but this is probably not so. The existence of seasonally different pre-recruit mortality levels and of a generation time of one year would lock together environmental effects and possible stock recruitment relationships and optimise stock reproduction. Garcia (1983) proposed a three dimensional interpretation of a stock recruitment relationship in shrimp (Fig. 8).

The bottom plane of the figure shows the seasonal cycle of population fecundity, assumed to depict also the seasonal spawning intensity with the shaded blocks accounting for natural variability of fecundity. Vertical plane I shows the seasonal cycle of recruitment with the shaded blocks again accounting for natural variability in recruitment. The darker three dimensional blocks identified by the month of spawning (J, F, M, etc) give the SRR area and therefore the level of pre-recruit survival for the months of spawning considered. The true SRR therefore, is three dimensional and depends on stock size, recruitment and time. The vertical plane II shows the apparent stock recruitment relationship as a projection of these SRR areas on the recruitment stock plane.

The figure emphasises the differences that exist, despite a similar shape, between this interpretation which shows the result of a long-term adaptation of the animal to its oscillating environment and the traditional stock recruitment relationship which is supposed to depict the effect of fishing on stock size and consequent recruitment.

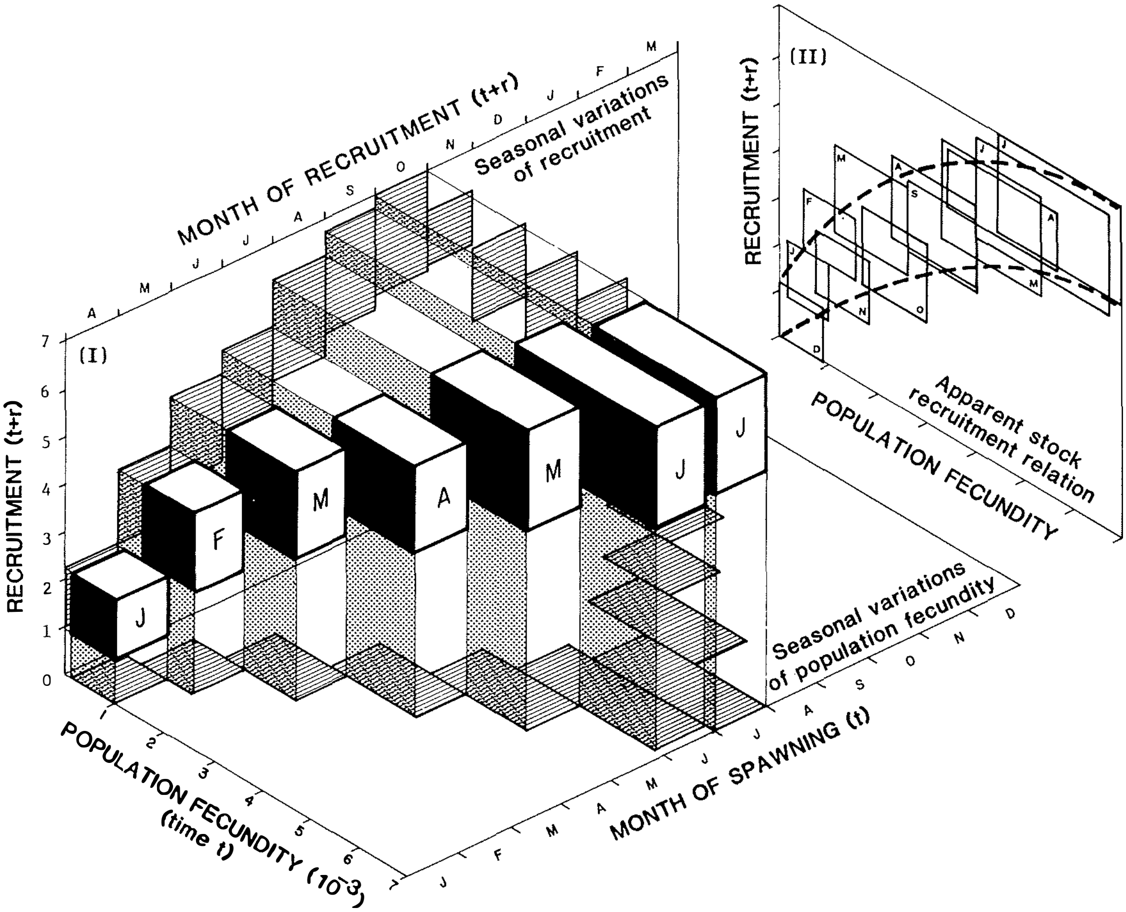

Figure 8. Seasonal patterns of population fecundity as an index of spawning stock sizes (at time t), recruitment (at time t+r) and apparent stock recruitment relationship (modified from Garcia 1983). Age at recruitment considered constant (r=3) for all monthly cohorts (eg shrimp spawned in January are recruited in April).

The important mechanisms that operate in the reproduction of penaeid shrimp populations need to be carefully considered before making biological inferences from a bivariate stock recruitment plot. This does not intend to rule out the possibility of a negative effect of fishing on recruitment. The effect of fishing on spawning capacity per recruit of the main cohort and on the seasonal fecundity cycle is potentially very drastic when fishing mortality approaches or passes the level of natural mortality (Garcia 1977a; Garcia and Le Reste 1981), and it is obvious that beyond a critical level of fishing mortality (Fig. 7) some serious and abrupt detrimental effect might happen, (eg the disappearance of the main spring generation spawning).

The progressively greater mismatch between the seasonal environmental cycle and the overall population fecundity and spawning cycles, which are continuously altered by increasing fishing mortality might result in an apparent SRR as effort increases because of the subsequent progressive increase in average pre-recruit mortality and reduction in recruitment resulting from a given stock size at the population level and on a yearly basis. It is not easy to demonstrate this effect, however, under moderate levels of fishing. A first approach might be to use multivariate models with effort, stock size, recruitment level and environmental indexes as variables following an approach similar to the one used for the Peruvian anchoveta by Csirke (1980).

Yield per recruit models

Yield per recruit models are proving to be very useful for the single species approach to shrimp management. The models of Thompson and Bell (in Ricker 1975), Beverton and Holt (1957), or Ricker (1975) have been widely used. They are justified when recruitment has not been shown to be dependent on stock size. They are flexible enough to be adapted to short time intervals and can easily be used to model for example (1) the interaction between artisanal inshore fishery on juveniles and trawl fishery on subadults and adults offshore (Garcia 1977a, 1978; Grant and Griffin 1979; Willmann and Garcia in press); (2) the effects of closed seasons (Garcia and Van Zalinge 1982) or (3) the effects of other changes in fishing patterns. They can also be used as a basis for simulation models with recruitment and fishing effort varying seasonally in order to try and reproduce the seasonal patterns characteristic of the resource. The results can be expressed, on a per recruit or on an absolute basis when an estimate of the current level of recruitment is available. They can also be expressed in value terms and used for economic analysis (Garcia 1977a; Clark and Kirkwood 1979; Lucas et al 1979). Finally they are useful for investigating the evolution of potential fecundity per recruit when fishing pressure increases (Garcia 1977a). The Thompson and Bell model is particularly appropriate because of its flexibility, capacity to use observed length at age or value at age data, and easily understood form for non-scientists like fishery administrators, (see for example Garcia and Van Zalinge 1982; Willmann and Garcia in press).

Because of the values characteristic of penaeids for natural mortality (M), growth rate (K), and critical length (l_c) and asymptotic length (L_∞), the yield per recruit (Y/R) increases exponentially towards a quasi asymptote with increasing fishing mortality (F) and Y/R_{max} is reached only at unreasonably high level of F. This casts doubts on Y_{max} as an objective for management but does not affect the intrinsic validity of the model.

Use of the De Lury-Leslie estimators

The use of the De Lury-Leslie methodology for estimating fishing mortality and population size in shrimp goes back to Iversen (1962) who used it on *P. duorarum.* The method (see Garcia and Le Reste 1981 for a review) is usable only if F is sufficiently high to affect significantly the stock size in a time interval short enough for M to be negligible, unless M is counterbalanced by recruitment. For short-lived animals like shrimp, changes in catch per unit effort (CPUE) during time intervals small enough for M to be neglected, are likely to be also largely due to behavioural changes in catchability and this complicates the interpretation of the data.

This method, correctly used by Iversen and also by Clark and Caillouet (1973) in conjunction with tagging data has been very widely used in the last 10 years in Latin America. The tendency has been, however, to plot the CPUE in numbers for the whole stock against cumulative catch for a long period of time (many months) starting after the recruitment has been completed. Within such a time interval the decrease in numbers is not only due to fishing but also to a significant natural mortality. In that case the slope of the regression is not $F/f=q$ but $F/f+M/f=q+M/f$ (Ricker 1975) where F=fishing mortality, M=natural mortality, q=catchability, and f=fishing effort. When this is not taken into account serious biases are introduced in the calculated F and, consequently, in M when this last parameter is estimated by difference between total mortality (Z), independently obtained, and biased F. The problem can be solved if M is known independently (Yew-Hu and Condrey 1985).

The other potential errors in the application of this estimator to shrimp should be carefully examined. By applying (correctly) the method only to the portion of the year where the CPUE decreases (and recruitment can be considered terminated) it is obvious that the Y axis intercept (in theory equal to q x initial population size (N_0) would be proportional to the population size at the starting point of the analysis and not proportional to the overall recruitment that entered the fishery in the preceding months. This value, better called qN'_0, depends not only on the true total recruitment but also on fishing mortality applied during the progressive recruitment period. It is therefore not a stable recruitment index. If the recruitment period is well determined and lasts for say, three months, a better, and more stable recruitment index might be obtained, as a first approximation, by the value of y when $x=-1.5$ months (assuming knife edge recruitment).

Forecasting models

Because of the high spatio temporal heterogeneity of shrimp resources and their year-to-year fluctuations in recruitment and abundance, there is need to develop short term predictive models to guide the fisheries. Many attempts have already been made and a review can be found in Garcia and Le Reste (1981) and Witzell and Allen (1983). Generally, empirical regressive models have been used relating total catch to some environmental parameter. The relationship can be quite good. In most instances the real predictive ability of these models cannot be assessed from the literature as the model has generally been elaborated using all the data available and the test of the model in the following years has either not been made or not reported in the literature. Predictive models using a pre-recruit abundance index seem to work better, especially when using juvenile abundance during migration as a predictor. These models can be used to predict total annual catch.

The inclusion of effort as a variable in predictive models might improve their predictive ability in most cases. When long time series of data on the fishery and environmental data known to affect shrimp catch are available, multivariate autoregressive integrated moving average (ARIMA) models could be tried for forecasting. An example of application to crustaceans is given by Fogarty (1984) which shows that annual and monthly catches could be predicted for the Maine American lobster (*Homarus americanus*). This methodology does not seem to have been applied yet to penaeid shrimp.

When detailed information on the biological patterns of migration, recruitment, distribution and spawning, as well as on population parameters of growth and mortalities are available, detailed forecasting is possible when data on recruitment strength of the main generation can be rapidly obtained, for example, through reporting by professional trawlers of their CPUE early in the season. Detailed forecasting of the CPUE and catch structures by month (and possibly by area) and of the likely extension of the profitable fishing season would be very useful for fleet management. The appropriate time structured simulation models are available (based on Y/R models for instance) and are presently used in operations research in a limited number of countries like Australia (Kesteven et al 1981) and Cuba (Baisre 1983). Structuring the models also in the space dimension to predict CPUE by areas could be done in theory when good information is available on the dispersion rate of shrimp from the nurseries to the various grounds. However, in most cases the variability of the spatial structure of the stock may be so high in the short term and so stable (and therefore known to fishermen) in the medium term that the exercise might not be worth its cost.

Alternative models and techniques

The modern trend for tropical fisheries is to make better and more complete use of length frequency distributions for parameter estimations (Pauly et al 1984, Munro 1984). Some of these methods still need further examination to test their sensitivity and accuracy (Majkowsky 1982, Hoenig et al 1983) but the trend will persist and the use of these techniques will be developed in the near future (see for instance Sainsbury 1982). When using length converted catch curves (Pauly 1983, 1984b) or various types of length cohort analyses (Jones 1979, or Jones and Van Zalinge 1979), there is a problem in using an age length relationship (average length for a given age) for calculating the average age for a given length. Jones (1985) points out that the L_∞ values can be biased downwards and suggests some ways of correcting them, as well as adjusting the K values accordingly. Bartoo and Parker (1983) stressed that, using the usual growth curve parameters, the calculated ages for given length are increasingly overestimated as the lengths approach L_∞. Majkowski and Hampton (1983) have shown that, in fact, the errors increase rapidly on both sides of the length frequency distribution, when they are converted to distribution of ages. They state that this leads to errors, for instance, in recruitment indices based on CPUE of small fish. It can be expected that errors in estimates of exploitation rates are also likely to occur. Pereiro and Pallares (1984) show that the bias introduced by inappropriate growth parameters can be very high. The bias could be reduced by starting the backward analysis at a length as close as possible to the upper limit of the length interval for which growth parameters are valid and by using a final length group (l+) for which the lower limit is as far as possible from L_∞.

Sampling produces another difficulty in the application of these methods which often uses stationary (annual) length frequency distributions. In short-lived animals, such as shrimp, the validity of the results depends largely on the representativeness of the annual aggregated size distribution and therefore on sampling. Single monthly size distributions of catches, or aggregated distributions from one single trawl survey cannot be used to estimate mortalities as the essential condition of

Table 1. Estimates of annual natural mortality M and fishing mortality at full exploitation, F_{MSY} (or equivalent) for penaeid shrimp. Z = Instantaneous rate of total mortality, f = fishing effort and q = catchability. SE = standard error.

Area and species	M	F_{MSY} (or equivalent)	Reference (method)
Gulf of Mexico			Rothschild and Brunenmeister 1984
P. aztecus	2.8	(0.36)[1]	(tagging)
P. aztecus	1.8-2.5	—	(average age and regression of Z on f)
P. aztecus	1.8	—	(decline in CPUE of cohorts)
P. aztecus	1.9	1.1[2]	(decline of CPUE)
P. setiferus	2.2	1.5[2]	(decline of CPUE)
Ivory Coast			Garcia 1977a,b
P. notialis	3.0	2.1[3]	(tagging and production modelling)
P. notialis	2.5	1.9[3]	(catch curve, relation Z/f and production modelling)
Madagascar			Le Reste 1978, for M and q; Marcille 1978
P. indicus	2.5	1.3-1.5[3]	(tagging and production modelling)
Australia			Lucas 1974, Lucas et al 1979
P. plebejus	2.4	—	(tagging)
P. merguiensis	2.4	(12.0)[4]	(tagging)
Mean ± 2 SE	2.4±0.3	1.6±0.3	

[1] Unlikely low value for such an old and intensive fishery—not used
[2] Close to full exploitation
[3] Full exploitation
[4] Exceptionally high value—very flat topped yield per recruit curve. Yields level off between 1.8 and 2.4 $year^{-1}$ on their Fig. 4.

equilibrium is not met. Similar problems in sampling length frequency distribution of pandalid shrimp are discussed by Frechette and Parsons (1983). Problems of sampling (of the population by the fleet and of the fleet by the scientist) seem to be largely responsible for a lot of chaotic length frequency distribution series found in the literature and lead to dubious estimates of growth parameters, no matter what sophisticated or objective methodology is used.

Commercial size categories which are used for reporting landings contain similar information but have seldom been used. They could potentially be very useful. They often represent an exhaustive compilation of the size structure of the annual landings and the categories used are standard for most fisheries around the world. The information is very often easily available, at least for the industrial trawl fisheries together with elementary data like catch and nominal effort.

In theory this information could be used for length cohort analysis with unequal time intervals (Jones and Van Zalinge 1979). The additional difficulty here is that when sexes have very different growth rates and therefore different K and L_∞ values, it is not advisable to analyse a mixed catch structure using average growth parameters. The sex ratios within each commercial category should be taken into account in order to split the annual data for mixed sexes into monosex catch structures. A similar procedure applying the size to sex ratio relationship to length frequency data was advocated by Garcia and Albaret (1977) for *P. notialis* (Fig. 9) in Ivory Coast. Such relationships have also been used by Lhomme and Garcia (1984) for *P. notialis* in Senegal and Marcille (1978) for *P. indicus* in Madagascar. These studies show that the sex ratio to size relationships are similar from year to year for a given stock, different from stock to stock and of course from species to species.

The problem of using appropriate growth parameters when studying commercial categories data are similar to those for length frequency data. The Jones and Van Zalinge (1979) method developed in Kuwait has apparently been used up to now only in Kuwait (Mathews and Al Hossaini 1982). It seems to generate excessively high mortality values (Z = 12 to 38 $year^{-1}$ for some species) and

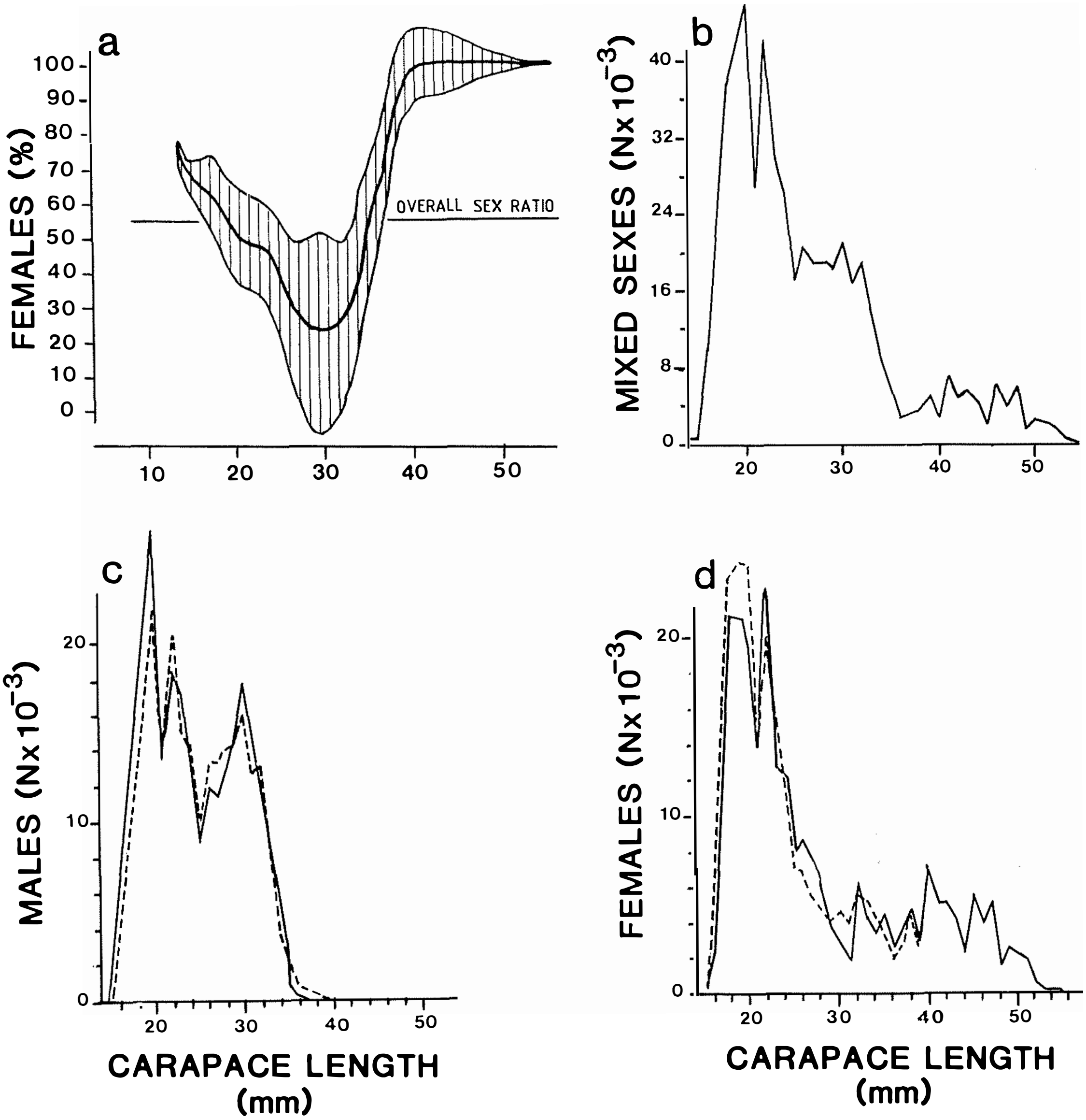

Figure 9. Example of determination of length frequency distribution by sexes from a mixed distribution using a relationship between size and sex ratio. **a.** Size sex ratio relationship (obtained from a one year trawl survey program in 1969). **b.** Mixed sexes distributions of landings in April 1974 (the distributions by sexes are known but have been pooled to test the method). **c.** and **d.** Comparison between the observed (continuous line) and calculated (broken line) distributions (from Garcia and Albaret 1977).

needs more testing in order to assess its practical value.

Comparative population dynamics

Comparative studies could potentially be very useful for tropical regions where a large number of species and stocks and a low number of scientists occur. Some generalisations might therefore provide useful first estimates when data are scarce.

Growth

The Von Bertalanffy model seems appropriate for shrimp (Parrack 1979; Frechette and Parsons 1983) despite the fact that growth in

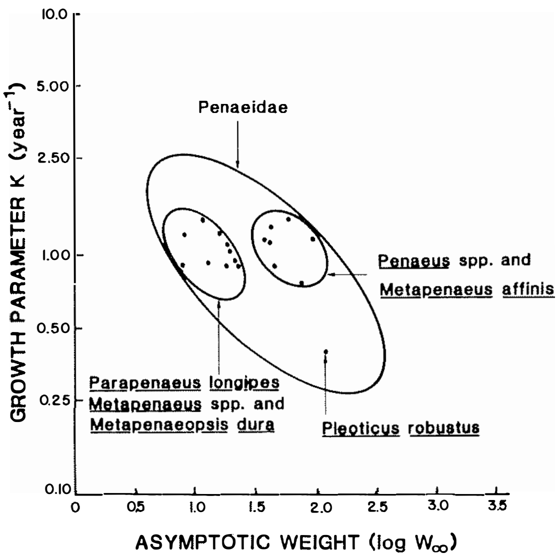

Figure 10. Comparison of growth parameters (K and log W_{∞}) for penaeid shrimps (redrawn from Pauly et al 1984).

crustaceans is not continuous but stepwise. Pauly (1980), Munro and Pauly (1983) Pauly and Munro (1984) have developed simple methodologies for comparing growth. These tools could be used to investigate similarities in penaeid shrimp as in Fig.10. The chain of programs (ELEFAN) applied to shrimp by Pauly et al (1984) can be a useful tool for growth analysis if critically used, especially when seasonal changes in growth are suspected and the seasonal temperature cycle consists of a single annual oscillation (one warm and one cool season of equal duration).

When the growth of females is known, the slower growth of males which is much more difficult to analyse by modal progression may be obtained through the relationship between size of males and size of females in various trawl samples taken at various depths (Fig.11). Comparisons between species or regions could be simplified. Pauly (1984a) showed that different growth curves (with different growth parameters) corresponding to different environmental conditions could be produced with a single set of K and L_{∞} by taking the seasonality of growth into account in a seasonally oscillating Von Bertalanffy growth model.

Natural mortality

Some of the M values obtained in the 1960s which attained 26.4 year^{-1} are clearly unrealistic and the values regularly obtained in the past 10 years by analytical methods are around 1.2 to 5.4 year^{-1} for adult shrimp at sea. Table 1 shows that when the most extensive analyses are considered, values of M are around 0.20 month^{-1} or 2.4 year^{-1} for adult *Penaeus.* The case of the smaller genera (*Metapenaeus, Trachypenaeus, Xiphopenaeus, Parapenaeopsis*, etc.) is less well documented and their most likely values for M are still to be determined. Natural mortality estimates in the juvenile phase are also seriously lacking. Doi (1981) reported a value of M=0.18 month^{-1} for *P. japonicus* and Lucas (1974) gives a value of 0.44 to 0.88 for *P. plebejus.*

Optimum fishing mortality and F_{MSY}

As recruitment is likely to vary from year to year, management may be based on some predetermined effort level. In this case, the value of F corresponding to the level of maximum sustainable yield (F_{MSY}) could be considered a management objective but, because of the general criticism about this parameter (Gulland 1969, Larkin 1977, Sissenwine 1978) it could be considered as a reference mortality level to exceed or not depending on management objectives. A review of F_{MSY} values or equivalents (Table 1) leads to a mean value of 1.6 year^{-1} ± 0.3. This value is lower than the mean value of M=2.4 year^{-1} ± 0.3 in the same papers, confirming the more general conclusion of Deriso (1982) about the relationship between M and F_{MSY}.

Few stocks in the world seem to have experienced levels of F largely above M, perhaps because this is economically difficult. The case of the banana prawn stock in the Gulf of Carpentaria, Australia, with F/Z = 0.78 to 0.86 is in this regard a notable exception (Lucas et al 1979).

Discussion and conclusions

A lot of progress in research has been achieved in the last two decades, particularly for the larger shrimp of the genus *Penaeus.* Some important aspects will remain obscure and more research effort is needed in order to improve our understanding and management ability.

In the first sections of this paper I have insisted on the need to integrate and cross check all the information available in both the time and space scales in order to build up a basic life history model. This information includes: seasonal

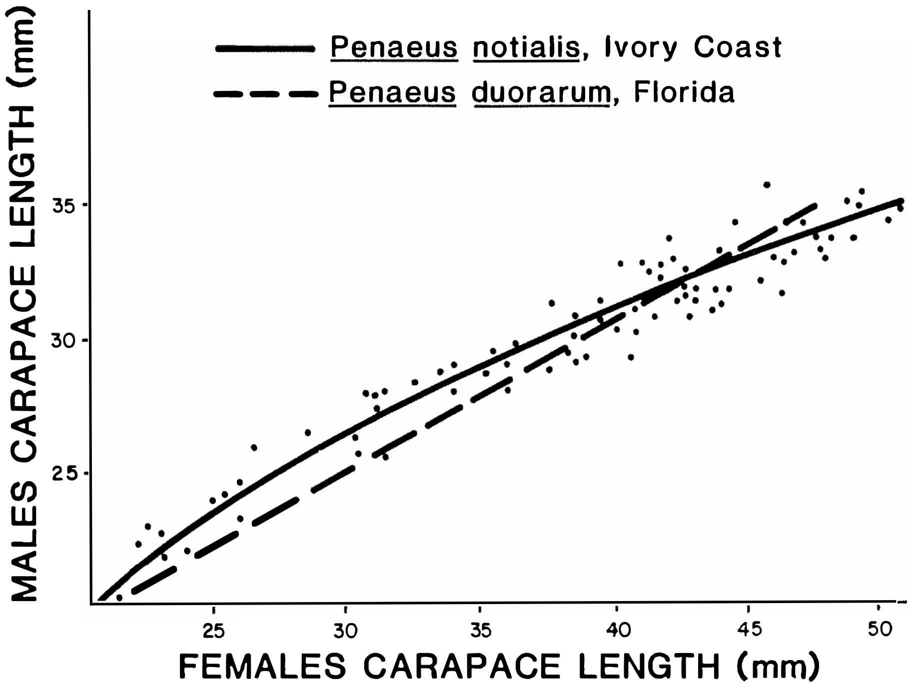

Figure 11. Relationship between mean size of males and females in trawl samples (from Garcia and LeReste (1981). Data for *Penaeus duorararum* from Iversen et al (1960). Dots and solid line indicates *P. notialis,* broken line indicates *P. duorarum*.

variations of recruitment, average size of massive spawning, adult abundance, fishing effort, modal progressions in monthly size frequencies offshore, weekly modal progressions inshore, bathymetric distribution of abundance, and of effort. This integration is important as the information published by different authors on these various aspects for the same stock and fishery are sometimes contradictory.

When a coherent life history model is available, a time structured simulation model should then be produced and tested on its ability to reproduce the observed seasonal patterns and length frequency distributions. It might then, and only then, be used for evaluating the effect of changes in fishing pattern or mortality levels on the population and on the fishery.

The use of a comparative approach could help by bridging the parameter gap for some species. This comparative approach should be fruitful as far as growth is concerned because much data are already available for various species. It is probably useful also for mortality estimates in the genus *Penaeus* but dramatic scarcity of data limits its application for the small shrimp (*Metapenaeus, Xyphopenaeus, Parapenaeopsis,* etc).

The reproduction mechanisms should be studied more intensively, and particularly the link between spawning and recruitment (and vice versa) at the seasonal level. This is necessary in order to understand the stock and recruitment relationship and also to assess the effect of fishing on the spawning potential and reproductive capacity of the stock.

In order to progress rapidly, particular effort should be made on sampling catches for size distributions by sexes and/or improving the present use of commercial categories, together with more and critical use of the length based methodologies. These methodologies need to be tested for sensitivity to error in input parameters and have been particularly scrutinised at the International Conference on the Theory and Application of Length-Based Methods for Stock Assessment organised by ICLARM in Mazara del Vallo, Italy, in February 1985 (Pauly and Morgan unpublished). The proceedings will be published in 1985 in the ICLARM Report series.

The available forecasting models for annual catch for abundance should be tested against time and the results should be published no matter whether they are positive or not. Finally, it must be remembered that a shrimp fishery has a heterogeneous and changing spatial structure which is very important to understand, if serious errors are to be avoided in stock assessment and management. Consequently, surveys (or detailed logbooks) are necessary to map the distribution of the resource and of the effort. The size structure may help identify migration routes sometimes more surely than tagging. The monitoring of concentrations of fishing effort by areas or depth will be fundamental when planning a tagging experiment, when standardising effort for production modelling, when trying to identify age specific fishing patterns and, last but not least, when trying to assess the potential effect of closed seasons or closed areas.

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Appraisal of some factors relevant to the development of penaeid prawn population reproductive models

Abstract: The duration of the ovary stages and the spawning periodicity of *Penaeus esculentus* were investigated. Young adult *P. esculentus* matured and spawned under laboratory conditions without use of artificial induction techniques. Both ovary maturation and spawning occur during one intermoult period, with no evidence of multiple spawning during a single moult cycle. Maturation and spawning during successive moult cycles occurred only with eyestalk ablation. The ripe ovary stage occupied approximately 31% of the intermoult period, with the spent stage apparent for only 6% of the intermoult period. Field observations of *P. esculentus* in Moreton Bay, Queensland, revealed continuous spawning of the population over the lunar month, with no evidence of synchrony of spawning. These findings provide support for assumptions previously made in studies of penaeid reproductive dynamics.

Introduction

The description of spawning seasons and spawning areas have been important components in studies of reproductive dynamics of several commercially important prawn species (Cummings 1961; Rao 1968; Thomas 1974; O'Connor 1979; Penn 1980; Kennedy and Barber 1981; Matthews 1981; Motoh 1981; Crocos and Kerr 1983). Spawning seasons for penaeid prawns have been ascertained in most studies either by changes in the percentage of ripe females in the catch (Cummings 1961; Rao 1968; Chong 1979) or by changes in gonad index (Thomas 1974; O'Connor 1979). These approaches do not take account of the effect of varying fecundity with size of a spawner, or the effect of large seasonal fluctuations in abundance of adults, and therefore numbers of spawners, which occur in penaeid populations. More refined quantification of reproductive output is possible with the use of an index of population fecundity which takes into account both abundance of the spawning population and the contribution of eggs relative to individual female size (Penn 1980; Crocos and Kerr 1983). Calculation of such an index on a temporal and spatial basis provides accurate estimates of spawning seasons and spawning areas.

The use of this method in previous studies, however, involves several assumptions concerning the maturation and spawning process. The method assumes that spawning in the population is asynchronous and that the duration of the ripe ovary stage is less than the sampling frequency. The validity of these assumptions is critical when considering the relationship between the proportion of ripe females recorded in a population and the actual level of spawning activity over a sampling period. If individuals in the population spawn in synchrony, then the sampling period must be determined so as to provide a meaningful estimate of spawning activity. Similarly, if spawning can occur more than once between sampling periods, or if the ripe stage has a duration which may extend over more than one sampling period, then the actual level of spawning activity would be under- or over-estimated, respectively.

In order to refine the population fecundity index model this study examined the possibility of lunar synchrony of spawning, and attempted to establish a time scale for the maturation process of *Penaeus esculentus* from Moreton Bay, Queensland (27° 25'S, 153° 20'E).

Methods

Spawning synchrony

Sampling was carried out during the peak of the October to November spawning seasons of 1981 and 1982 so that the overlying pattern of seasonal variation in spawning activity would not influence detection of any lunar cycle during this period. Up to 40 female *P. esculentus* of reproductively active size (>30 mm CL) were collected from a trawler in Moreton Bay on alternate nights for six weeks during the spawning seasons. On several nights fewer than 40 females were available from the catch so the sample comprised the total catch, otherwise the first 40 females encountered were taken as the sample. Prawns were chilled on ice and returned to the laboratory each morning. Ovary samples taken from the first abdominal segment of each female were prepared histologically and examined microscopically. Five stages of ovarian maturity were distinguished: immature; developing; early ripe; ripe (spawning imminent); and spent (recently spawned) (Crocos and Kerr 1983). The combined proportions of females ready to spawn (ripe ovary stage) and those which had recently spawned (spent ovary stage) were defined as the active spawners in the population. The proportion of females actively spawning was estimated both on a two-daily basis, and also on a lunar-quarter basis by grouping samples from up to three days before and after the lunar quarter. The data were also split into two size groups, 30 to 36 mm CL and >36 mm CL to test for variation of spawning activity with size.

Duration of maturation process

Adult *P. esculentus* were collected by trawling during February 1983 in Moreton Bay and held in the laboratory. Techniques of artificial induction of maturation such as eyestalk ablation were not used to establish ovary stage duration. It was considered that these techniques although accelerating ovarian maturation do not provide representative temporal information on the maturation process. Some eyestalk ablated animals were included for comparative purposes only. Prawns were held in 2 m diameter x 900 mm circular tanks with sand substrate and flow-through seawater at 26° C and a daylength of 14.5 h. Each of three tanks was stocked with five adult immature females (30 to 36 mm CL) and three adult males (30 to 34 mm CL). To compare the temporal maturation response of unablated and ablated females, two tanks were stocked with unilaterally eyestalk ablated females under the same environmental conditions. Stage of ovarian development was monitored by examination on capture three times weekly and, in the case of females showing ovary development, daily, by observation using a strong light in the tank. Females were code-marked by snipping the uropods to allow monitoring of moulting, mating, maturation, and spawning on an individual basis.

Results

Spawning synchrony

Short-term variation in the proportion of active spawners was evident from both the 1981 and 1982 data (Fig. 1), however, no discernible pattern of variation which may have suggested a regular cycle occurred (Table 1). When considered separately, proportions of ripe and spent females sampled on any particular day varied, but once again there was no indication of a regular pattern.

When the data for each lunar quarter were pooled, there appeared to be a relatively constant level of spawning activity for the period of each lunar quarter with no suggestion of spawning in synchrony with the lunar cycle (Fig. 2). Subdivision of this data into two size groups also showed no significant pattern of spawning activity for different sized spawners during a lunar month (Fig. 3). The 30 to 36 mm CL group (predominantly 32 to 36 mm CL) showed a more constant level of spawning activity compared to the larger females (predominantly 37 to 40 mm CL). This variation in the latter group was not statistically significant and probably reflected the lower numbers and slower turnover rate of the large females. Analysis of variance relating proportion of spawners to moon phase, year, and size of prawn showed no significant effects or any suggestion of a spawning cycle within the time period studied (Table 1). Spawning therefore appears to occur at a nearly constant level throughout the lunar month.

Duration of maturation process

Maturation responses

Maturation of females with intact eyestalks followed the temporal pattern summarised in Fig. 4a. Ovarian development beyond the immature stage did not occur until the third or fourth intermoult period ($\bar{x}$ = 3.6 intermoult periods, SD = 0.60, n = 12) after commencement of the experiments. During the first days of the

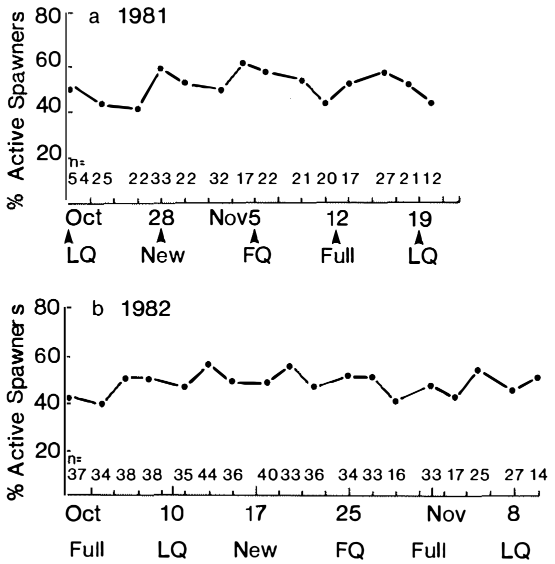

Figure 1. Proportion of active *Penaeus esculentus* spawners during the spring spawning periods of **a.** 1981, **b.** 1982. Arrows indicate lunar quarter dates; New, New Moon; FQ, First Quarter; Full, Full Moon; LQ, Last Quarter. Number of females sampled on each date indicated as n.

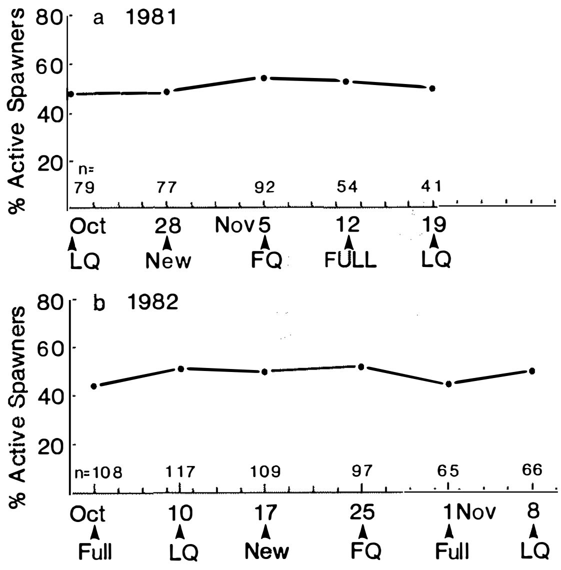

Figure 2. Proportion of active *Penaeus esculentus* spawners by lunar quarter during the spring spawning periods of **a.** 1981, **b.** 1982. Arrows indicate lunar quarter dates. Pooled numbers of females sampled for each lunar quarter indicated as n.

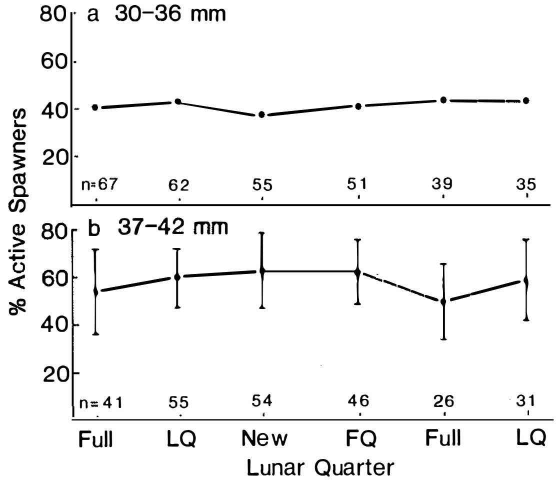

Figure 3. Proportion of active *Penaeus esculentus* spawners by lunar quarter during the spring spawning period of 1982. **a.** Females 30 to 36 mm CL, **b.** Females 37 to 42 mm CL. Vertical bars represent 95% confidence intervals of the mean for each quarter. CL = carapace length; n = number of females.

maturation-moulting cycle, the ovary appeared visually immature. Increase in size and pigmentation of the ovary, indicating the early ripe stage (vitellogenesis), occurred 6 to 11 days ($\bar{x}$ = 8 days) after the moult. Once ovary development began, maturation through the early ripe and ripe stages and spawning, occurred during the same intermoult period. Multiple spawnings within the same intermoult period were not observed. Ovaries were completely spent after a spawn; no partial spawnings were observed. Maturation and spawning in successive moult cycles was not observed in females with intact eyestalks.

Table 1. Analysis of variance relating proportion of *Penaeus esculentus* spawners to moon phase, year, and size of prawn. CL = carapace length.

Source	d.f.	Sums of squares	Mean squares	F-ratio
Proportion versus				
Moon	2	0.0083	0.0042	0.62 NS
Year	1	0.0053	0.0056	0.79 NS
Size				
30 to 36 mm CL	2	0.0149	0.0075	0.43 NS
>36 mm CL	2	0.0761	0.0380	2.42 NS
Interaction				
Moon, Year	2	0.0335	0.0168	2.47 NS
Error	28	0.1896	0.00676	

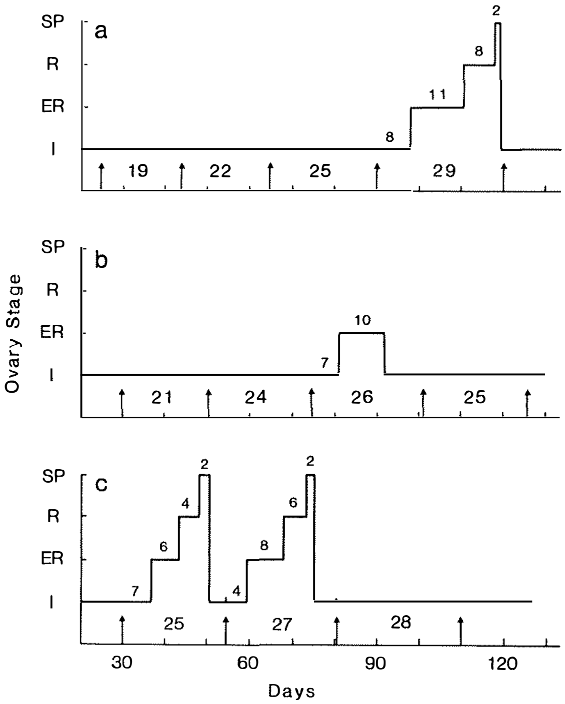

Figure 4. Maturation and spawning responses of *Penaeus esculentus* held in the laboratory. **a.** Maturation and spawning of eyestalk intact females. **b.** Regression of ovary without spawning, after initial development to the early ripe stage. **c.** Maturation and spawning in successive moulting cycles by eyestalk ablated female. I, immature or resting ovary stage; ER, early ripe; R, ripe; SP, spent. Vertical arrows indicate ecdysis, numbers between arrows indicate intermoult period (days), numbers on ovary stage profile indicate days spent at each ovary stage.

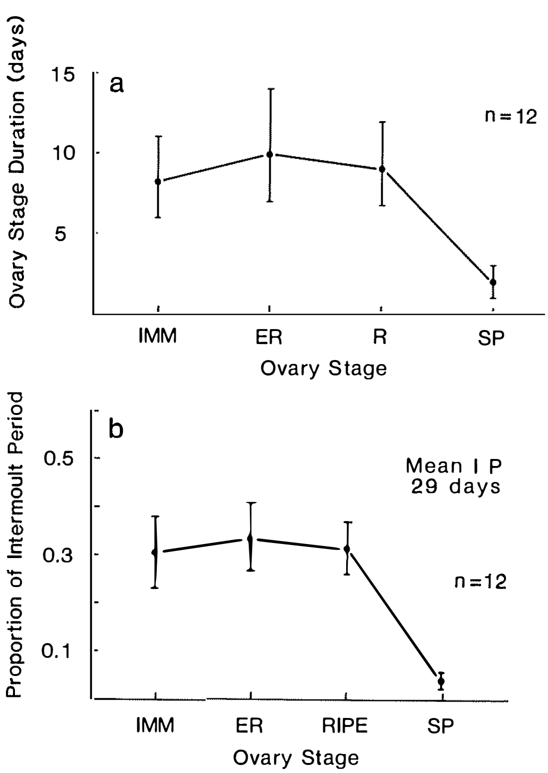

Figure 5. Duration of ovarian developmental stages of *Penaeus esculentus* held in the laboratory. **a.** Mean duration and range of stages (days). **b.** Duration of stages as a proportion of the intermoult period. IMM, immature or resting ovary stage; ER, early ripe; R, ripe; SP, spent. Vertical bars represent one standard error of means. IP = intermoult period; n = number of females.

Commencement of ovary maturation in a particular moulting cycle did not always result in complete maturation and spawning during that moulting cycle. In three out of 15 cases, maturation to the early ripe stage occurred but the ovary regressed to the immature stage without spawning (Fig. 4b).

Maturation of eyestalk ablated females began two intermoult periods ($\bar{x}$ = 2.2, SD = 0.40, n = 10) following ablation. Multiple spawning within a moulting cycle did not occur, but maturation and spawning in two successive moulting cycles was observed for two ablated females (Fig.4c).

Duration of ovary stages

In a maturation cycle, ovaries remained undeveloped for a mean period of 8 days (range 6 to 11 days). The early ripe ovary stage had a mean duration of 10 days (range 7 to 14 days) while the mean duration of the ripe ovary stage was 9 days (range 7 to 12 days). The spent stage was clearly identifiable only by visual inspection for the period following spawning and prior to the ensuing ecdysis, a mean period of two days (range 1 to 3 days) (Fig.5a). For moulting cycles within which maturation and spawning occurred, the mean intermoult period was 28.7 days (SD = 4.06, n = 12), so the immature, early ripe, ripe, and spent ovary stages occupied 28%, 35%, 31%, and 6% respectively, of the intermoult period (Fig.5b).

Discussion

Although lunar reproductive rhythmicity is known to occur among some marine animals (Korringa 1947; Ross 1983) information for penaeid prawns is scant. For *P. duorarum* in Florida, Munro et al (1968) measured relative abundance of first protozoeae larvae over the lunar cycle and used this to estimate the spawning intensity five days previously. An increase in spawning intensity was observed during the last lunar quarter, but this relationship accounted for only 10% of the variation in spawning intensity. Since the moulting cycle and the maturation and spawning cycle in penaeid prawns are related (Crocos and Kerr 1983), it would be reasonable to expect lunar synchrony in moulting if synchrony in spawning was to occur. White (1975) suggested synchrony occurred in moulting of *P. esculentus* in Exmouth Gulf, Western Australia, however, this was at a low level with the percentage frequency of moulting prawns ranging only from 4 to 10% during the lunar cycle. Peaks of moulting did not always coincide with the same phase of the lunar cycle, and the level of moulting activity was less cyclic during the spawning season. Therefore, when the scant evidence of a lunar cycle in moulting, seen by White (1975), is coupled with no evidence of a lunar cycle in spawning, seen in the current study, there is little support for a lunar cycle of reproduction of *P. esculentus.* Rather, turnover of active spawners throughout the month appears to be continuous. If this is the case for other penaeids, this result supports the assumption of lack of synchrony in spawning inherent in the reproductive models used by Penn (1980) and Crocos and Kerr (1983). Therefore, sampling strategies for reproductive studies do not have to account for the timing of spawning periodicity within a particular time frame.

Successful maturation of penaeids in captivity is not straightfoward and requires particular conditions which may vary with species (Primavera 1985). Maturation of *P. esculentus* in this study involved experiments with a range of environmental conditioning regimes, details of which will be reported elsewhere, but basic requirements have been summarised in this paper. The immature, early ripe and ripe ovary stages occupy similar proportions of the intermoult period (28%, 35% and 31% respectively) and the spent stage occupies a relatively small proportion, approximately 6% (Fig. 5a). The duration of the spent stage may, however, have been biased by the definition of this stage used in this study. Due to difficulty of visual recognition of the transition phase between the spent ovary stage and the subsequent resting immature stage, the spent stage was defined as the period between spawning and the next moult. Histological examination of spent stages has revealed persistence of the spent condition for one or two days into the next intermoult period (Crocos and Kerr 1983). Hence the duration of spent stages is probably under-estimated in this study.

Duration of the developed ovary stages (early ripe and ripe stages combined) was reported as 12 to 14 days by Arnstein and Beard (1975) for eyestalk ablated *P. orientalis.* Although this is a shorter duration than observed for the developed stages of unablated *P. esculentus* in this study (14 to 26 days), ablated *P. esculentus* had a combined developed stage duration of 10 to 14 days. This shows that eyestalk ablation accelerates ovary maturation. Also, maturation response of unablated females occurred only after 3 to 4 intermoult periods in the laboratory, whereas ablated prawns responded in the first or second intermoult period after ablation. These differences suggest that use of unablated females in the laboratory would be more suitable for obtaining estimates of ovary stage duration comparable with the situation in the wild. Although maturation and spawning in successive moult cycles was observed only in eyestalk ablated females in this study, the possibility of spawning in successive moult cycles for unablated females cannot be dismissed. Due to the long maturation response time for unablated females (duration of experiments up to 140 days), monitoring of spawners for more than one intermoult period after the first spawn was done for only two of the 12 spawns recorded, so the potential for successive spawning has not been examined thoroughly.

In this study the duration of the ripe ovary stage of *P. esculentus* was approximately 9 days or 30% of the intermoult period. If this result is applicable to *P. merguiensis* then the assumption of ripe ovary stage duration being less than the 28 day sampling frequency used by Crocos and Kerr (1983) is justified. For *P. esculentus,* proportions of ripe stage females, or ripe and spent stages combined (duration of 8 to 15 days), would provide a reliable indicator of spawning activity for a particular month. However, if the combined early ripe and ripe stages were used (14 to 26 days duration) an over-estimate of spawning activity might result as the combined duration might exceed the monthly sampling frequency. This is particularly relevant when the intermoult period may be longer due to lower temperature or for larger sized spawners.

This insight into the temporal aspects of the maturation and spawning process thus provides a better basis for the design and interpretation of the results of field based reproductive studies of penaeid prawns. Early studies relying on the percent frequency of ovary stages to estimate spawning activity without a knowledge of ovary stage duration, and therefore turnover of spawners (Cummings 1961; Rao 1968; Thomas 1974; Chong 1979; Motoh 1981) were prone to over- or under-estimate the actual level of spawning activity, and could only describe broad trends of reproductive output. Furthermore, use of seasonal trends of percentage gravid females in a population has been shown to be insufficient to ascertain seasonal patterns of reproductive output (Penn 1980; Kennedy and Barber 1981; Crocos and Kerr 1983). Development and refinement of a population fecundity index based on a more precise estimate of active spawners, and which takes account of abundance and relative fecundities of spawners, has provided for a more meaningful description of the population reproductive dynamics.

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Stock recruitment relationships for the tiger prawn, *Penaeus esculentus,* fishery in Exmouth Gulf, Western Australia, and their implications for management

Abstract: An unusual reduction in the catch of tiger prawns, *Penaeus esculentus,* from the Exmouth Gulf multispecies prawn fishery has been investigated. Examination of the interaction between the stock to recruitment relationship (incorporating environmental variables) and the alternate recruitment to spawning stock relationship for the tiger prawn stock has indicated that the combination of normal environmental conditions and high levels of effective effort as occurred in the post-1979 period was responsible for the fivefold decline in catch from 1980 to 1982.

Management measures involving total protection of the spawning stock and severely reduced fishing effort on recruits are described and early indications of a recovery in recruitment are reported. Long term management options for reducing effective effort are discussed and the implementation of an industry funded buy-back scheme to remove vessels is noted.

Factors including the vulnerability of tiger prawns to trawl capture, the bioeconomic effects from the multispecies nature of the fishery and the past history of limited entry management, which have contributed to the ability of fishing to influence future recruitment in the Exmouth Gulf fishery are discussed.

Introduction

Although the relationship between stock and recruitment is considered fundamental to management of fisheries (Gulland 1978), such relationships have received little study for penaeid prawns because clear cases of recruitment overfishing of penaeid stocks have not been reported (Garcia 1983).

However at the FAO workshop on the scientific basis for the management of penaeid shrimp (Key West, Florida) in November 1981 (Gulland and Rothschild 1984) a number of papers expressed concern that recruitment overfishing may now be occurring. These papers were later extensively reviewed by Garcia (1983) who concluded that to date none of the available data provided a satisfactory example of a penaeid stock recruitment relationship (SRR). Since 1980, however, there have been significant declines in the level of catch from the two major stocks of *Penaeus esculentus* in Shark Bay and Exmouth Gulf on the Western Australian coastline (Fig. 1). This situation in the Exmouth Gulf stock has proved particularly suitable for the study of SRR, and a detailed analysis of the data from the fishery has shown relationships between spawning stock and recruitment and recruitment to spawning stock (RSR). (Penn and Caputi in press).

The specific purpose of this paper has been to examine the roles of fishing effort and environmental factors in the SRR and RSR and to report on the management measures being used to assist the fishery to recover to its former production levels.

The Exmouth Gulf fishery commenced in 1963 based on daylight fishing for schooling banana prawns, *P. merguiensis,* but changed to an entirely night fishery for tiger prawns, *P. esculentus,* as banana prawn catches declined. Since 1968 virtually no banana prawns have been taken, leaving tiger prawns as the dominant species in the fishery up to 1981. The fishery also produces significant but generally smaller quantities of western king prawns, *P. latisulcatus,* and endeavour prawns, *Metapenaeus endeavouri* (Table 1).

Table 1. Catch in tonnes (heads-on) and effort (actual hours trawled) in the Exmouth Gulf from the start of fishing in 1963 to 1984. NM indicates no market,* includes effort data for both day and night fishing, S indicates small catches of <1000 kg.

Year	Catch (t)				Thousand hours trawled	Maximum no. of vessels
	Penaeus merguiensis	*Penaeus esculentus*	*Penaeus latisulcatus*	*Metapenaeus endeavouri*		
1963	52	15	1	NM	1.8*	12
1964	60	34	17	NM	2.1*	6
1965	57	135	16	NM	8.4*	13
1966	39	421	72	NM	11.1*	15
1967	22	704	41	NM	16.7*	17
1968	S	212	167	NM	17.7*	17
1969	S	473	77	105	26.2	17
1970	S	888	208	295	38.8	20
1971	S	234	135	150	29.7	20
1972	S	673	364	210	45.0	22
1973	S	596	278	277	47.3	22
1974	1	515	206	223	41.5	22
1975	2	1239	312	450	45.1	22
1976	17	745	233	286	49.7	22
1977	1	639	341	237	51.0	22
1978	S	882	377	423	54.4	22
1979	S	572	272	328	51.1	23
1980	S	647	216	191	52.7	23
1981	S	320	298	256	46.7	23
1982	S	116	374	239	42.2	23
1983	S	77	309	268	37.9	21
1984	S	167	316	252	38.5	17

The Exmouth Gulf fishery

The fishery has been subjected to controlled expansion since 1965, when a system of limited entry management was introduced (Bowen and Hancock 1982). Initially 15 licences were issued, followed by increases to 17 in 1967, 20 in 1970, 22 in 1972, and 23 in 1979.

During the early years of the fishery, vessels were generally converted rock lobster vessels which trawled for prawns during their winter off season. This practice ceased after 1971 when rock lobster vessels were no longer permitted to operate in the fishery and the fleet was replaced with specifically designed, more efficient prawn trawlers of approximately 19m in length. Another major change in efficiency also occurred in the mid to late 1970s, when all of the existing trawlers were equipped with Kortz propeller nozzles which increased towing power by 20 to 30%. This allowed higher trawl speeds and therefore higher levels of effective effort. During the same period (1975-76) mechanical prawn peeling machines were introduced which allowed previously unprocessable small prawns to be caught and marketed. This allowed the fishery to start earlier each season and for fishing to be more concentrated on small prawns in the nursery areas. A further increase in efficiency of the fleet occurred in 1980-81, when four large trawlers of 23 m in length entered the fishery as replacements for smaller vessels. The record high international prices for tiger prawns in 1978 and 1979, and the existence of a Federal government subsidy for building vessels above 21 m in length, undoubtedly contributed towards the move to larger vessels by competing vessel owners.

As a result of the poor catches experienced in 1981 and 1982, a number of the larger trawlers left the fishery early each season. In 1983, two vessels did not fish at all during the year, and in 1984 this number increased to 6.

Methods and materials

Data collection and processing

Measurement of the abundance of prawns in Exmouth Gulf has been based on daily catch and effort recorded in research logbooks, with the catch adjusted by the end of trip landings. Since 1970, all trawlers have completed research logbooks and provided landing statistics to give an approximate 95% coverage of reliable data. Prior to 1970, and particularly during the early years 1963 to 1967 when both day and night fishing occurred, the catch rate data were less reliable and have therefore not been used in this study. However the total landings by species has always been reliable, because essentially all of the catch has passed through two local shore based factories from which accurate records were available.

The procedures for calculating indices of abundance from raw logbook records and landed weights have been given in Hall and Penn (1979). These involve standardisation of fishing effort (method of Gulland 1956) by adjusting fishing power for each species, so that hours of fishing in each year are comparable with the 1973 level. The standardised effort and catch data have also been used to calculate the effective effort applied to the tiger prawn stock each year using a method described in Hall and Penn (1979).

Biological data on sizes of prawns and spawning condition of females have been obtained from both routine factory samples and research charter vessel survey records. (Penn and Caputi in press). The factory sampling project has been run in parallel to the research logbook program throughout the history of the fishery (Bowen and Hancock 1982).

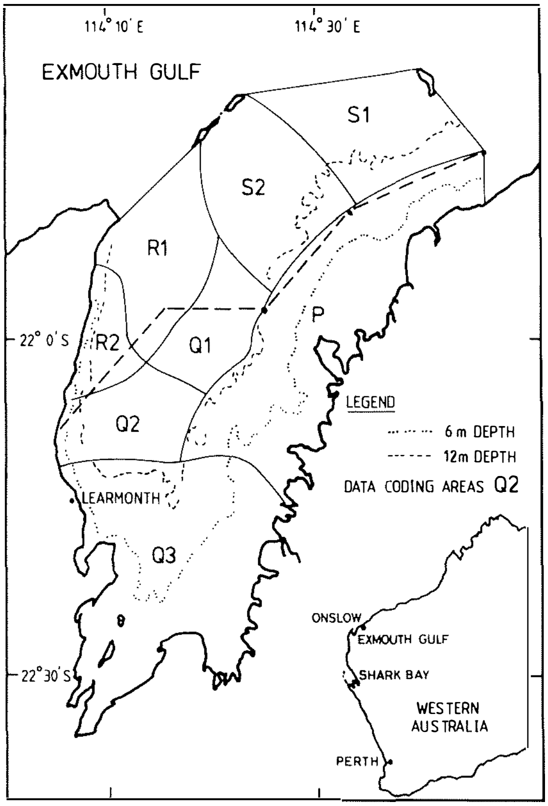

Figure 1. Exmouth Gulf showing the fishing ground coding areas and the temporary closure line (---) introduced in August 1982 to protect stocks of the tiger prawn, *Penaeus esculentus.*

Spawning stock indices

An important feature in the analysis of the tiger prawn fishery is that it can be regarded as a single unit stock within Exmouth Gulf. The nearest significant population of the same species is in Shark Bay (Penn and Stalker 1979) 300km to the south and tiger prawns are unknown along the intervening coral reef coastline. To the north, small catches of tiger prawns are occasionally taken, but they are generally too small and too remote (200km) from Exmouth Gulf to be expected to have any impact on the recruitment.

Data on spawning cycles for the Exmouth Gulf tiger prawn stock in the early years of the fishery have been reported by White (1975). A peak in spawning activity by 0+year class prawns (ie 10 to 12 months old) was found to occur in the August to October period of each year. More recent surveys (1975, 1977, 1982 to 1984) of spawning stocks have confirmed and extended these observations. The more recent data shows that the spawning season begins in July-August of each year and continues through summer at least until the identity of the age group is lost in March when the new recruits appear in the catches. The distribution of the spawning stock in October when the proportion of spawning females reaches a peak is primarily in the 13 to 20m depth zone in the centre of the Gulf (Fishing area Q1, Fig. 1).

During the August to March period, individual female tiger prawns are considered to undergo a series of spawnings, as has been shown for another penaeid (*P. latisulcatus*) in Exmouth Gulf (Penn 1980).

To produce an index of the spring spawning stock, Penn and Caputi (in press) have used the mean catch rate from the Q1 fishing ground for the months of August, September and October each year. The months after October when spawning was still in progress were not included because of the lack of sufficient commercial catch data for this period in early years. Since 1982 when the area was closed to fishing, the index has been based on survey catch data (60h trawling per month). Spawning indices for 1970 to 1983 are given in Table 2.

Recruitment indices

The major period of tiger prawn recruitment to the trawl grounds resulting from the spring spawning begins in February and extends to May each year. During this time large numbers of small (approximately six months old) tiger prawns are caught commercially on the shallowest trawl areas (5 to 11 m) along the eastern border of the Gulf (Fishing areas P and Q3 on Fig.1). This distribution of prawns has been independently verified by research vessel survey data which showed that newly recruited prawns are restricted to the eastern shoreline and that individual size increases with depth as they migrate towards the north central section of the Gulf (Q1 area).

To obtain an index of recruitment to the fishery Penn and Caputi (in press) have selected the average catch rate (kg per standardised hour) in the Q3 fishing area for the months of March, April and May each year as being the most reliable recruitment index for the stock (Table 2). However since 1982 when fishing on recruits was restricted, the index was based on April and May catch rates.

Environmental data

The stock under study is located in an open marine embayment on a desert coastline (mean rainfall 292mm, mean rain days 23 and mean evaporation 1070mm annually; Bureau of Meteorology unpublished weather records) which provides a relatively stable hydrological environment, not affected by any significant river flow into the Gulf.

The only major exception to this environment stability, which may affect the postlarval to juvenile phase of the life history, is the occurrence of occasional severe tropical cyclones during summer and autumn. These events are responsible for all of the major rainfalls during summer and autumn, and in addition generate heavy wave action and coastal flooding due to the tidal surge related to the extremely low barometric pressure. Severe cyclones producing in excess of 200mm of rainfall occurred only twice in January and February and three times in March over the past 31 years. Rainfall values for Learmonth (Fig.1) during January and February (the critical recruitment period) for the years of the study, 1970 to 1984, are included in Table 2.

Results and discussion

Stock recruitment relationship

A Ricker (1975) stock recruitment curve adjusted by rainfall using multiple regression techniques was fitted, resulting in the following equation (Fig.2)

$$RI_t = 3.71\, SI_{t-1} e^{(0.053\, SI_{t-1} - 0.0029\, RJ_t + 0.0030\, RF_t)}$$

Table 2. Spawning stock, recruitment, and cyclone indices for the Exmouth Gulf stock of tiger prawns, *Penaeus esculentus,* for the years 1970 to 1984. The spawning index is for the months August to October in fishing area Q1 (Fig.1), the recruitment index is for March to May in area Q3, and the cyclone index is the monthly rainfall at Learmonth in the Gulf.

Year	Spawning Index	Recruit Index	Cyclone Index Jan.	Cyclone Index Feb.
70-71	18.0	9.9	353	19
71-72	5.7	19.1	0	1
72-73	12.8	21.0	1	5
73-74	10.0	18.5	102	22
74-75	8.2	37.5	0	213
75-76	24.0	26.8	23	38
76-77	10.1	22.1	2	1
77-78	10.4	26.9	4	10
78-79	11.3	19.2	0	0
79-80	7.4	19.7	14	41
80-81	6.0	12.4	18	19
81-82	3.2	7.1	85	28
82-83	2.4+	9.3+	0	0
83-84	3.9+	16.3+	0	54

+indicates preliminary estimates including survey data for March when there was no commercial fishing.

where RI_t is the recruitment index of year t, SI_{t-1} is the spawning stock index of the previous year, and RJ_t and RF_t are the rainfall (mm) occurring in January and February respectively just prior to the recruitment to the trawl grounds in March-April. The fitting of the equation to the data resulted in a multiple correlation coefficient of 0.97 and residual mean square of 0.030. The parameters of the equation are all significant at the 0.001 level except for the February rainfall parameter whose significance level was 0.008. The significance of the January and February rainfall parameters is mainly due to the cyclones which occurred in 1971 and 1975 respectively. The reason for rainfall having both positive and negative values in the equation, is that cyclone related environmental factors appeared to have the potential to both increase and decrease recruit survival depending upon the timing of the cyclone.

In physical terms, cyclones passing through or near Exmouth Gulf have a number of effects on the nursery environment which may alter prawn survival. For example: cyclones cause heavy rainfall and runoff which alters salinity and increases turbidity; wind generated waves disrupt the coastal zone; and the associated tidal surge causes widespread flooding over a

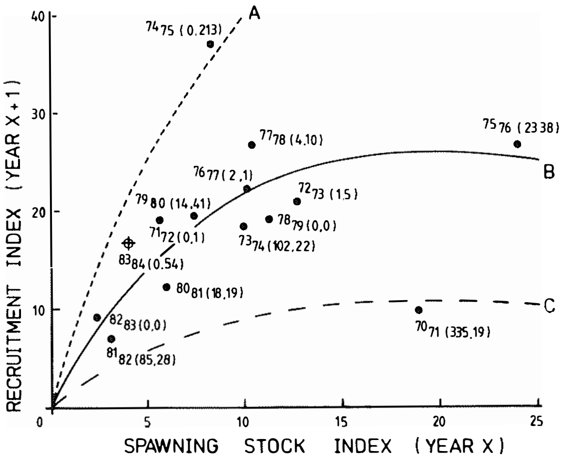

Figure 2. The relationship between spring spawning stock, autumn recruitment and January and February rainfall for the Exmouth Gulf stock of the tiger prawn, *Penaeus esculentus.* Preliminary data for 1983-84 is shown ⊕

short period. In terms of survival, these changes in the environment (apart from increased turbidity) appear likely to have a detrimental effect on the small juveniles when they are concentrated in the shallow subtidal nursery areas presumably occupying a typical seagrass habitat (Young and Carpenter 1977). After the juveniles have moved offshore into 5 to 11 m depths, usually in February each year, cyclone effects are less likely to cause mortality and in fact the increased turbidity is likely to be beneficial in reducing predation.

We have used January and February rainfall as independent variables, and although the end of January appears as the reversal time for the effect of rainfall (cyclone) having a negative and positive effect, in reality, a clear or static change over time is unlikely. Factors such as the spread of recruitment over time, the timing of the tidal cycle in relation to the calendar year, preceding growth rates etc, would all be expected to be important. In addition, the effects of individual cyclones, particularly the strength of the tidal surge and wind waves can vary with the direction from which the cyclone approaches the Gulf. As a consequence when considering the validity of the environmental factors in the equation it should be noted that the relationship is largely determined by two extreme data points (1971 and 1975). The only other major early cyclone in the history of the fishery occurred on 21 January 1967 (361 mm rainfall) outside of the period of the present data set. This cyclone, however, corresponded to a good tiger prawn catch of 704t (Table 1) which adds further emphasis to the uncertainty of this factor in recruit survival. Because of the foregoing uncertainty about the effects of severe cyclone activity and the rarity of such events during the 14 years of the present data set, the environmental aspects of the relationship have been suggested as a working hypothesis until more data are available. That is, severe cyclones may be expected to cause significant departures (in either direction) from the predicted recruitment from a given breeding stock. It should be noted however, that during the overall downward trend in recruitment and spawning stock during the post-1975 period, no unusually severe cyclone event has occurred.

In evaluating the spawner to recruit relationship fitted to the data, possible biases in the spawning stock and recruitment indices as well as environment indices need also to be considered. These include any effect of bias in the measure of effort, the possibility of auto correlations in the yearly data as described by Garcia (1983), the impact of effort expended during the periods used to calculate indices of SI and RI etc. These factors have been discussed in detail by Penn and Caputi (in press), but they have not been found to present significant difficulties in this particular data set.

In summary, Fig.2 shows that there is a strong relationship between stock and recruitment when rainfall is taken into account but that rainfall was dominant in only two of the 14 years of the study. In the average rainfall situation the recruitment is a direct function of spawning stock levels.

Recruitment spawning stock relationship

To complement the spawning stock recruitment relationship given in the previous section, the relationship between recruitment each year, effective effort on recruits (ER) and resultant spawning stock in spring later that year was determined as

$$SI_t = c\,(RI_t)e^{-d\,ER_t}$$

This resulted in the parameters c and d taking values of 1.27 and 0.0232 (S.E. 0.0075) with a multiple correlation coefficient of 0.94 and residual mean square of 0.052. The parameter associated with effective effort (d) was significant at the 0.01 level. The raw data points for the period 1970 to 1983, and predicted effort lines representing 40 and 60 effective effort

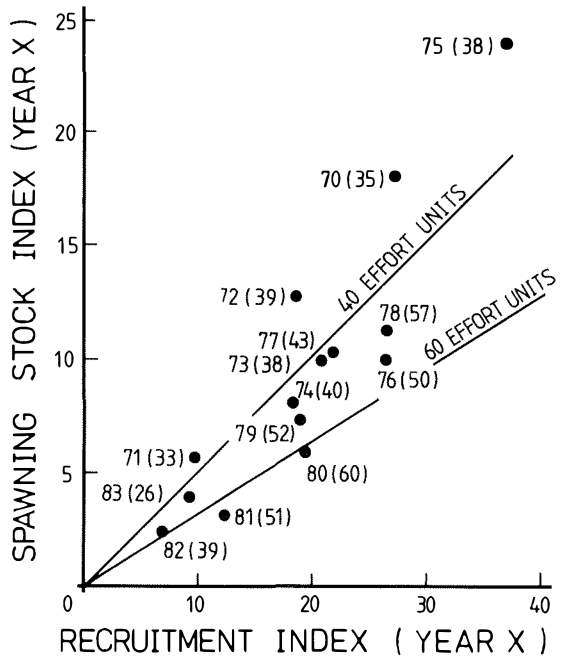

Figure 3. The relationship between recruitment, effective fishing effort (recruitment to spawning season) and resultant spawning stock for the Exmouth Gulf tiger prawn, *Penaeus esculentus*, stock from 1970 to 1982. Year and effective effort units are given as: 1970(35).

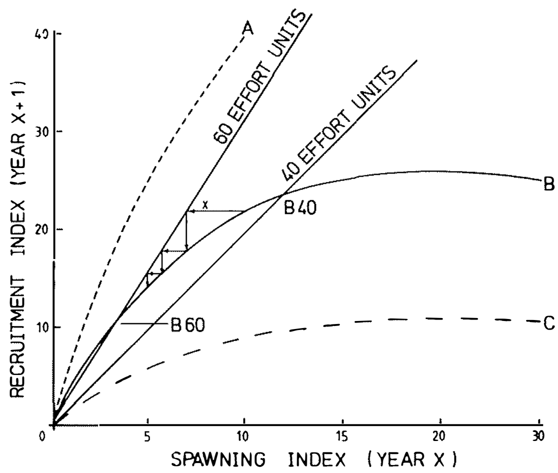

Figure 4. The interaction between the two relationships, stock to recruitment and recruitment to spawning stock from Exmouth Gulf stocks of the tiger prawn, *Penaeus esculentus*. Two levels of effort units are indicated. B is the predicted curve for the most common environmental conditions, A is for most advantageous and C for the least. Line X shows the direction of movement of the relationship under constant high effort relative to curve B.

units are given in Fig. 3. This relationship shows that for any given year, the effect of increasing effort from a low level (40 units) to a high level (60 units) on a given level of recruitment can be expected to reduce the spawning index by approximately 37%.

Examination of the residuals in the recruitment to spawning stock equation does, however, indicate that a number of the raw data points do not fit the equation particularly well. These years 1970, 1972, 1975, 1978, on closer examination were all found to be years when the recruitment was late ie higher recruitment catch rates occurred in May, than in March. However, the addition of a further parameter to correct for this bias was ruled out at this time, because of the shortness of the data set. Other potential sources of bias in the relationship include: the assumptions of both constant natural mortality (M) and catchability (q) from year to year during the period from recruitment to spawning; the possibility that there may be increases in vessel efficiency not fully accounted for in the standardisation of effort; and the problems related to redistribution of effort with the advent of the prawn peeling machine in 1976. These sources of possible bias in the relationship have been considered unlikely to radically alter the significance of the RSR. (Penn and Caputi in press).

Although most of these factors are accounted for in the RSR relationship (Fig. 3) by the use of effective effort in the regression, effective effort cannot be used directly for management purposes. In practice, any decision to reduce effective effort can of necessity only control actual hours fished and/or the distribution of effort on the stock.

Management implications

An understanding of the interaction between the SRR and RSR relationships is fundamental to the development of a management strategy to optimise effort levels applied to the stock. For this purpose the relationships provided in Figs. 2 and 3 have been combined (Fig. 4) along the lines of Garcia's (1983) proposed stock recruitment surface model which takes into account natural (environmental) variability in recruitment levels.

Fig. 4 illustrates the interaction between the two relationships (SRR and RSR) at two effective effort levels. These data suggest that under the most common environmental conditions of little rainfall ie less than 100mm, in either January or February (predicted curve B) which occurred in 12 of the past 14 years, the maximum effort level which could allow stable recruitment to occur is of the order of 40. At higher levels of effort ie near 60 as occurred in 1978 to 1980, the SRR curve under normal conditions (curve B) intersects the effort line corresponding to 60 units only at very low levels of stock and recruitment (B60). At this level of effort and typical conditions of environment, recruitment level (and hence spawning stock size) can be expected to move towards this point B60 near zero with each passing year (line X starting at spawning index of 10 on Fig. 4).

However, if advantageous environmental conditions such as those in 1975 (ie curve A) were to occur continuously, then effective levels in excess of 60 units could still allow high but stable recruitment to be maintained. Conversely under continuously poor environmental conditions (ie curve C) an equilibrium situation could be maintained only at effort levels of less than 40 units.

In the event of a once only low recruitment such as occurred in 1971, the data (Fig. 4) suggest that for the stock to recover quickly an appropriately low level of effort would be required in that year and in one or two following years if normal environmental conditions returned. This in fact occurred naturally in 1971 (Table 1). Similarly in the event of a single, unusually high recruitment as occurred in 1970 an increased level of effort could be applied to maximise the catch, but only in that year. If however, effort is not increased in this situation, as happened in 1970 there is a considerable safety margin in spawning stock levels and a significant carry over catch (1+ year prawns) for the following season as has occurred before (White 1975).

Before using these relationships for management purposes, it must however be recognised that although the Exmouth Gulf environment is particularly stable and the basic relationships are highly significant statistically, there is variation about each line which makes precise prediction difficult. In the case of the SRR, however, additional years of data should provide more information about the predictability of curve B, but will have little impact on the curves representing the levels of recruitment related to extreme cyclone events which have occurred only three times in the history of the fishery. However, in the case of the effort lines on the RSR (40, 60) the degree of confidence in the lines should improve more rapidly with additional years of data. Also further work on this relationship both to improve the vessel standardisation (fishing power) methods and the measurement of effective effort is being undertaken.

Because the occurrence of a cyclone is an infrequent event, a practical management strategy for the stock can be based only on the average environmental situation (curve B in Fig. 4), but with contingency plans to decrease effort when low recruitment levels occur. Appropriate effective effort levels for the future when the breeding stock has recovered would be around the 40 unit level, which should, under typical environmental conditions, maintain the stock at about position B40 ie a recruitment index level of approximately 23 and a corresponding spawning index of approximately 11. To translate such a recruitment index into an expected recruitment catch at that effort level, a relationship between RI, recruit catch and effective effort is required. Work to refine this relationship is yet to be completed, however in practice past catch records can be used directly to indicate the likely level of equilibrium recruitment catch. Years which generally fit the recruitment index, effort situation described by the B40 point (Fig. 4) were 1973 and 1977, when recruit catches of approximately 360t were taken in the period between recruitment and spawning. The total tiger prawn catch taken in each year (Table 1) however, also comprises catch taken after mid-September, some carry over of 1+ year prawns and possibly some early recruitment of individuals spawned in autumn (March to May) of the preceding year. These catches would add to the catch taken between recruitment and the middle of the spawning season.

Because the spawning stock was low in 1982 (Fig. 2), management of the Exmouth Gulf stock since then has been directed at rebuilding the spawning stock. This has been achieved by direct area closures (the area south and east of broken line, Fig. 1) to protect both spawners and recruits. Although the general closure introduced on 15 August 1982 has been maintained to the present time (May 1985), restricted fishing ie roster fishing by one third of the fleet per night, was allowed for short periods during the recruitment season of April to May 1983 and April to June 1984. While the biological optimum solution may have been a complete closure of the fishery until spawning stock recovered (Clark 1976), this phased approach, which has resulted in a slower rebuilding of the breeding stock, did allow for some tiger prawn production which supplemented the catches of king and endeavour prawns and maintained the viability of the fleet in the interim. The level of fishing effort allowed on tiger prawns since 1983 has been determined primarily from the relationship given in Fig. 4 and from similar relationships between catch rates at a series of points in time between the recruitment period and spawning.

The impact of these management measures to date was an initial decrease in catch during 1983, which resulted in a near doubling of the spawning stock index in spring 1983. In 1984, recruitment levels increased by a factor of 2 over 1983, due to both improved spawning stock levels and environmental conditions which allowed a catch of 167t while leaving the SI at approximately 7. This progression suggests that with continuing controls on fishing effort and average environmental conditions the recruitment levels should return to the pre-1979 levels by the 1986 fishing season. At that stage management measures aimed at stabilising the effective effort level close to 40 units will be needed to maintain spawning stock and recruitment levels in the range of the mid-1970s, without the need for continuing the present difficult system of roster fishing. Mechanisms for long-term effort reduction being considered include:

(1) A later opening date for the start of the season, which will move the catching period back towards the spawning season.

(2) A proposal to firstly reduce gear sizes and then to reduce vessel numbers by allowing amalgamation of gear entitlements which would allow the remaining vessels to have greater fishing power and efficiency.

(3) A direct reduction of vessel numbers by an industry funded buy-back scheme.

A buy-back scheme was implemented in February 1985 and four vessels have been removed permanently from the fishery to bring the fleet size down to 19 vessels.

General discussion

Although a number of penaeid stocks have suffered recruitment variations which may have involved recruitment overfishing (Penn 1984) satisfactory SRRs have yet to be accepted for these species (Garcia 1983). The documented SRR for tiger prawns (Penn and Caputi in press) is therefore unusual, but does provide an opportunity to look for more general features in the Exmouth Gulf fishery situation which may help identify other stocks susceptible to recruitment overfishing.

One such feature of the Exmouth Gulf fishery is the apparent differences in resilience to the high effort levels, of the two major species in the fishery. In the absence of significant tiger prawn stocks during the period 1981 to 1984, fishing pressure was largely redirected at the second most valuable species, the western king prawn, in the northern sector of the Gulf, without any apparent decline in yield (Table 1). This difference in the response of western king and tiger prawns to fishing pressure, was however anticipated from previous behavioural studies in the mid-1970s (Penn 1984). This work indicated that tiger prawns were likely to have a higher vulnerability to trawl capture than king prawns, making them more susceptible to fishing pressure. A further observation in Penn (1984), that banana prawns, *P. merguiensis*, were likely to be considerably more vulnerable to fishing pressure than tiger prawns is also noteworthy in the present circumstances, since banana prawns on which the fishery initially developed in 1963 have not been commercially significant since 1967 (Table 1).

Another factor of general importance which appears to have contributed to this specific case of recruitment overfishing, was the existence and distribution of the two alternative species. Those species, combined with the catch of tiger prawns in individual trawl shots, allowed for example, fishing of the concentrated tiger prawn spawning stock down to the minimal catch rates of approximately 2 kg h^{-1} in 1982 (when fishing was unrestricted). Effectively, the western king prawn provided a subsidy which allowed effort to continue to reduce the tiger prawn stock during the recruitment decline. In a similar way, the past history of profitability due to the limited entry management of the Exmouth Gulf stock (Bowen and Hancock 1982) has also indirectly provided a financial subsidy for continued fishing after stock levels had declined. In an open fishery situation, the low recruitment catch rates of early 1982 would probably have resulted in a movement of vessels out of the area and prevented the severe reduction in spawning stock achieved by the following spring.

The preceding features of the Exmouth Gulf fishery are of general interest in the further understanding and identification of stocks which may be susceptible to recruitment overfishing. Their direct impact however, on the Exmouth Gulf tiger prawn stock, has been to alter the usual balance (Garcia 1983) which frequently favours environmental factors over spawning stock in the control of recruitment levels. There is little doubt that this unusual situation in Exmouth Gulf has contributed significantly to our ability to illustrate a relationship between spawning stock and recruitment. In practical terms the present study has however now shown that the possibility of recruitment overfishing of penaeid stocks can no longer be disregarded in management terms. As observed by Walters and Ludwig (1981) 'in the long term view of management it is simply irrelevant to comment that recruitment can often be predicted more accurately from environmental factors than from spawning stock, because it is the spawning stock which can be controlled through management decisions'.

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Modelling the recruitment processes of the banana prawn, *Penaeus merguiensis,* in the southeastern Gulf of Carpentaria, Australia

Abstract: Two approaches have been used to address the problem of identifying the main factors which have caused the wide year-to-year fluctuations and downward trend in catches of *Penaeus merguiensis* since 1974 in the Karumba region of the southeastern Gulf of Carpentaria. Firstly, the year-to-year variation in catch was examined and related to environmental variables. Secondly, detailed data on the population dynamics of postlarvae, resident and emigrating juveniles, were collected and related to both environmental and biological variables. In both studies the importance of rainfall in determining the strength of recruitment into the offshore fishery was recognised. Juvenile prawns were observed to emigrate from the estuarine nursery areas in response to increased rainfall, smaller prawns requiring heavier rainfall to stimulate their migration. As a result, within the observed range of juvenile densities, the number of emigrants was higher in years of increased rainfall and was largely independent of the number of resident juveniles. A multistage model which described the stock recruitment relationships between the four main life history stages incorporated the combined effects of rainfall and juvenile numbers. Testing the model against the catch and rainfall data for the last 14 years suggested that both spawning levels and juvenile densities have remained sufficiently high for rainfall to be the most important factor in determining offshore catches. The multistage model has provided a useful tool for examining the possible effects of lower spawning stocks and juvenile abundances, but at present, the long term trends in catches and short term predictions for the future can be made on the basis of a simple catch rainfall model.

Introduction

All penaeid prawn populations are characterised by large year-to-year variations in yield although it has been suggested that those species which utilise estuaries as nursery areas for the juvenile phase are subjected to the widest fluctuations (Kirkegaard 1975). Catches of banana prawns, *Penaeus merguiensis,* in the Karumba region of the southeastern Gulf of Carpentaria (Fig. 1) have ranged from 3854t in 1974 to 333t in 1983 (Somers and Taylor 1981 and data of Commonwealth Department of Primary Industry, Canberra). Catches have shown a downward trend since 1974. During the life cycle of a penaeid prawn, many biological and environmental factors affect the survival of the various life history stages both prior to and after the commercial fishing season. The effect of fishing adds an additional mortality factor which affects adults and subsequent population fecundity. Each life history stage is spent in a different environment and the relative importance of the many inter-related biological and physical factors will vary for the different stages. It is, therefore, rather surprising that several successful predictive models based on the relationship of the offshore catch to one or two environmental variables have been developed. Environmental factors include temperature, (Williams 1969; Barrett and Gillespie 1973, 1975 and Hunt et al 1980), rainfall (Gunter and Edwards 1969; Ruello 1973; Le Reste 1980 and Vance et al in press) and river discharge (Subrahmanyam 1966; Barrett and Gillespie 1973, 1975 and Glaister 1978). These models depend heavily on one or two driving forces in the system which presumably control the survival of earlier life history stages. Although useful in short term forecasting, the models contain little information on the mechanisms which cause the population fluctuations. They also assume that there is no relationship between the stock density of one generation and the recruitment of the following generation. Stock recruitment models, on the other hand, which assume that the number of recruits is fixed at some earlier life history stage and ignore subsequent biological and environmental effects would also appear to be rather limiting. The success of these models especially in cases where recruitment is related to spawning stock 6 or 12 months earlier (or in some analyses to the level of recruitment in the previous year) is rather dubious (examples given by Morgan and Garcia 1982; Rothschild and Brunenmeister 1984 and Changcheng 1984). As pointed out by Garcia (1983) the relationships could easily be artefacts of serial changes in environmental variables. Obviously the more closely related the life history stages (for example, postlarvae and juveniles) the more chance that their abundances are correlated in some predictable way but this is not necessarily the case. To fully understand the dynamics of penaeid populations it is becoming increasingly obvious that a combination of both environmental effects and stock recruitment relationships must be considered (for an example see Penn and Caputi 1985). It is also important to consider all life history stages, and sound biological data on the underlying recruitment mechanisms must be considered before the relationships can be accepted.

The life history of *P. merguiensis* in the southeastern Gulf has been described in detail by Rothlisberg et al (1985). Two peaks in spawning activity occur each year; one in spring (September to November) and the other in autumn (March to April) (Crocos and Kerr 1983). Seasonal changes in offshore currents, coupled with the vertical migratory behaviour of larvae, however, result in a proportionally higher percentage of the larvae reaching the estuaries in spring than in autumn (Rothlisberg et al 1983). Most of the larvae spawned in autumn appear to be lost to the system. Following a juvenile period of one to three months the prawns originating from the spring spawning emigrate offshore during the summer monsoonal period (Staples 1980b and Staples and Vance in press) and recruit into the fishery from January to May. Thus, although the generation time is six months, and two main cohorts of larvae are produced each year, the effective life history is an annual cycle starting with spawning in spring, a juvenile phase in summer, and an offshore young adult phase in autumn. Commercial fishing effort concentrates on the autumn prawns during their first spawning season. The escapement from the fishery provides the spring spawners which initiate the next annual cycle.

A study of *P. merguiensis* was started in 1975 to determine the causes of the wide fluctuations and downward trend in catches of this species in the Karumba region of the southeastern Gulf. Two approaches to the study were used. In the first approach, the variability in catches was examined and correlated with a range of environmental variables (Vance et al in press). In the second approach, detailed data were collected on the abundance of immigrating postlarvae, resident juveniles and emigrants in the Norman River in the southeastern Gulf from 1975 to 1979 (Staples and Vance 1985, in press). The results of this latter study were extended by Staples (unpublished data) who added results on juvenile abundances collected by Hynd (1974, unpublished data) and spawning stocks to develop a multistage recruitment model which examined the relationship between each stage of the life history. The model incorporated both stock recruitment relationships and the effect of environmental factors into the analysis of catch variability. The present paper presents an overview of the whole study, and then examines the significance of the findings with respect to the commercial fishing for *P. merguiensis* in the southeastern Gulf of Carpentaria.

Materials and methods

Environmental data

Most environmental data for the examination of *P. merguiensis* catch variability were obtained from the Australian Bureau of Meteorology (Australian Bureau of Meteorology, Melbourne). Factors examined included rainfall, temperature, river discharge and wind speed and direction. For the complete analyses published by Vance et al (in press), the Gulf of Carpentaria was divided into six regions corresponding to the six statistical commercial catch regions (Fig. 1). This paper summarises results for the Karumba region in the southeastern corner of the Gulf. Details of analyses and methods of significance testing are given by Vance et al (in press).

Postlarval and juvenile sampling

Sampling techniques used to estimate postlarval and juvenile *P. merguiensis* abundances are described by Staples (1980a, b) and Staples and Vance (1985, in press). A fixed station 2 km upstream from the mouth of the Norman River

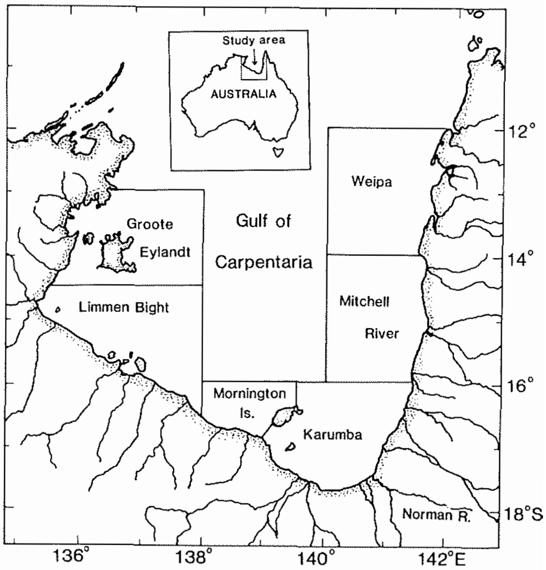

Figure 1. Gulf of Carpentaria showing the six statistical regions used for recording catches of the banana prawn, *Penaeus merguiensis.*

(Fig. 1) was sampled weekly for juvenile prawns from September 1975 to September 1979 using a 1 m wide beam trawl with a 2mm mesh net and 1 mm mesh codend. Sampling was conducted at the time of low tide when catchability is at a maximum (Staples and Vance 1979). Juvenile catches expressed either as no. min^{-1} or no. m^{-2} trawled, averaged over the period from September to December were used as an index of juvenile prawn abundance. Set net sampling during this four year period also provided estimates of both the immigration rate of postlarvae and the emigration rate of juveniles. Postlarvae were sampled using an array of 0.5 x 0.5 m plankton nets of 1 mm mesh suspended from buoys near the estuary mouth during the flood tide. Immigration rate was calculated as no. h^{-1} caught during the period of maximum tide flow. Set nets measuring 1.0 x 0.5 m fitted with a 2 mm mesh were deployed during the ebb tide and the no. m^{-2} h^{-1} caught in the surface waters was used to describe the emigration rate of juveniles from the estuary.

Adult and spawning stock estimates

Annual yield estimates for the Karumba region have been given by Somers and Taylor (1981) for 1970 to 1979 and the Commonwealth Department of Primary Industry, Canberra, for later years. Estimates are based on total landing figures for the northern Australia prawn fishery apportioned into regional catches on the basis of logbook statistics. Average logbook return rate was 58% of the fleet for 1970 to 1979. Because the fishery is extremely seasonal and has been heavily exploited since the early 1970s (Lucas et al (1979) estimated an exploitation rate of 85% for the period 1974 to 1976) the total catch rather than the catch per unit effort was considered a better indicator of recruitment and adult abundance. Under these circumstances any changes in effort will be reflected in the length of the fishing season not the total catch taken. Estimates of the spring spawning stock were also obtained from logbook records for the period September to November each year. Although fishing in the Karumba region during this period is mainly for tiger prawns, *P. esculentus*, incidental catches of *P. merguiensis* are recorded in logbooks. The spawning index was estimated by the average catch of *P. merguiensis,* in kg boat-day^{-1}, of tiger prawn fishing during September to November.

Results

Environmental catch relationships

Vance et al (in press) found a significant positive correlation between summer monsoonal rainfall and the following autumn catch of *P. merguiensis* in the Karumba region of the southeastern Gulf of Carpentaria, from 1970 to 1979 (Fig.2). Including data for more recent years, the correlation is now $r=0.864$, d.f. = 13, $P<0.01$ and explains about 75% of the observed variation in catches. The introduction of other environmental variables through the use of multiple regression analyses failed to significantly increase the level of explained variation. This does not mean that other factors are not involved but simply that the present data and techniques employed could not detect them. Although catches followed rainfall fairly closely in most years, the catches of 1972 and 1976, in particular, were considerably lower than expected. The ecological studies described in the following sections attempted to further explain the causes of the year-to-year fluctuations especially in the years when rainfall alone gave poor predictions.

Ecological studies

When the postlarval immigration rate, resident juvenile population abundance, spawning stock index and rainfall of the previous year for the period 1975 to 1979 were all compared, Staples and Vance (1985) found that all these variables were closely associated (Fig. 3). Postlarval

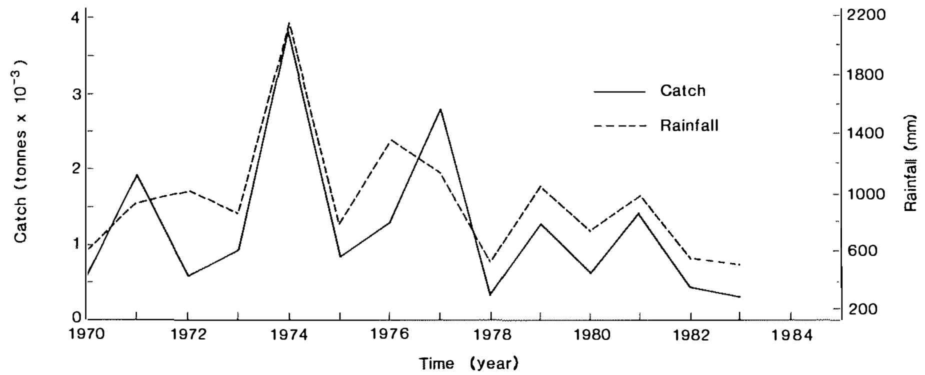

Figure 2. Catch of *Penaeus merguiensis* and rainfall for the Karumba region of the southeastern Gulf of Carpentaria, 1970 to 1983.

immigration and resident juvenile abundance increased following years of higher rainfall. Spawning stock followed similar trends with high abundance in 1976-77 and low abundance in 1978-79 following the dry year of 1977-78. As both adult abundance and rainfall are themselves highly correlated (Vance et al in press), the effects of the two variables on postlarval immigration cannot be separated empirically. As a predictive tool, however, the suggested relationship between spawning stock and subsequent juvenile abundance warranted further examination.

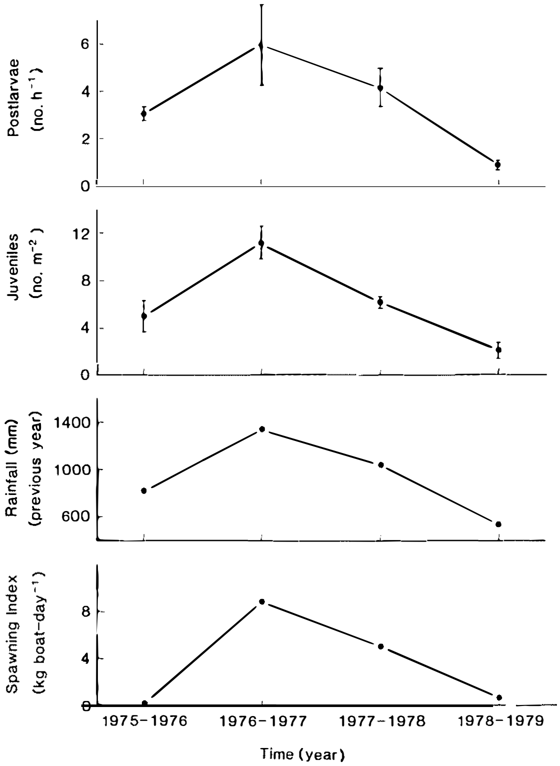

Figure 3. Year-to-year variation in postlarval immigration and juvenile abundance of *Penaeus merguiensis* in the Norman River from 1975 to 1979 shown together with annual rainfall of the previous year and index of spawning for the Karumba region of the southeastern Gulf of Carpentaria. Vertical bars indicate ± standard error of the mean. (Data from Staples and Vance 1985).

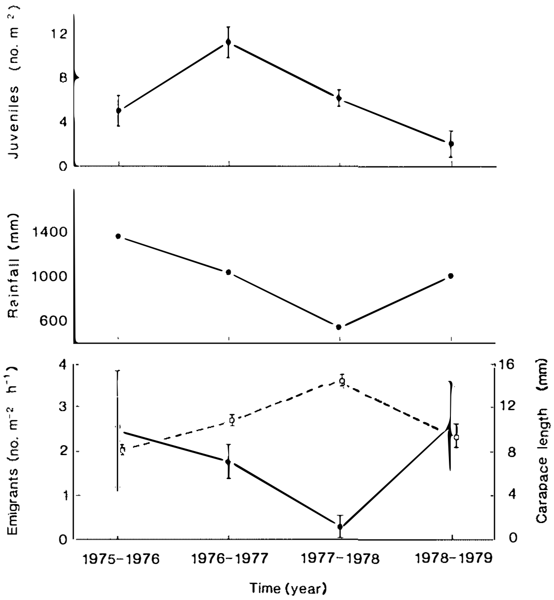

Figure 4. Year-to-year variation from 1975 to 1979 in the abundance of juvenile *Penaeus merguiensis*, annual rainfall, rate (●) and size (□) of emigrating juveniles from the Norman River. Vertical bars indicate ± standard error of the mean. (Data from Staples and Vance in press).

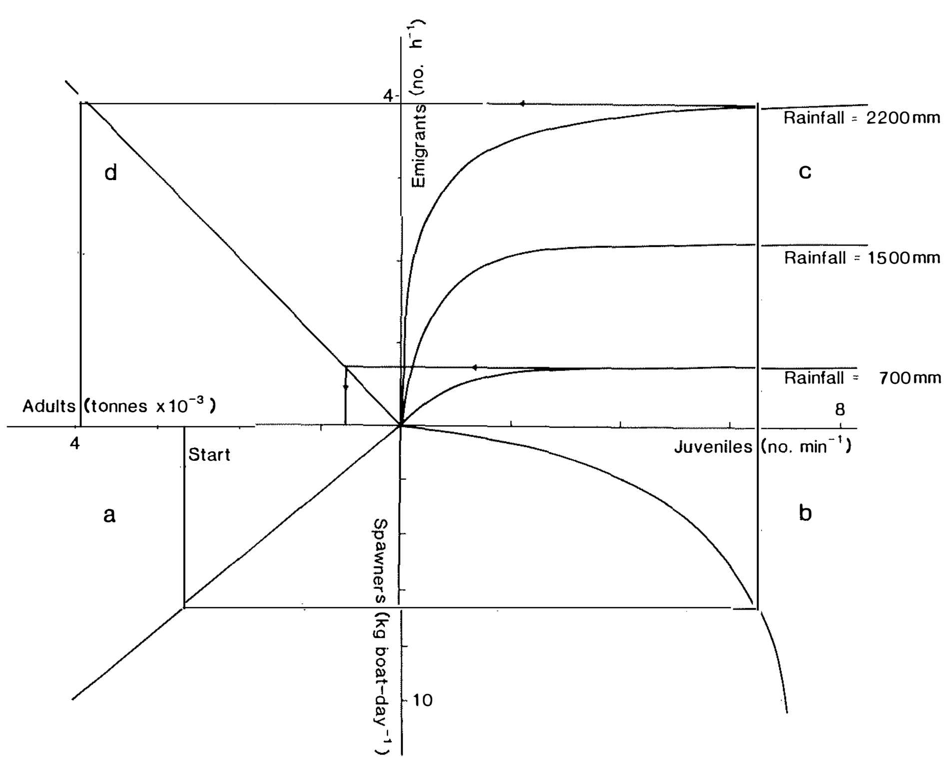

Figure 5. Multistage recruitment model for *Penaeus merguiensis* showing relationships between **a.** Adult catch : spawning index **b.** Spawning index : juveniles **c.** Juveniles : emigrants and **d.** Emigrants : adult catch in the Karumba region of the southeastern Gulf of Carpentaria. Solid line with arrows traces the changes in relative abundance through each stage of the life cycle.

After two to three months in the estuary, the number of juveniles emigrating from the Norman River depended largely on the amount of rainfall recorded during the summer wet season of the same year (Staples and Vance in press) and appeared to be largely independent of the abundance of resident juveniles in the estuary (Fig. 4). Thus the highest emigration rates occurred during the 1975-76 and 1978-79 wet seasons, despite the relatively low number of juveniles resident in the estuary. The lowest emigration occurred during the dry year of 1977-78. However, whereas the number of emigrants increased with increasing rainfall, their mean size decreased (Fig. 4). In years of lower rainfall only a few larger prawns emigrated, whereas in wetter years, a much larger proportion of the resident population, including small juveniles, emigrated. Over the ranges of resident population sizes seen during the four years, it was the proportion of the population that emigrated, rather than its absolute size which determined the strength of the offshore migration. However, this conclusion must be restricted to years of relatively high juvenile densities (zero juveniles must result in zero emigrants) and Staples and Vance (in press) suggested an asymptotic function to describe the juvenile to emigrant relationship which allows the number of emigrants to be dependent on both the abundance of resident juveniles and rainfall at low juvenile densities, and mainly rainfall at higher juvenile densities.

Staples and Vance (in press) also showed that the commercial catch in the Karumba region fluctuated in accordance with the changes in the emigration rate of juveniles from the Norman River estuary during the study period.

Multistage model

The relationships between each successive life history stage described on the basis of the short term biological data on postlarvae and juveniles collected from 1975 to 1979, were further expanded by incorporating estimates of juvenile numbers and adults obtained during the early 1970s. The relationships considered were (Fig. 5):

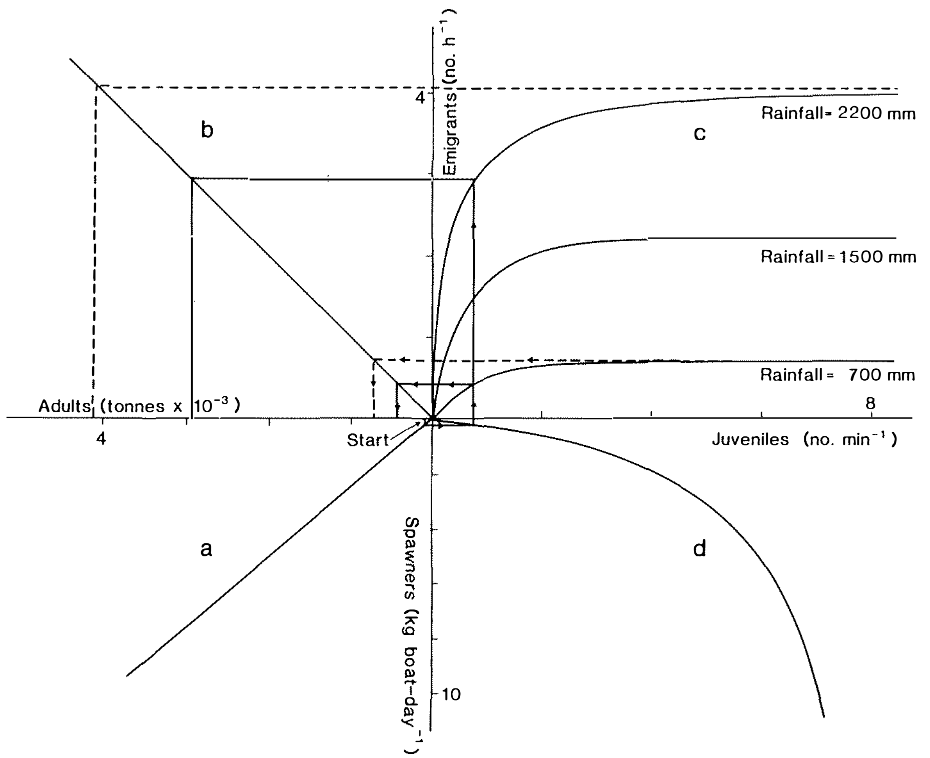

Figure 6. Multistage recruitment model for *Penaeus merguiensis* showing depressed estimates of emigrants and adult catch (solid lines with arrows) compared with rainfall predictions resulting from low initial adult stocks and spawners (broken lines).

a. adult catch : spawners which was approximated on the basis of a simple linear model, b. spawners : juveniles fitted as a hyperbolic curve (Beverton and Holt 1957), c. juveniles : emigrants using a modified Ricker stock recruitment curve (Ricker 1975) and d. emigrants : adults which was again approximated by a simple linear regression. Details of fitting each of these relationships will be published elsewhere. When combined, the relationships between each of the four life history stages can be used to describe the population changes throughout an annual cycle. The model suggests that when the adult catch of any year is large, both the spawning stock and subsequent juvenile populations will also be large (Fig.5a, b) but the number of emigrants and the size of the next year's catch will be largely determined by the amount of rainfall occurring during the juvenile stage of the life history (Fig.5c, d). With a range of rainfall from 700 to 2200mm the catch will range from approximately 750 to slightly less than 4000t. When the catch of one year is small, on the other hand, the resulting low density of spawners and juveniles will depress the adult stock to levels below those expected on the basis of rainfall alone (Fig.6). In the case of very small catches in one year, the population can enter a downward spiral where each subsequent year's catch is below that of the preceding year.

Using the recorded rainfall and commercial catch of *P. merguiensis* as inputs into the model, the relative abundance of spawners, juveniles, emigrants and subsequent catch of the following year were estimated. In all years, the estimated juvenile population on the basis of the strength of the previous season's estimates of adult stock and spawners remained relatively high and the model gave predictions which did not differ markedly from those made on the basis of rainfall alone ($r=0.865$, d.f.$=13$ for the multistage model compared with $r=0.864$, d.f.$=13$ for the rainfall model) (Fig.7). From the multistage model the expected catches for the low catch years of 1972 and

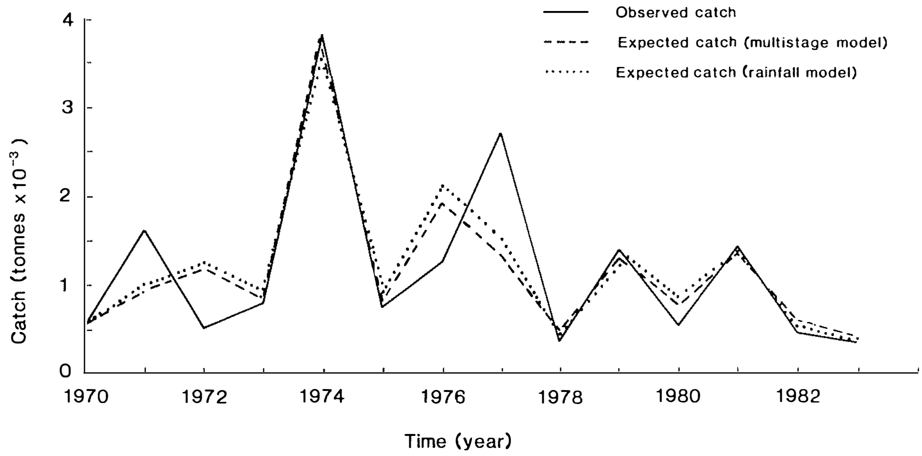

Figure 7. Observed and expected catches of *Penaeus merguiensis* in the Karumba region of the southeastern Gulf of Carpentaria estimated from the rainfall and multistage models.

1976 were only slightly closer to the actual catch than those expected on the basis of rainfall alone.

Discussion and conclusions

The main aim of this study was to identify and describe the factors affecting the year-to-year variation in the catch of *P. merguiensis* in the Karumba region of the southeastern Gulf of Carpentaria. Both a simple correlative approach and a detailed ecological study have identified the driving force of the system to be the monsoonal rainfall. In the first approach, the close link between rainfall and catch was demonstrated and in the second, the mechanisms underlying the correlation were identified and the effects of other biological and physical factors examined. Development of the multistage model combined all the known information on each life history stage of *P. merguiensis* and provided a better explanation of the importance of the rainfall effect. The multistage model indicates that provided the level of spawning and subsequent juvenile population numbers are relatively high, the catch of the next year is determined largely at the juvenile estuarine stage and can overide any previous relationships between spawning stock and juvenile numbers. Only in years of reduced spawner and juvenile abundances will the number of emigrating juveniles and recruitment into the fishery be affected by the number of resident juveniles. In these years, catches will be lower than the expected catch based on rainfall data. Using the model to estimate expected catches using catch and rainfall data for the past 14 years gave similar results to those produced by the simple rainfall model. This comparison suggests that spawners and resident juvenile prawn numbers over the past 14 years did not fall to levels at which their low abundance affected catches. The exact juvenile abundance at which a significant influence will be felt, however, is difficult to determine from the existing data. The present model is based on the results for only nine years of catch and juvenile abundance estimates. It indicates that densities have to fall to levels well below those previously observed before they markedly affect catches, an important conclusion which requires further substantiation. Further support was provided by the detailed ecological studies which showed that although juvenile numbers varied by a factor of four between 1975 and 1979, the emigration and offshore catches behaved quite independently of these fluctuations. In view of the present evidence, therefore, it seems valid to use the simple rainfall model to examine trends in the fishery and make predictions about future catches.

When the residuals of the rainfall model (difference between expected catch and the observed catch) were examined over time (Fig. 8), no long term trends were evident. The decline in catch seen over the past nine years, therefore, can be adequately explained by a similar decline in rainfall over the same period. For short term forecasting it is also possible to modify this model to include total rainfall up to the end of January which enables prediction of the catch six to eight weeks before the opening

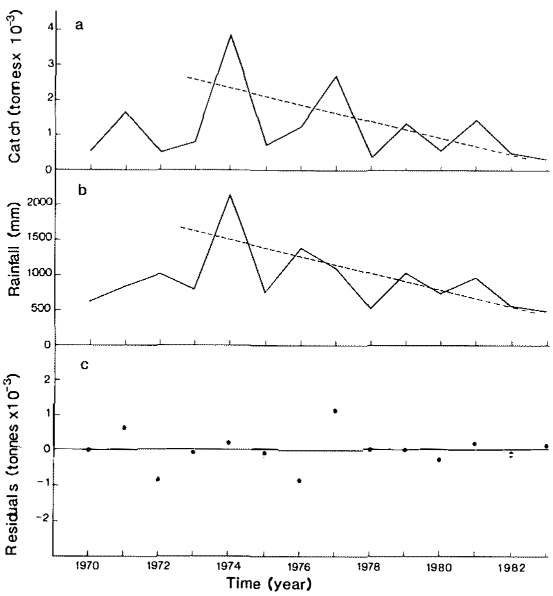

Figure 8. Long term trends in **a.** Catch of *Penaeus merguiensis* in the Karumba region of the southeastern Gulf of Carpentaria **b.** Rainfall over the same period and **c.** Residuals (difference between expected catch on the basis of rainfall and actual recorded catch). Trend in catches and rainfall shown by broken line. (Redrawn from Vance et al in press).

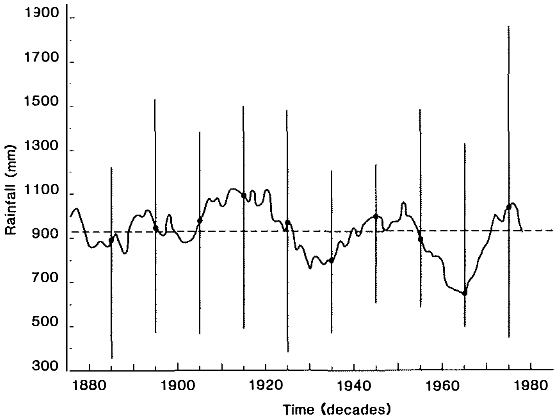

Figure 9. Five year moving average of rainfall in the Karumba region of the southeastern Gulf of Carpentaria for the period 1880 to 1980. Mean and ranges of rainfall observed for each decade shown by solid points and vertical bars. Broken line indicates 100 year mean.

of the fishing season. These predictive relationships are given by Staples et al (1984) and Vance et al (in press). The trends in rainfall were also examined over longer time scales and some speculation on long term catches of *P. merguiensis* are possible (Fig.9). Rainfall during the 1970s was slightly above the 100 year average and the decade also experienced one of the widest ranges of rainfall observed this century. Nicholls (1981) has observed that rainfall in northern Australia can be predicted from long term barometric changes observed in northern Australia and therefore from the Southern Oscillation Index (Quinn and Neal 1983) but no definite cycles in rainfall could be detected from the long series of rainfall data. Expectations of the industry were greatly influenced by the catches of 1974, but the likelihood of a high rainfall similar to that of 1974 occurring in the immediate future appears to be small. Providing spawning stocks and juvenile prawn densities are not reduced further by overfishing, future *P. merguiensis* catches in the Karumba area can be expected to fluctuate between 200 and 2500t with an average of 1100t.

The significance of the more complicated multistage model becomes more apparent if we consider what could happen if recruitment overfishing occurred in the Gulf. The rainfall model provides an estimate of catch based on rainfall alone. If the actual catch falls below the lower 95% confidence limit of the prediction, the model indicates that low spawning stocks and juvenile densities are involved and appropriate management measures may need to be implemented. Following the low rainfall experienced since 1982 and 1983, the rainfall and catch predictions of 1984 were of particular interest. Rainfall in 1984 was 772mm, which although below the long term average was an increase over the past two years. Preliminary estimates for 1984 indicate that catch has also increased although the catch was only just above the lower 95% confidence limit of the predicted value. Given the combination of a low rainfall over the past few years and a very high exploitation rate, the situation in the Karumba region of the Gulf of Carpentaria requires close monitoring in the future.

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Maximising value per recruit in the fishery for banana prawns, *Penaeus merguiensis*, in the Gulf of Carpentaria

Abstract: A computer model is described which is used to analyse the relationship between monetary value per recruit and opening date of the fishing season for banana prawns, *Penaeus merguiensis*, in the Gulf of Carpentaria. The model requires input on the size composition of the fishable stocks, prevailing market values for the various size grades, rates of exploitation during the fishing season, and rates of growth. If the size composition of the stock can be ascertained prior to the fishing season and the other inputs are known, then it is possible to set an opening date which results in maximum revenue. Attempts have been made to assess the size composition of banana prawn populations in the Gulf of Carpentaria prior to the fishing season. These attempts, which have met with mixed success, are also described.

The model has also been used to analyse length frequency data from the banana prawn fishery so that value per recruit could be expressed as a function of opening date rather than size at first capture. This analysis has shown that despite marked regional and annual variability, if value per recruit in this fishery was to be maximised via a fixed annual opening date, that date would be in mid-April.

Introduction

Maximising yield per recruit is an objective common to most managed fisheries. Although, in theory, it is possible to manipulate yield per recruit through controls on fishing effort and on length at first capture, in practice it is usually only the latter which is feasible. An increase in fishing effort in a fully developed fishery may result in a marginal gain in yield per recruit but this is usually more than offset by the increase in costs of fishing. In the Gulf of Carpentaria fishery for banana prawns, *Penaeus merguiensis*, (Fig. 1), seasonal closures have been considered the most appropriate means of achieving an appropriate length at first capture (Anon. 1982).

Although regulations governing closures were implemented in the banana prawn fishery from as early as 1971, these were aimed more at protecting spawning adults than achieving a maximum yield per recruit. The closed areas and periods varied from year to year although in general the opening date for the fishing season was in mid-March (Anon. 1982).

Lucas et al (1979) carried out a yield per recruit analysis using the model of Beverton and Holt (1964) and data collected from the fishery during the period 1974 to 1976. As most of the catch from the fishery was exported and the monetary value per kilogram varied with the size of prawns, the authors extended this analysis to obtain the corresponding measure of export revenue or value per recruit. Estimates of length at first capture were obtained which would provide maximum export revenue under the prevailing levels of fishing mortality and market values by size grade. The temporal distribution of average prawn size obtained from commercial catch sampling was used as a guide for selection of the best seasonal closures for the fishery. With the observed variability in average size of banana prawns, the authors could find no reason to change from the mid-March opening for the fishing season.

This paper describes further modification of the value per recruit model which allows direct assessment of optimal opening date from the

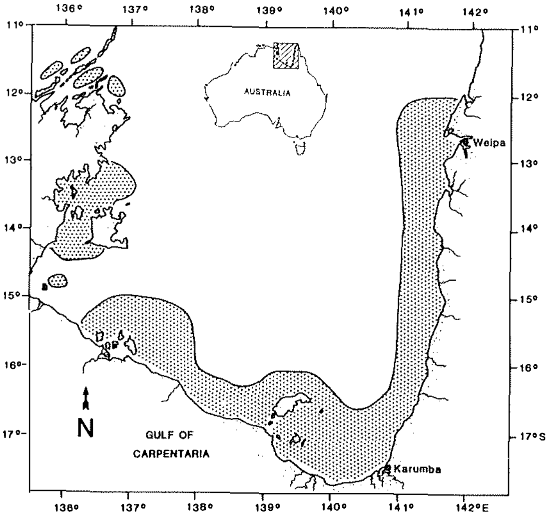

Figure 1. Gulf of Carpentaria showing the major fishing grounds for banana prawns, *Penaeus merguiensis.*

size composition of the stock rather than from a comparison of the average size with the previously determined length at first capture. The model has also been made more flexible than the simple Beverton and Holt model in that fishing effort need not be assumed as constant and that growth rates for the two sexes may be considered separately. In applying this model to the banana prawn fishery, monetary value per recruit has been reassessed using 1981 levels of fishing effort and relative market values current at the time of the assessment.

The size composition data used in the application of the computer model have come from two sources. In the first instance, commercial catch size composition data from the period 1974 to 1979 have been used to provide a more precise and up to date picture of the annual and regional variability of optimal opening dates for the fishery. As well as this application, attempts have been made to obtain the size composition of the fishable stock through a preseason survey of the fishery, thereby using the model to calculate the appropriate opening date prior to the commencement of the fishing season.

Development of the model

The original yield equation developed by Beverton and Holt (1957) was of the form—

$$(1)\quad \text{Yield} = \int F N_t W_t \, dt$$

where F = instantaneous fishing mortality coefficient
N_t = number of prawns alive at age t
W_t = weight of an individual prawn at age t

N_t is described by the negative exponential model—

$$(2)\quad N_t = Re^{-M(t_c - t_r) - (F+M)(t - t_c)}$$

where R = number of prawns which recruit to the fishery at age t_r
M = instantaneous natural mortality coefficient
t_c = age at which fishing commences

The weight (W_t) of an individual prawn at age t is described by the Von Bertalanffy equation—

$$(3)\quad W_t = W_\infty(1 - e^{-K(t - t_0)})^b$$

where W_∞ = asymptotic weight
K = growth coefficient
t_0 = constant
b = 3

Lucas et al (1979), in analysing the value of the catch in relation to length at first capture and level of fishing mortality, added a stepwise value function (V_t) to this Beverton and Holt yield model. The monetary value of prawns at age t is a stepwise function because of the marketing classification of prawn size into several grades, the value per kilogram of which increases with size of prawn.

$$(4)\quad \text{Value} = \int F N_t W_t V_t \, dt$$

In order for the model to provide an answer to the question of the optimal opening date for the fishing season rather than the optimal length at first capture, the size of animals in the population has to be tied to a date. To achieve this, the model has been restructured in such a way that, given the size composition of the population on a specified date, the model will provide the relationship between the date of commencement of fishing and the monetary value of the catch that would result. The concept of age classes in the original model has been replaced by one of size classes in the computer model. Transformation of the age variable to that of size is as described by Beverton and Holt (1964) whereby from equation (3)—

$$(5)\quad (W_t/W_\infty)^{1/b} = 1 - e^{-K(t - t_0)}$$

As the restructured model considers animals of all sizes, the number of recruits (R) at age t_r in equation (2) has been replaced by the sum of the number of recruits

$$(\sum_i \sum_j R_{ij})$$

in each size class i and sex j at a specific point in time (t_r) prior to the commencement of fishing (t_c). The underlying assumption that animals recruit at age t_r is replaced by the assumption that the population has fully recruited by t_r irrespective of the size of the animals.
Thus equation (2) becomes—

$$(6)\quad N_t = \sum_i \sum_j R_{ij} e^{-M(t_c-t_r)-(F+M)(t-t_c)}$$

In practice, t_r is a date corresponding to a measure of the size composition of the fishable stock after recruitment is complete but before the optimal opening date t_c.

The method adopted in ascertaining the optimal opening date is to calculate the monetary value per recruit for each component of the size class distribution and to accumulate the results with a percentage weighting to provide a measure of the value per 100 recruits. This process is carried out for each day commencing at the date t_r. This change in approach however, did mean that the increased computational burden had to be transferred to a computer.

A major advantage in using a computer model is that it allows a closer simulation of the real world. In this regard, the allometric parameter b in the growth model need not be assumed to be 3 but can be estimated from the relationship between length and weight—

$$(7)\quad W = aL^b$$

where W = weight
L = length
a, b = allometric constants

Furthermore the growth rate for each sex can be considered separately and hence there need be no assumptions with regard to the sex ratio of the fishable stock.

In the Beverton and Holt model, the fishing mortality coefficient (F) is assumed to be constant over time. In the analysis by Lucas et al (1979), F was estimated as the mean fishing mortality during the fishing season. This constraint is removed in this modification to the model. The coefficient is replaced by the function F_t which itself is computed by the function—

$$(8)\quad F_t = qf_t$$

where q = catchability coefficient
f_t = fishing effort at time t

In practice, F_t is described by a stepwise function with the mortality coefficient taking a different value each week of the fishing season. As a result, the integral to calculate the total monetary value from the fishery becomes the sum of a series of integrals over time intervals within each of which, both the fishing effort and the value per kg remain constant. The intervals $(t_k, t_{k+1}), \ldots$ over which the integrations are performed are not equal in length but correspond to a change in the level of fishing effort or, for that particular size class, a change in market value as the size class grows through to a new market grade.

The resulting model can be expressed most simply by using the following transformation (see Gulland, 1969 Section 9.2)—

$$(9)\quad y_t = e^{-K(t-t_o)}$$

from which

$$(10)\quad dt = -dy/(Ky)$$

and equation (4) becomes

$$(11)\quad \text{Value}_{t_c} =$$

$$\sum_i \sum_j R_{ij} W_{\infty j} y_{t_r}{}^{-m_j} \sum_k V_k g_{jk} y_{t_c}{}^{-g_{jk}} \int_{y_{k+1}}^{y_k} y^{(m_j+g_{jk}-1)} (1-y)^{b_j} dy$$

where $g_{jk} = F_k/K_j$

$m_j = M/K_j$

The computer program which simulates this model is written in FORTRAN IV. The intervals $(y_k, y_{k+1}), \ldots$ are calculated for each R_{ij} and t_c before integration can be performed. Integration is performed using the Gaussian numerical method with three intervals. The optimal opening date (t_c) is chosen such that Value_{t_c} is at a maximum.

Application of the model

Since the fishery for banana prawns in the Gulf of Carpentaria commenced in 1968, the level of

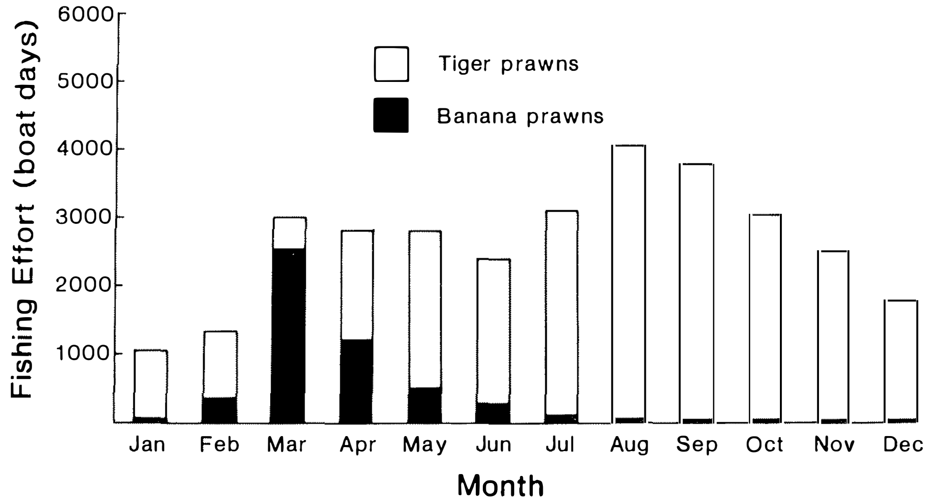

Figure 2. Histogram of monthly fishing effort in 1982 for both the banana prawn, *Penaeus merguiensis,* and tiger prawn, *P. esculentus* and *P. semisulcatus,* fisheries in the Gulf of Carpentaria.

exploitation has increased rapidly to the extent that the fishing season has shortened from a duration of several months to that of a few weeks. As the banana prawn catch rate declines, fishermen divert their attentions to the less rewarding but more predictable fishery for tiger prawns, *P. esculentus* and *P. semisulcatus.*

The monthly fishing effort for 1982 (Fig. 2) has been separated into the two components of the fishery. The fishing effort on banana prawns declined exponentially corresponding to the decline in catch per unit effort. At the same time, fishing effort on tiger prawns increased correspondingly.

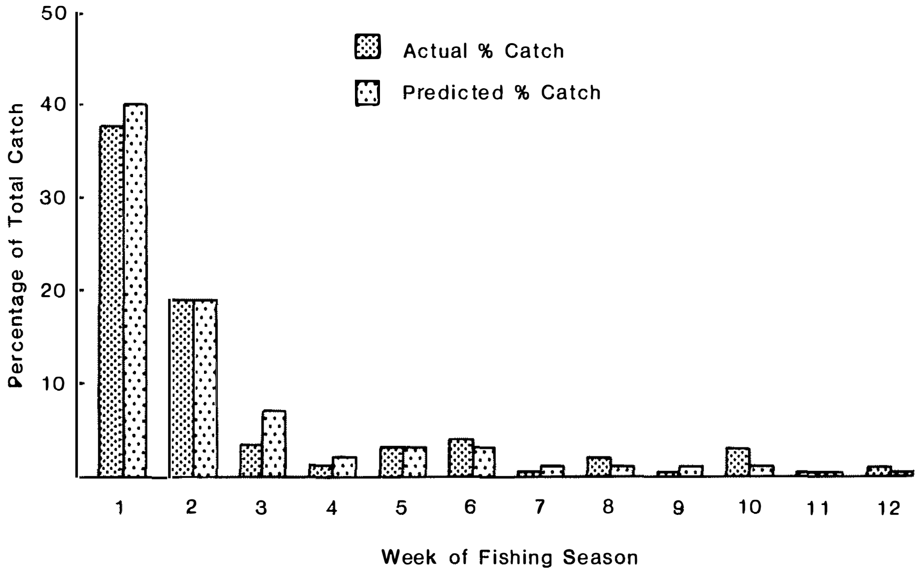

Figure 3. Actual and predicted values of the percentage by week of the total catch of banana prawns, *Penaeus merguiensis,* during the 1982 fishing season in the Gulf of Carpentaria.

In order to provide an appropriate stepwise function (F_t) to describe the prevailing pattern of fishing mortality on a weekly basis, an estimate of the catchability coefficient (q) was obtained using the cohort analysis described by Pope (1972). The estimate of the natural mortality coefficient (M) used in this analysis and in the computer model was 0.05 week^{-1} (Lucas et al 1979). The catch and effort data used to estimate q were for the years 1974 to 1981 and represented that of the whole Gulf fishery. The estimate of q (0.51 x 10^{-3}) obtained from this analysis was tested by using it to predict the pattern of catch in 1982 from the pattern of effort in that year (Fig. 3).

Growth of banana prawns (sexes combined) was described by Lucas et al (1979) using a Von Bertalanffy model with growth parameters estimated from modal progression in size composition data. The data were in the form of percent by weight of catch in each commercial market grade for each month of the 1968 fishing season in the Weipa region of the fishery. Problems of analysing these data were that there was no separation of the two sexes nor was there any upper bound for the largest size category.

More recent length frequency data collected by sampling commercial catches in the western Gulf of Carpentaria have allowed estimates to be made of maximum attainable sizes for each sex. As a first approximation these maximum sizes have been used as estimates of W_∞ for each sex with the other Von Bertalanffy parameter K as measured by Lucas et al (1979).

Analysis of commercial catch samples

Banana prawn length frequency data were obtained from commercial catch samples taken throughout the fishing seasons in the years 1974 to 1979. The average size of prawns in the samples collected in the years 1974 to 1976 was used by Lucas et al (1979) as a monitor for recruitment into the fished population in the estimation of mortality rates and later as a guide in the selection of an opening date for the fishing season from the estimated optimal length at first capture. In this analysis, the length frequency data rather than the average size of prawns, have been used in order to estimate the optimal opening date directly using the computer model.

As the model requires an estimate of the size composition prior to fishing, these data have been back-calculated to a length frequency on 1 March each year and added together. To achieve the back-calculation, the boundaries for each 1 mm size class were transformed according to the growth rate and the days between 1 March and the date on which the sample was obtained. The frequency of occurrence of animals across the size class was assumed constant and the frequency of that size class was redistributed accordingly. Lack of information prevented calculation of appropriate weighting factors for individual samples and each was assumed to be an independent estimate of the size composition of the fishable stock.

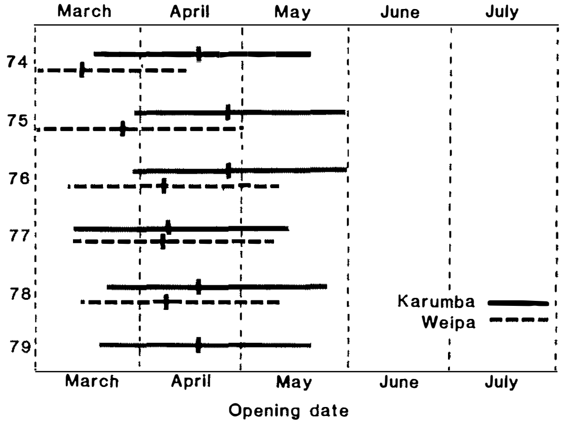

Figure 4. Optimal opening dates from 1974 to 1979 for the Gulf of Carpentaria based on the size composition of banana prawns, *Penaeus merguiensis*, from each of the regions around Weipa and Karumba. The range of opening dates which would have resulted in export revenue to within 5% of the maximum possible is shown. No data was collected from Weipa in 1979.

The most comprehensive coverage of commercial catch samples over the period 1974 to 1979 came from two regions within the Gulf of Carpentaria fishery: around Weipa in the northeast and around Karumba in the southeast (Fig. 1). The size composition data from these two regions were used as input to the model with fishing mortality parameters referring to the Gulf as a whole. The question which was thus being addressed was: "If the regional size composition was representative of the fishery as a whole, what was the optimal opening date under the prevailing pattern of fishing effort?" The results of this analysis are presented in Fig. 4 together with the range of dates that would have resulted in revenue within 5% of the maximum possible. It can be seen from these results that there is significant annual and

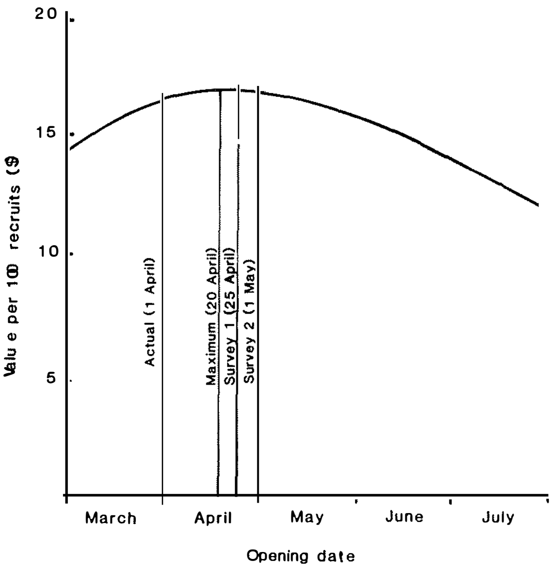

Figure 5. The relationship between value per 100 recruits and opening dates based on the size composition of banana prawns, *Penaeus merguiensis,* in the Weipa region in 1983. The optimal opening date (20 April), the actual opening date (1 April) and those estimated from the preseason surveys (25 April and 1 May) are also shown.

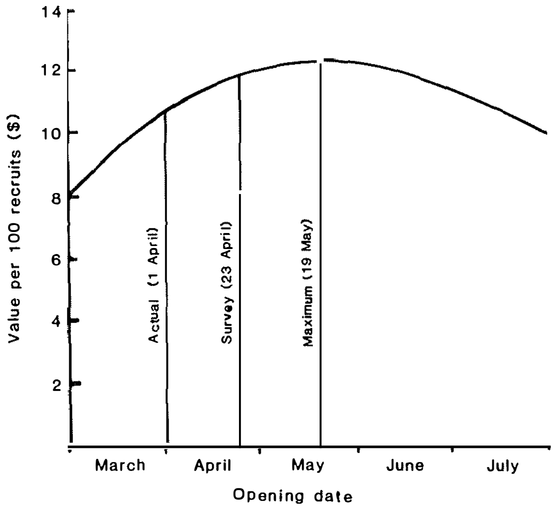

Figure 6. The relationship between value per 100 recruits and opening dates based on the size composition of banana prawns, *Penaeus merguiensis,* from the 1984 fishing season in the Gulf of Carpentaria. The optimal opening date (19 May), the actual opening date (1 April) and that estimated from the extensive preseason survey (23 April) are also shown.

regional variability in optimal opening dates, however it should be noted that in nearly all cases an opening date of mid-March was substantially sub-optimal. If the fishery was to be regulated by a fixed opening date common to all regions then, on the basis of this analysis, this date would be in mid-April.

Preseason sampling

A flexible annual opening date based on the size composition prior to the fishing season would at least alleviate the problem of annual variability in optimal opening date shown above. To test the feasibility of obtaining reliable estimates of the size composition prior to a fishing season, a sampling program was carried out in the Weipa region in March and April 1983.

The sampling program was divided into two six-day surveys (four and two weeks prior to the opening of the fishing season on 1 April) followed by a comprehensive survey of the commercial catch during the first week of the fishing season. Three vessels were deployed in the first survey and six in the second. Each vessel operated independently so that an assessment could be made of the necessary level of sampling required for a reliable estimate of the optimal opening date. The objective of each survey was an assessment of the size composition of the banana prawn population. From the size composition obtained in each survey, corresponding opening dates were calculated using the computer model.

Generally speaking, there was very close agreement between the results from each of the surveys and those of the commercial catch sampling (Fig. 5). An analysis of sampling intensity (Cochran 1963) indicated that an opening date calculated on the results of one vessel undertaking such a survey in the Weipa region would result in revenue within 2% of the maximum possible with a 95% degree of confidence.

Using this level of sampling as a guide, a sampling program for the whole fishery was implemented in 1984 with the deployment of ten vessels covering all of the major fishing grounds in a six-day period from 3 March. As with the 1983 program, the results of the preseason survey were again compared to those obtained from a comprehensive survey of commercial catches during the first week of the fishing season (1 April to 7 April). The results from this study (Fig. 6) however, did not reach the degree of precision predicted by the 1983 Weipa study. Continued recruitment of small prawns after the completion of the sampling program caused by late seasonal rains (Staples 1980) resulted in the estimated opening date (23 April) being some three weeks too early. It should be stressed however, that although this date would have resulted in revenue some 3% below the maximum possible, the actual opening date (1 April) resulted in revenue 12% below the maximum.

Discussion

As the computer model still has the original simple Beverton and Holt yield per recruit model as its basis, the sensitivity to changes in mortality and growth parameters is the same as for the simple model. The major difference which occurs with the change from the use of average length to length frequency is that the curve relating value per recruit and opening date becomes much flatter, as the whole population is not assumed to be growing (and thus passing through marketing grades) in unison. In the analysis of length frequency data from the years 1974 to 1979 (Fig. 4), the range of opening dates within which 95% or more of the potential revenue would have resulted was approximately two months in all cases. Beyond this range the potential revenue falls away more rapidly, an additional two weeks resulting in another 5% reduction in revenue. In contrast to this, the relationship between potential revenue and length at first capture as described by Lucas et al (1979) shows marked changes corresponding to the boundaries of each of the marketing grades.

Conclusions

This computer model provides a convenient means of analysing yield and monetary value per recruit in situations where the size composition of the fishable stock can be ascertained. The output of the model provides an explicit solution to the problem of defining the optimal opening date for the fishing season.

The advantages in using a computer model are related to the degree of computational complexity that is possible with this type of model. It has been possible to incorporate sex specific growth rates, fishing mortality rates which vary with time, and a function which relates value per kilogram to the size of prawns caught. The model is thus flexible enough to make it possible to cope with annual changes in fishing patterns and also the size composition of the stocks or in the relative value of prawns of different sizes on export markets. By using the size composition of the stock rather than the average size of individuals, all of the relevant information is used in ascertaining the optimal opening date.

The application of the model to the Gulf of Carpentaria banana prawn fishery has been successful in providing a useful picture of the annual and regional variability in optimal opening dates as well as showing some promise as a tool in fine tuning the opening date of the fishing season through preseason surveys.

Acknowledgments

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Fisheries biology

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Review of the penaeid prawn fisheries of Australia

Abstract: An account is given of the historical development of the prawn fisheries of Australia on a state-by-state basis, with particular emphasis on the considerable expansion which has taken place in this industry in the past decade, and the increased espousal of limited licence regimes as a tool with which management authorities hope to combat the economic problems arising from such expansion in combination with other factors. The current status of each of the major fisheries is described in terms of species fished, the marketing regimes about which the fisheries are oriented, the numbers and size structure of the fishing fleets exploiting each fishery, the types of gear in use, and the legislative systems involved in their management.

Introduction

Australia may not hold an important place in the general world fisheries scene, but in regard to prawns and prawning, its status has some significance internationally. More than 50 species of penaeid prawns are found in Australian waters, and according to a survey carried out in 1981, Australia was ranked 15th among the major prawn producing countries of the world, sixth in terms of the value of its prawn exports, and fourth in the world in relation to per capita consumption of prawns (Anon. 1983).

The aim of this review is to present a broad picture of the historic development of the prawn fisheries around Australia and to provide a background for specific papers on the management and future development of these fisheries.

The early development of Australian prawning, and indeed of its history up to 1973, was dealt with in a background paper to the First National Prawn Seminar (Ruello 1975). As 11 years have elapsed since that review, this paper will briefly recapitulate the main features of the period then reviewed, in addition to describing the changes which have taken place over the past decade.

Apart from the comprehensive account of past events by Ruello, there are two publications which give excellent coverage of the biological and operational aspects of the Australian prawn fisheries. These are Grey, Dall and Baker's illustrated handbook entitled A guide to the Australian penaeid prawns (Grey et al 1983), and an article by Alexander (1984).

Both papers are recommended for details of the identification and distribution of the main commercial species around Australia.

State-by-state review

New South Wales

Commercial fishing for prawns in Australia commenced around the Sydney area in the early years of the 19th century, with the use of scoop and hauling nets. Transport difficulties and the lack of ice hampered the spread of fishing outwards from the Sydney region, but by 1850 prawning was being carried out in the Hunter River in the Newcastle region, and by 1889 a small fishery had been established in the Clarence River (Fig. 1).

The introduction of prawn trawls to New South Wales (NSW) in 1926 saw a considerable expansion in the industry as fishermen were now able to pursue the prawns into the deeper waters of the coastal lakes and rivers. A further

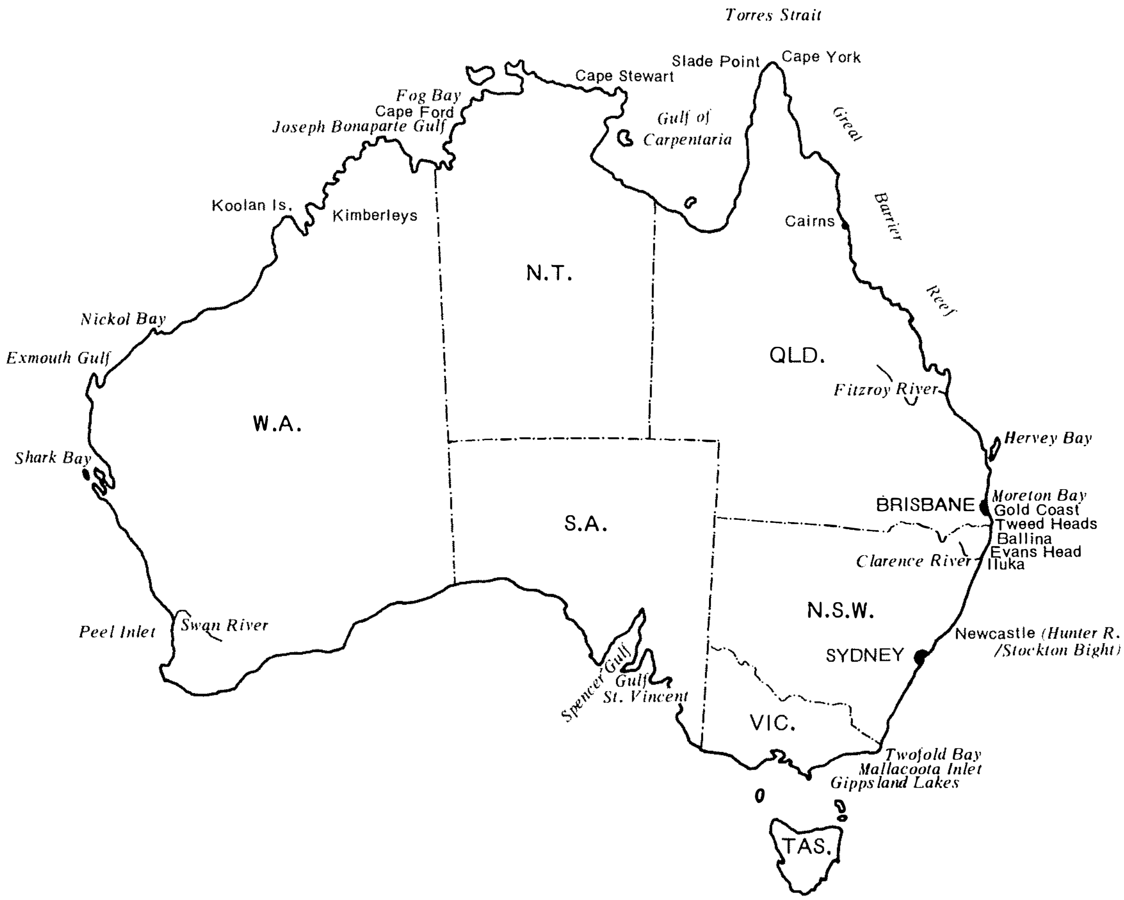

Figure 1. Place names mentioned in the text.

innovation was the introduction of set pocket nets in 1932. These were particularly effective in the tidal races which are a feature of the entrances to the coastal lakes. However, prawning as a commercial operation did not move into ocean waters until 1947, despite the fact that various research and finfish trawlers had been picking up large prawns at sea over a period of half a century. Dakin (1935, 1938) and others had also drawn attention to the offshore breeding migration of eastern king prawns, *Penaeus plebejus,* and school prawns, *Metapenaeus macleayi,* from the estuaries into the open sea.

Once ocean trawling for prawns commenced with the discovery by Danish seiners of large quantities of school prawns in Stockton Bight near Newcastle, it spread very rapidly to the NSW north coast centres such as Iluka, Evans Head, Ballina and Tweed Heads. Initially the fishery was oriented towards school prawns, being generally restricted to daylight hours in waters less than 55 m. However, under the influence of work by Racek (1957, 1959), which demonstrated the offshore abundance of *P. plebejus* and brown tiger prawns, *P. esculentus,* operations soon moved into night trawling in deeper waters, resulting in a spectacular increase in the industry.

Following this period of rapid expansion in the 1950s, which saw prawning established as a substantial element of the fishery scene in about 20 localities along the coast from Tweed Heads in the north to Twofold Bay in the south, NSW prawning has settled down into a relatively stable, decentralised industry, oriented very much more towards the domestic market than is the case in most other states. There has been comparatively little development in either fishing vessel design or in the fishing operations themselves since the 1960s, apart from exploitation of royal red, *Haliporoides sibogae,* and other deepwater prawns following exploratory fishing surveys by the NSW Fisheries research vessel Kapala.

The NSW prawn trawling fleet consists of a little more than 450 vessels, of which 298 are involved in the offshore trawl fishery. The latter range in size from 12 to 25 m, though few exceed 19 m. Most tow triple-rig trawls. The inshore fleet ranges from 6 to 21 m in length, the smaller boats being mostly single-rig vessels. Annual catch (which includes that taken by methods other than trawling), averages slightly more than 2000t. (Glaister and McDonnall 1983; S. Montgomery[1], pers. comm.; Anon. 1982).

Queensland

Commercial prawning operations in Queensland (Qld) probably also commenced along the river shores of southern Qld in the 1840s, using scoop and scissor nets to take the smaller varieties, namely greasyback, *M. bennettae,* and school prawns, *M. macleayi.* Later, juvenile banana prawns, *P. merguiensis,* in the Fitzroy River were probably taken by these methods.

Seine nets were not as much a part of the early Qld scene as they were in NSW, probably because the latter fishery tended to develop along the sand beaches of Sydney Harbour and the shallow coastal lakes, whereas in Qld the fishery was mainly in the rivers, where bold banks and mangroves made seining difficult.

However, after the turn of the century, seining and the use of set pocket nets (locally called stripe nets) developed in suitable locations, and beam trawls were introduced into the Brisbane and Fitzroy Rivers, based on gear in use around the Greek islands.

Despite the fact that several government sponsored trials utilising the vessels Waterlily and Otter in 1886 or 1887, the Ostrea in 1902 (Welsby 1967), and the Endeavour in 1909 (Schmitt 1926), had indicated the presence of large prawns in Moreton Bay and offshore waters, it was not until 1950 that commercial otter trawling commenced in Moreton Bay and eventually spread to the Gold Coast and Hervey Bay in 1954.

The Challenge survey in 1957-58 (Anon. 1959) helped to spread the development of prawn trawling up along the entire Qld east coast, as well as outwards into deeper water off the established southern Qld grounds.

Between 1963 and 1965, a joint Commonwealth-Queensland survey under the leadership of I.S.R. Munro, established the presence of banana prawns, *P. merguiensis,* and brown tiger prawns, *P. esculentus,* in the southeastern Gulf of Carpentaria (Munro 1983), and paved the way for the establishment of what is now Australia's richest prawn fishery. When this fishery first developed, the main interest centred on fishing concentrated schools of banana prawns. The presence of these schools was indicated by distinctive mud boils on to which the vessels were directed by aerial spotting.

This fishing regime saw some extraordinary catches made with individual vessels taking several tonnes of prawns in a matter of only a few minutes' trawling. It was also estimated by Commonwealth Scientific and Industrial Research Organization scientists (Lucas et al 1979) that very high proportions (about 80%) of the available stock of banana prawns were taken each year, giving rise to fears that this might be one prawn fishery where recruitment could be drastically affected by fishing operations.

The banana prawn season, that is the period within which the mud boils appear and concentrated target fishing for this species takes place, has drastically shortened from five or six months to a matter of a few weeks. With this change, there has been a corresponding increase in the relative importance of the steadier but less spectacular fishery for brown tiger prawns and for endeavour prawns, *M. endeavouri,* to the extent that the latter species now provides more than half the catch.

In 1977, the Qld Gulf of Carpentaria grounds, in common with those in the western half of the Gulf and most of the trawling grounds off the rest of the Northern Territory coast, were incorporated into a limited licence fishery with a Declared Management Zone (DMZ) stretching orginally from Slade Point to Cape Ford, but later extended further westward to Koolan Island. This fishery, which is known as the Northern Prawn Fishery (NPF), is managed jointly by the Commonwealth, Queensland, the Northern Territory and Western Australia.

In 1984 there were 292 entitlements existing for this fishery, of which 262 related to vessels actually fishing. About 200 of the vessels were Queensland based, 30 were based in the Northern Territory and most of the remainder came from Western Australia.

Annual production for the DMZ of the NPF has

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fluctuated in recent years from 7000 to 12000t, of which slightly less than half comes from the Queensland side of the Gulf. The NPF boats are generally larger than those in any other Australian prawn fishery, ranging in size from 12 to 32m, most being about 21-22m. This is not necessarily the most efficient size but it is just above the limit (21m design load waterline length or 150 gross construction tons) which attracts a Commonwealth shipbuilding subsidy.

In his review, Ruello (1975) said that "although the east coast of Queensland is widely believed to be heavily or over-exploited, there are still new prawn grounds to be discovered and fished." In 1984 that statement is no longer true. Most of the gaps seem to have been filled in. The Torres Straits are heavily fished, and the inter-reef areas of northern Qld are yielding an annual catch of the order of 700t of red spot king prawns, *P. longistylus,* a species which a few years ago was regarded as a comparative rarity. Recent surveys funded by the Fishing Industry Research Trust Account, and carried out by officers of the Qld Department of Primary Industries in collaboration with individual fishermen have indicated that the fisheries for the deeper water prawns such as royal red prawns, *Haliporoides sibogae,* and scarlet prawns, *Plesiopenaeus edwardsianus,* also known as giant scarlets, could be expanded. However, the marketing problems associated with these species and the fact that only a small proportion of the fleet would be capable of fishing the depths in which they are found suggest there is unlikely to be a spectacular potential for expansion in this direction.

By 1979, under the stimulus of a series of good seasons and buoyant overseas markets, the Qld east coast trawling fleet had grown to approximately 900 vessels, and there were reliable indications that 400 or more additional trawlers were being built around Australia with the intention of participating in the Qld fishery. Unilaterally, the Qld government placed a freeze on the licensing of additional trawlers, other than those which met certain conditions of commital. Although some NSW vessels not previously licensed in Qld persisted in fishing in Commonwealth waters off the Qld coast the freeze did manage to hold the Qld east coast fleet to about 1100.

Western Australia

Although small subsistence fisheries for the western school prawn, *M. dalli,* have existed in Peel Inlet and the Swan River for about a century serious commercial fishing for prawns did not commence in Western Australia (WA) until 1962, following a series of surveys by the research vessel Lancelin (Ruello 1975).

The tropical Western Australian coastline is a very arid one, and for those used to the estuary dependent prawn resources of the eastern states, it was perhaps surprising when large quantities of prawns were found in such localities as Shark Bay, Exmouth Gulf and Nickol Bay. The remoteness of these areas, necessitating the development of shore processing facilities in areas of low population density, slowed down the rate of development and helped the WA government to keep a tight control over the expansion of these fisheries right from their inception. As a result, WA has not been plagued by some of the goldrush type development which characterised other parts of tropical Australia, and the attendant problems of such expansion.

Western Australia was also fortunate in that these three fisheries are all based on relatively enclosed bays and inlets lying within the state's territorial waters, and consequently the decision to establish completely effective limited licence fisheries was able to be made unilaterally by the WA government, without involvement of Commonwealth authorities.

The Shark Bay fishery is limited to 35 boats, and produces an annual average catch of 1920t. Exmouth Gulf produces 1230t annually from 23 licensed boats, and Nickol Bay 160t from 16 boats (Bowen and Hancock 1982). Some increasing production, of course, is taking place along the northwestern coast of WA outside these three areas, mainly as the result of incidental fishing by vessels with NPF endorsements en route to or from the grounds off the Northern Territory or in the Gulf of Carpentaria. The catches are still relatively minor, but the WA government has recently moved to extend its limited licence regimes to the Kimberley region of this coast.

Northern Territory

Although comparatively late on the prawning scene, the Northern Territory (NT) fishery has had a spectacular growth from a production of zero to nearly 5000t in less than 20 years. The fishery was pioneered by a Japanese company but in 1968 the NT administration embarked on a deliberate program to develop the fishery and encourage Australian participation (Ruello 1975).

In the years since the Ruello review, the main developments have been the extension of trawling for banana prawns, *P. merguiensis,* into Fog Bay and the Cape Stewart grounds in 1974 and into the Bonaparte Gulf for the Indian banana prawn, *P. indicus,* in 1979. In 1977 all the NT waters east of Cape Ford were incorporated into the jointly managed limited licence fishery known as the NPF. Of the 292 vessels endorsed for operations in the NPF, about 200 are currently licensed in the NT, and of these about 30 have a home base in the NT (J. Glaister[2] and R. Buckworth[3], pers. comm.).

There also exists within the NT a handful of smaller boats which fish west of Cape Ford. These are being incorporated into the NPF fleet under special arrangements associated with the western extension of the DMZ of the NPF.

South Australia

Despite a series of exploratory trawling ventures dating back to 1948, prawn fishing did not start in earnest in South Australia until 1967, when a rich resource of the western king prawn, *P. latisulcatus,* was discovered in Spencer Gulf. The South Australian government almost immediately instituted a limited licence regime, and based it on a zonal system covering all the state's waters, (Olsen 1975).

A fleet of 59 vessels produces an annual catch of between 2000 and 3000t. The vessels, which include both double- and triple-rigged vessels, range in size from 10 to 25m, with an average of 18m in Spencer Gulf and 14m in Gulf St. Vincent (R. K. Lewis[4], pers. comm.).

Victoria and Tasmania

Victoria has a very small fishery for eastern king, *P. plebejus,* and school prawns, *M. macleayi,* in and adjacent to the Gippsland Lakes and Mallacoota Inlet. However, it is not significant in the national sense, annual production being of the order of 10t. Tasmania does not appear to have any prawn resources.

Status of fisheries

The foregoing has been an account of the historical development of Australia's prawn fisheries, based on state boundaries. For those interested in the future management of this industry, however, it may be more useful to record the status of fisheries from a viewpoint which plays down the role of state boundaries and which tries to look at fisheries as entities comprising recognisably distinct groups of fishing units exploiting common stocks of prawns, regardless of the home base of the individual units participating.

In practice, of course, because of overlaps, extensions and various political, geographical and biological factors, this local compartmentalisation is impossible to achieve in a rigid sense except for some of the smaller fisheries in the west and south. However, if one accepts the absence of sharply defined demarcations and the existence of some element of subdivision derived from political influences, one can recognise the following distinct fisheries or groups of fisheries around the Australian coastline (see Table 1).

The Northern Prawn Fishery

Australia's major fishery, the NPF, with its DMZ, stretches from Slade Point to Cape Ford and was extended west to Koolan Island in 1984.

The NPF is a multi-species fishery, temporally and spatially separated into banana prawn and tiger/endeavour prawn fisheries. There are six main species comprising three species pairs—*P. merguiensis* and *P. indicus; P. esculentus* and *P. semisulcatus,* and *M. endeavouri* and *M. ensis.* The individual components of these species pairs are not readily distinguished by fishing operatives and are lumped together in the fishery production statistics, complicating matters for fisheries managers.

The annual catch varies from 5000 to 14000t, taken by a fleet of 262 medium to very large multi-rigged trawlers, and is processed primarily for export. There is a large component of company owned vessels with varying degrees of control of operations on a fleet basis. (O'Dea and McNamara 1984).

The NPF is a limited licence fishery under joint management by the Commonwealth, Qld, NT and WA governments.

The Queensland East Coast Fishery

Queensland has a complex of sub-fisheries, comprising those in the Torres Strait, along the Coral Coast (a name I have coined to designate the area between the tip of Cape York and Hervey Bay—those latitudes generally

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[3] R. Buckworth, NT Dept. of Ports and Fisheries, Locked Bag 100, Darwin, NT 5794, Australia
[4] R.K. Lewis, SA Department of Agriculture, GPO Box 1625, Adelaide, SA 5001, Australia

Table 1. Summary of status of prawn fisheries

	Northern Prawn Fishery	Queensland East Coast	New South Wales	South Australia	Western Australia
Target	multi-species	multi-species	multi-species	single-species	multi-species
Annual catch (t)	5 000 to 14 000[1]	>14 000	2 000	2 000 to 3 000	3 300
Fleet numbers	262 (292 entitlements)	1 000 to 1 100[2]	450	59	74[3]
Vessel sizes	12 to 32 m	5 to 24 m (20 m maximum in territorial waters)	6 to 21 m	10 to 25 m	13 to 24 m
Type of rig	multi-rig	mostly multi-rig, a few single-rig	both multi- and single-rig	multi-rig	multi-rig
Market orientation	export	export, domestic and bait	mainly domestic	export and domestic	mainly export
Licence regime	limited	limited in state waters, changing to limited elsewhere	changing to limited	limited	limited in most areas
Legislative control	joint Commonwealth three states	mostly state based	mostly state based	almost entirely state based	almost entirely state based

[1] Range of annual catch for period 1974 to 1983, but includes product landed outside the DMZ between Cape Londonderry, WA and Bowen, Qld

[2] Includes some NPF vessels, but excludes several hundred very small beam trawlers in the rivers

[3] Excludes some NPF vessels

dominated by the Great Barrier Reef), off the subtropical or southeastern Qld open coast, and within the partly enclosed Moreton Bay. Also included are the various localised river beam trawl sub-fisheries exploiting juveniles of some of the species hunted by the otter trawl operators in offshore areas.

There is a great deal of overlap between the various otter trawl subdivisions, and with the NSW fishery. In fact, the demarcation between the latter and the Qld southeastern coast sub-fishery is essentially a political one. The Qld east coast fishery is a multi-species fishery—almost every Australian species of prawn has been taken in one area or another. The annual catch in recent years is not known with any certainty. Australian Bureau of Statistics figures of between 10000 and 14000t for the total Qld catch are gross underestimates. The east coast catch alone is probably in excess of these figures.

The Qld fleet is a markedly heterogeneous one, comprising between 1000 and 1100 otter trawlers from small to large size, plus several hundred beam trawlers. Marketing has an export orientation in the north and mainly supplies the domestic cooked market in the more populous south as well as bait from Cairns to the Gold Coast.

The east coast fishery has been a limited licence regime in Qld territorial waters since 1979. In 1984 an extension of such a regime into Commonwealth waters was being discussed with the Commonwealth and NSW.

The New South Wales Fishery

The NSW Fishery is mainly based on eastern king and brown tiger prawns offshore, and school and greasyback prawns close inshore and in estuaries, with some deepwater fishing for such species as royal red and scarlet prawns. Total catch averages a little over 2000t.

The NSW fleet numbers some 450 boats ranging in size from very small single-riggers to large multi-rigged vessels. Production is very largely destined for the cooked domestic trade. NSW has been the last great bastion of open licensing, but appears to be now joining the common trend towards limited licensing.

The South Australian Fishery

South Australia (SA) has the only single-species fishery in Australia, with an annual catch of 2000 to 3000t of western king prawns, taken by 59 medium to large multi-rigged trawlers in the two South Australian gulfs and some coastal areas, (R.K. Lewis, pers. comm.).

It has been a limited licence regime from the beginning, and has both export and domestic market elements. Very little of the catch is taken outside SA territorial waters and the regime of management is predominantly state based.

The West Australian Fisheries

The WA complex consists of four localised, state-based, limited licence sub-fisheries, two based on brown tigers and western kings, one on banana prawns, and the fourth on a mixture of tropical species.

The total fleet (excluding NPF boats) consists of 74, mainly large trawlers, multi-rigged, and producing an annual catch in the order of 3300t, destined mainly for the export market (Bowen and Hancock 1982).

Western Australia was the pioneer of limited licence fisheries, and three of these sub-fisheries were the first to be limited in Australia.

Other developments

On the technological side, the advances in the last decade tend to have been in the form of quiet evolution rather than cataclysmic revolution. Nonetheless, several significant improvements have occurred.

The trend towards double-rigging noted by Ruello (1975) certainly has continued to the extent that only some of the smaller inshore vessels now appear to be single-rigged. But the movement has gone much further than a mere change from single- to double-rigging. Double-, twin-, and triple-rigged gear are used by many of the larger vessels, and occasionally other experimental forms of multi-rigging are used.

Little change has taken place in otter-board design, but there has been some research into the advantages of bulbous-bow designs on the fuel efficiency of trawler hulls (Anon. 1984), and several boats are fitting false bows of this type (G. Goeden[5], pers. comm.).

[5] G.B. Goeden, Fisheries Research Branch, Queensland Department of Primary Industries, Bungalow, Qld 4870, Australia

In the area of post-harvest technology, there has been (at least for export oriented fleets) an almost complete transition from wet boat operation to dry refrigeration of product, and a decided swing towards the production of Individual Quick Freeze (IQF) packs.

In a number of areas, but particularly in the north, there has been a trend towards the development of fleet and company operations. The aerial spotting of mud boils was probably the first manifestation of this, but it has progressed further to the extent of encompassing the co-ordination of group fishing operations and strategy.

There has been a battle for survival amongst the processing plants. In the early 1970s there were more than a hundred applications for land for processing prawns at Karumba. The really non-efficient operators were eliminated a long time ago, but some long-standing processors dropped out only in the 1980s. It is to be hoped that these events may stimulate the two wings of industry to give some thought to their dependence on each other.

All these situations are, of course, due to the fact that times are getting harder in the economic sense. One obvious manifestation of these pressures has been the increasing interest in utilisation of bycatch, as profitability becomes harder to achieve.

Bycatch

Increasing use of bycatch has two conflicting effects. It increases the fisherman's income, but it also causes some concern in relation to conservation issues and leads to conflict situations with other users of marine biota. The following are a few examples of existing or potential management problems in this field.

Sea snakes

Sea snakes occur frequently in bycatch in tropical waters. Although in years gone past their usual fate was to be struck on the head and thrown overboard, they now find ready sale for the production of snakeskin fashion goods. This trade is strongly opposed by conservation groups, who claim that target fishing for sea snakes is practised by many trawlermen. In an attempt to resolve the situation, the Queensland Fish Management Authority is directing its control efforts towards the processing points, which are fortunately few in number because of the high quality standards demanded by the snakeskin market.

Pipe fishes

A surprisingly substantial trade has developed in the sale of specimens of the red-and-gold pipehorse, *Solegnathus dunckeri,* a large relative of the sea horses. These fishes, after reduction to a powdered state, find a ready market in the Orient as an aphrodisiac, presumably as a result of a diminution in world supplies of rhinoceros horn. As with the sea snakes, this is a potential item of conflict with conservation bodies.

Sand crabs and whiting

One of the major utilisable items in the incidental catch of trawlers is the sand crab or blue swimmer, *Portunus pelagicus.* This species occurs all around Australia, and in several states is the object of substantial commercial and recreational fisheries. As the crabbers and prawn trawlers frequently fish the same grounds, and as target fishing for this species by trawlermen is expanding, conflict situations between competing groups are on the increase.

Increased exploitation by prawn fishermen of some of the smaller whitings (*Sillago* spp.) is also causing concern to recreational fishermen.

Rock lobster

The latest management problem related to trawler bycatch fortunately appears to be confined to the Torres Straits. The local rock lobster, *Panulirus ornatus,* undertakes a seasonal spawning migration across the trawling grounds which makes the migrating population at this time extremely vulnerable to capture by the trawlers. The situation has significant social and political implications, as these lobsters are not only exploited by a dive-fishery in the Straits, but are also important items in the diet of the Torres Strait Islanders and certain Papua New Guinea native communities. The nature of the problem and the remoteness of its location militate against a simple and easy solution.

Conclusion

The foregoing account has of necessity been a general outline of the development of Australia's most dynamic fishery. During the 1950s and 1960s, this fishery expanded with some of the characteristics, atmosphere and colour of a gold rush. While the fishery as a whole has continued its expansion within the last decade, such growth has been made against the grim realities of excess fishing capacity, escalating costs (particularly in fuel) and increasing competition from foreign interests on the overseas market. A response to this situation has been the very much greater interest and role which industry has been taking in the management of this fishery in recent years. For an illustration of this, one only has to contrast the vigorous participation of industry in the Second National Prawn Seminar as compared with the situation in 1973, when only three people with any real interest in the catching side of the industry attended the First National Prawn Seminar, and even these three contributed little if anything to the discussions. While this change in attitude may have given government administrators new headaches, it is a welcome development from the broad viewpoint of efficient fisheries management.

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The Moreton Bay, Queensland, beam trawl fishery for penaeid prawns

Abstract: Voluntary logbook returns for October 1982 to January 1984 from 14 beam trawl operators indicated that the main prawn species in catches from the Brisbane, Pine and Caboolture Rivers was *Metapenaeus bennettae* at an average of 4.2 $t\,yr^{-1}$. In the Logan River, each boat caught near equal quantities of *M. bennettae* (0.9 $t\,yr^{-1}$), *M. macleayi* (0.73 $t\,yr^{-1}$) and *Penaeus merguiensis* (0.9 $t\,yr^{-1}$). Other penaeid species accounted for 0.045 $t\,yr^{-1}$ from all rivers. It was estimated that 267 t of prawns was taken from these four rivers from October 1982 to January 1984 and that 159t came from the Brisbane River. There was a marked seasonality in catch rates which were minimum during June to August and maximum in November when they averaged 13 $kg\ h^{-1}\ boat^{-1}$. It appears the Moreton Bay beam trawl fishery has a large overlap with the Moreton Bay otter trawl fishery with respect to *M. bennettae* stocks and has a potential overlap with the inshore *M. macleayi* fishery in southeastern Queensland.

Introduction

Beam trawling was introduced in the Brisbane River as an alternative to hand-held scoop or dip nets and was established in the rivers of Moreton Bay by 1950. This preceded the introduction of otter trawlers in Moreton Bay (Ruello 1974). In recent years there has been growing concern over the effects of river beam trawling on the economically more important Moreton Bay otter trawl fishery and on finfish stocks exploited by amateur fishermen. As a consequence a review of the Moreton Bay beam trawl fishery was undertaken by the Queensland Department of Primary Industries. This paper presents a brief description of the fishery, the composition of beam trawl samples obtained from the Logan River and an analysis of trends in data from voluntary logbooks.

Methods

Study area

The Logan River (Fig. 1) which has a catchment area of approximately 1 500 km^2 and the Albert River with a catchment area of 710 km^2, join and flow into the southern section of Moreton Bay. Six study sites were selected within the Logan River, extending from the mouth to the farthest upstream commercially trawled reach. These sites were situated 0.5, 5, 8, 12, 18 and 22 km from the mouth. An additional two sites were selected 2 km and 5 km outside the mouth in an area closed to commercial trawling. Water depths at the sites ranged from 1 m to 10 m at low tide.

Logbook information on beam trawl catches was obtained from fishermen in the Logan and Albert, Brisbane, North and South Pine and Caboolture Rivers. These rivers all flow into Moreton Bay which is sheltered from the Pacific Ocean by Moreton and North Stradbroke Islands.

Sampling gear

Samples from the Logan River were obtained with a 4.5 m Yankee Doodle design commercial beam trawl, with 28mm stretched mesh in both the net body and codend. The net was hung from a pair of steel frames separated by a 3.7 m beam. Each frame consisted of a 1 m upright welded to a flat skid at a point 100mm from the rear edge of the skid. The mouth of the trawl net was 3.7 m wide and 0.8 m high during trawl operation. A drop chain of 6mm links was hung from the rear edge of the skid. The bottomline

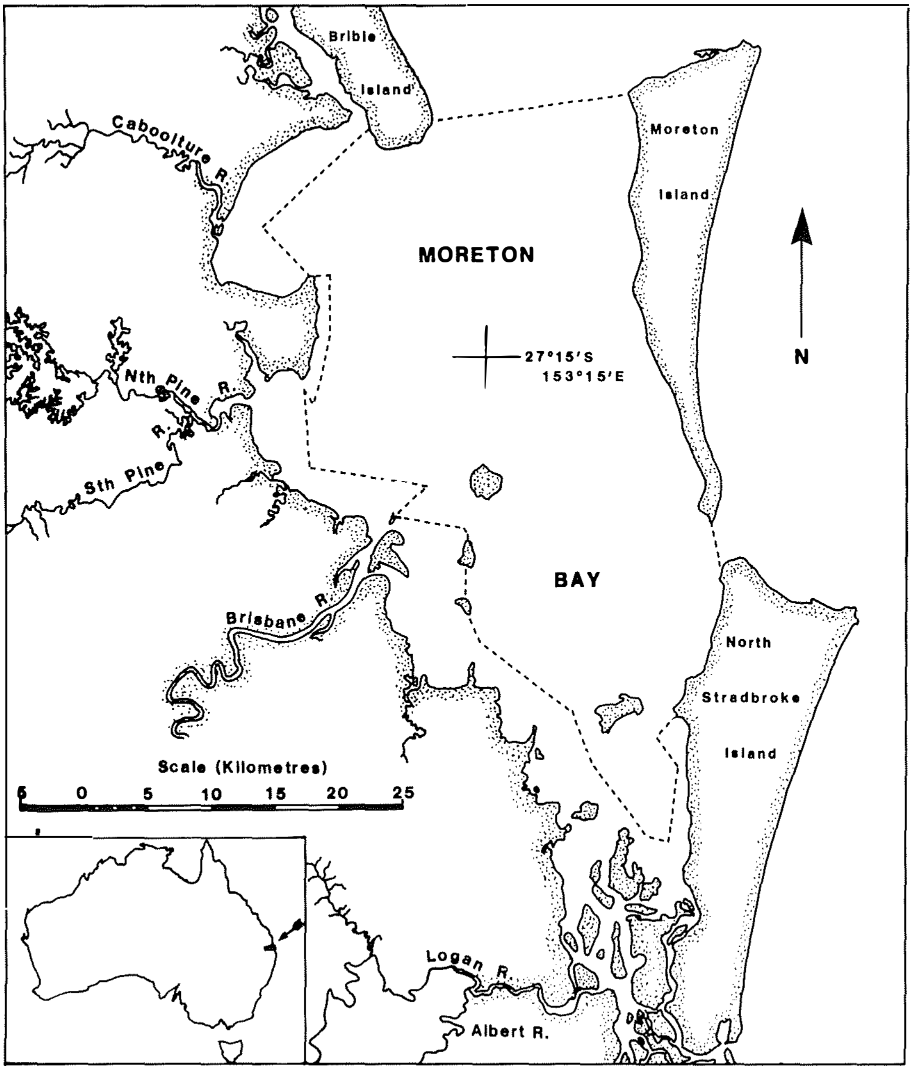

Figure 1. Moreton Bay and rivers in which beam trawlers operate. Broken line marks the foreshore area closed to trawling.

was attached to the upright 120mm above the skid. The drop chain was attached to the bottomline so that the bottomline lay 5 to 10cm behind and 5 to 10cm above the drop chain during trawl operation. Drop chains are commonly used on commercial beam trawls to minimise the entry of debris into the net. Conventional tickler chains are not usually used with river beam trawls. The net was towed behind an outboard powered 5.2m dinghy. The net was positioned 25m behind the boat when trawling to minimise the effect of propellor wash.

Sampling

Samples were taken during the day, as close as possible to the time of low water and within three days of new moon. Each sample was obtained by trawling at 0.85m s^{-1} (1.6 knots) for 10 min from a fixed starting mark. Two samples, taken in opposite directions, were collected monthly from each site over an 18-month period between August 1982 and January 1984. The catch from each trawl sample was stored on ice and taken to the laboratory where it was processed.

Data collation

Prawns were identified by reference to Dall (1957). Fish were identified by reference to Fischer and Whitehead (1974), Marshall (1964), Munro (1967) and Grant (1978). Where possible the classification of Fischer and Whitehead (1974) was accepted. Positive identification at the species level was not possible for some specimens of juveniles of the family Mugillidae. Mr R. Mackay of the Queensland Museum assisted in identifiying juvenile *Johnieops vogleri.* The abundance and wet weight of all species in each sample was recorded. Species were weighed in the laboratory on an electronic balance. The carapace length (CL) of all penaeid species was measured with dial calipers and recorded. In samples where large numbers of a penaeid species were present, 160 individuals of that species were randomly selected for measurement. A visual estimate of ovarian development and spermatophore development in penaeids was recorded.

Logbook methods

Fourteen commercial beam trawl operators voluntarily supplied catch and effort data from October 1982 to January 1984. Three operators worked in the Logan River, eight in the Brisbane River, two in the Pine River and one in the Caboolture River. Each logbook contributor recorded mesh size, net size, commencement time of first trawl, time of completion of last trawl and the weight of each species of prawn retained during the period of trawling.

Results

Commercial fishery description

The beam trawl fishery in the Moreton Bay region supplies prawn which is processed mainly as bait. Management regulations on the operation of beam trawls include a maximum vessel length of 9m, a maximum beam width of 5m, a minimum mesh size of 28mm and a ban on trawling over weekends. Area closures also apply, restricting the operation of beam trawlers to the lower 10km of the Pine and Caboolture Rivers, the lower 25km of the Brisbane River and the lower 30km of the Logan and Albert system. There is currently a restricted entry into the fishery which limits the number of commercial fishermen allowed to operate in the rivers of Moreton Bay to 70. Only 50 of these operate full time in the fishery.

Bycatch

Identification of 93 species representing 51 families was made from the monthly samples and included nine species of marketable prawn (eight penaeid and one carid species). More than 50% of the wet weight of the catch was unmarketable and was discarded by commercial fishermen. Penaeid prawn species made up 60% of the catch by abundance and 19% by weight. Eight species accounted for 92% of the catch by abundance and 12 species made up 90% by weight (Table 1).

Table 1. List of species from beam trawl samples from the Logan River and percentage contribution of each by abundance and by weight. Only species which made up more than 1% by abundance or by weight are included for species other than penaeids.

Species	Family	Percentage abundance	Percentage weight
Metapenaeus bennettae	Penaeidae	31.6	7.4
M. macleayi	Penaeidae	25.0	9.2
M. endeavouri	Penaeidae	0.001	0.001
M. ensis	Penaeidae	0.05	0.05
Penaeus esculentus	Penaeidae	0.14	0.19
P. plebejus	Penaeidae	0.04	0.02
P. merguiensis	Penaeidae	3.84	2.39
P. monodon	Penaeidae	0.002	0.002
Acetes sibogae australis	Sergestidae	1.75	0.07
Macrobrachium australiense	Caridae	2.51	1.67
Scylla serrata	Portunidae	0.17	5.35
Loligo chinensis	Loliginidae	0.11	12.41
Ambassis marianus	Ambassidae	3.18	1.67
Arius spp.	Ariidae	20.68	34.07
Dasyatus fluviorium	Dasyatidae	0.09	5.82
Johnieops vogleri	Sciaenidae	2.88	4.13
Acanthopagrus australis	Sparidae	0.87	3.5
Aseraggodes macleayanus	Soleidae	2.48	2.23
	Total	95.39	90.17

Altogether 34 species were edible and therefore considered to be of some commercial or recreational value. Two of these, the teleosts (*J. vogleri* and *Acanthopagrus australis*), made up 3.8% of the total catch by abundance and 7.6% by weight. The remaining edible teleost species each accounted for less than one percent of the total catch by both abundance and weight. *Johnieops vogleri* ranged in size from 20 to 260mm total length with a mean length of 76.9mm, *A. australis* ranged from 40 to 260mm total length and had a mean size of 92mm. Catch rates averaged 186 *J. vogleri* and 35 *A. australis* h^{-1}. A maximum catch rate for *J. vogleri* occurred in August 1982 (726 h^{-1}) and secondary peaks occurred in January 1983 (470 h^{-1}) and August 1983 (480 h^{-1}). A single peak in monthly catch rates for *A. australis* occurred in January 1983 (136 h^{-1}). Visual observations indicated that *J. vogleri* were usually dead when released from the codend

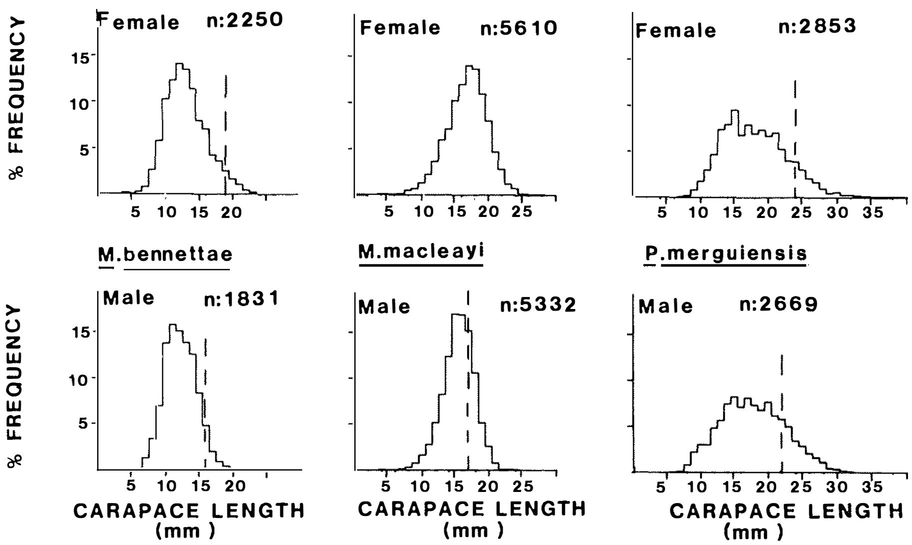

Figure 2. Size frequency of *Metapenaeus bennettae, M. macleayi* and *Penaeus merguiensis* from the Logan River. Broken lines indicate minimum size at which gonad development was observed.

but *A. australis* survived sorting and swam actively when returned to the water. *Arius* spp. (estuary catfish), *Metapenaeus bennettae* and *M. macleayi* collectively accounted for 77% of total catch numerically. *Arius* spp. were the most abundant species by weight at 38% of the total catch. The banana prawn, *Penaeus merguiensis,* the glassy perchlet, *Ambassis marianus*, the little jewfish, *J. vogleri,* the narrow banded sole, *Aseraggodes macleayanus*, and a carid, *Macrobrachium australiense*, each accounted for between 5 and 10% by both abundance and biomass. Estuarine stingrays, *Dasyatis fluviorum*, squid, *Loligo chinensis*, and mud crabs, *Scylla serrata*, were a major (5.8, 12.4 and 5.4% respectively) component of the total catch by biomass but only a small (0.1, 0.1 and 0.2% respectively) component by abundance.

Penaeid size frequencies

Size frequencies of the three most abundant penaeid species were unimodal (Fig. 2). Ovary development commenced at 18mm CL in *M. bennettae* and at 24mm CL in *P. merguiensis.* No ovary development was observed in female *M. macleayi* collected. Spermatophore development was visible at 16mm CL in *M. bennettae,* 17mm CL in *M. macleayi* and 22mm CL in *P. merguiensis.* Small (4.2 to 15.4) percentages of spermatophore bearing males of all three species were caught (Table 2). Less than one percent of female *M. bennettae* and *P. merguiensis* and no female *M. macleayi* caught had visible ovary development.

Penaeid size distribution

The three main commercial prawn species showed an overall decrease in mean CL with increased distance upstream (Fig. 3). Females were larger than males at each site for each species. Trends in size distribution along the river were similar for both sexes of each species. A sharp decrease in mean size for all species occurred at the shallow water site 5km from the mouth. There was also a decrease in CL outside the river for *M. bennettae* and *P. merguiensis* but not for *M. macleayi.*

Logbooks

Catch rates reported through the voluntary logbooks are presented in Table 3. *Metapenaeus bennettae, M. macleayi* and *P. merguiensis* were the main penaeid species

Table 2. Percentage of prawns caught in Moreton Bay rivers which displayed gonad development.

	Male		Female	
Species	n	% with developed gonad	n	% with developed gonad
Penaeus merguiensis	2500	4.2	2772	0.4
Metapenaeus bennettae	4601	9.2	7215	0.2
M. macleayi	3492	15.4	4227	0

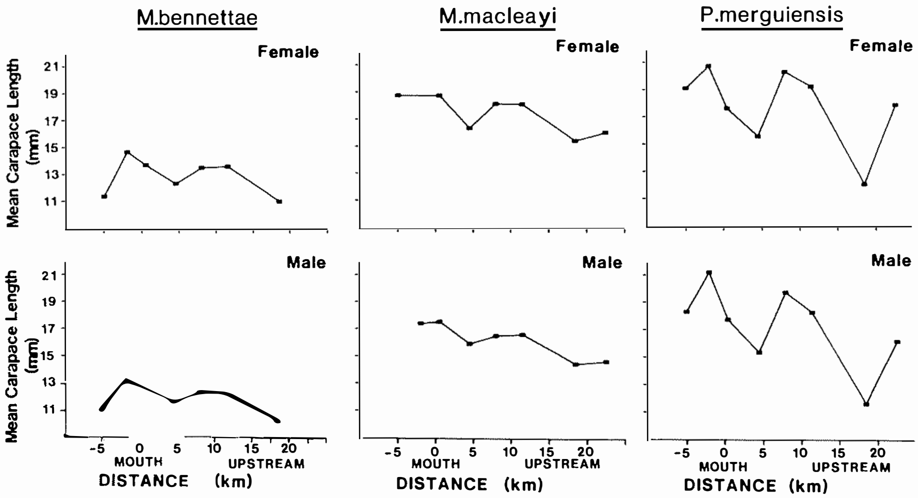

Figure 3. Mean carapace length plotted against distance from mouth in the Logan River for *Metapenaeus bennettae, M. macleayi* and *Penaeus merguiensis* (negative distances are indicated for sites outside the river).

caught. The small quantity of other species of prawn caught was a mixture of eastern king, *P. plebejus*, and tiger, *P. esculentus*, prawns. Composition of the catch varied considerably between rivers. *Metapenaeus bennettae* was the dominant species in the catch from the Brisbane and Pine Rivers (95 and 99.6% respectively). The catch from the Logan River was equally divided between *M. bennettae, M. macleayi* and *P. merguiensis.* The Caboolture River catch was mainly *M. bennettae* (59% of the catch) with some *M. macleayi* and *P. merguiensis* (28 and 12% respectively). An estimate of the quantity of prawn landed by the total beam trawl fleet in each river was made by multiplying the average catch per boat by the estimated number of boats working full time in each river (Table 3). These values are

Table 3. Prawn catch rates (t boat^{-1}) recorded in voluntary logbooks in southeastern Queensland rivers between October 1982 and January 1984.

Species	Logan River	Brisbane River	Pine River	Caboolture River
Metapenaeus bennettae	1.2	5.6	4.6	6.0
M. macleayi	0.97	0.003	0.02	2.9
Penaeus merguiensis	1.23	0.19		1.2
Other	0.01	0.1		0.1
Total	3.4	5.9	4.6	10.2
No. of contributors	3	8	2	1
Est. total no. of boats	12	27	8	3
Est. total catch (t)	41	159	37	30

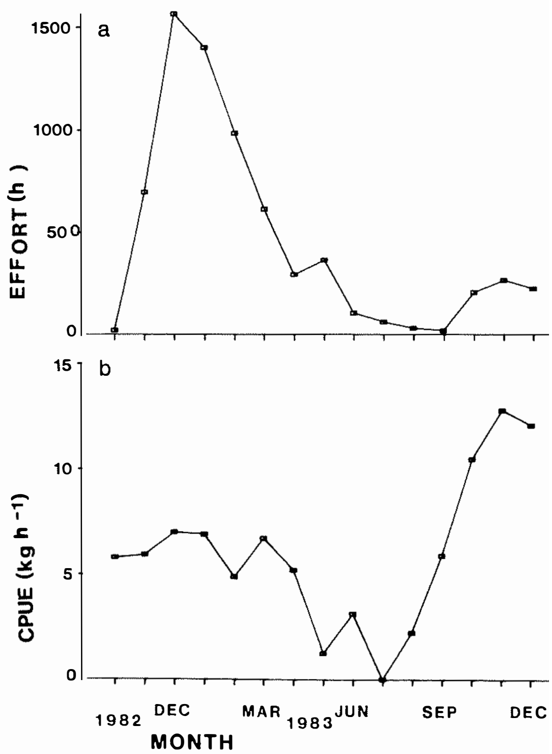

Figure 4. Catch statistics for *Metapenaeus bennettae* in the Brisbane River: **a.** total effort **b.** catch per unit effort (CPUE). Data are based upon logbooks for eight beam trawlers.

considered to be conservative as there seem to be an additional 20 boats working part time in these rivers. The largest number of logbook contributors operated in the Brisbane River. Monthly catch per unit effort and total reported effort for this area for *M. bennettae* shows a strong seasonality in catch rates which were at a minimum during July and peaked around November to December (Fig. 4). There was a large difference between the CPUEs for December 1982 and December 1983.

Discussion

The wide variety of species in the beam trawl samples indicates that a large number of species is potentially affected by beam trawling. The direct mortality effect of this fishery on these species is not known. It is possible that less common species have already been affected to the extent that they are no longer common in either the beam trawl bycatch or in the recreational fisheries. A distinction between affected species and species with low catchability is required to assess the impact of trawling on the less common species. *Johnieops vogleri* is likely to be of most concern since it is caught in relatively large numbers and does not appear to survive trawling. Anecdotal reports suggest it has become less abundant and its value as an angling species has decreased. *Acanthopagrus australis* is caught in considerable quantities at times but is not considered to be at risk since it appears to survive trawling. Pollock (1984) reported that catch statistics from 1945 to 1980 for Moreton Bay indicated little change in the abundance of this commercially and recreationally important species, while the beam trawl effort has increased substantially.

A major concern of prawn fisheries management in southeastern Queensland is the extent of the overlap between beam and otter trawl fisheries. The present findings clearly indicate that the Moreton Bay river beam trawl fishery is based mainly on *M. bennettae* and to a lesser extent on *P. merguiensis* and *M. macleayi.* The size composition and size at maturity show that this fishery relies to a large extent on juvenile prawn. The use of estuarine areas as juvenile habitats has been well documented for *M. bennettae* (Dall 1958), *M. macleayi* (Kirkegaard and Walker 1970; Ruello 1973) and *P. merguiensis* (Staples 1980 a, b). The present findings suggest that juvenile *M. bennettae* and *P. merguiensis* also utilise sheltered shallow foreshore areas since the size of prawns found in these areas is similar to that found in the upper estuarine reaches. The extensive shallow inshore coastal zones of Moreton Bay are likely to provide many recruits of *M. bennettae* to the deep water fisheries (Young 1978). These will supplement the recruitment of prawns from within the river. Since most of the shallow areas in Moreton Bay are closed to all forms of trawling these areas may provide a buffer to the overlap between the river beam trawl fishery and otter trawl fishery for these two species.

The present findings suggest that juvenile *M. macleayi* does not utilise shallow foreshore areas as nurseries and therefore there is no additional source of prawns for the offshore fishery other than those from the rivers. The extent of overlap between the river beam trawl fishery and the deeper water otter trawl fishery remains undetermined in the absence of reliable estimates of mortality and emigration rates. The catch of the Moreton Bay otter trawl fishery consists mainly of eastern king prawns, *P. plebejus*, brown tiger prawns, *P. esculentus,* and greasyback prawns, *M. bennettae*, (Anon. 1976; Dall 1979). The low number of *P. plebejus* and *P. esculentus* in beam trawl catches and *P. merguiensis* in otter trawl catches clearly indicates that the overlap concerns only *M. bennettae.* The catch rate, 50 kg day^{-1}, of *M. bennettae* by beam trawlers in the Brisbane River at the end of 1982 and in early 1983 is comparable to average catch rates reported from Moreton Bay otter trawl logbooks from 1970 to 1975 (Anon. 1976). This suggests a substantial overlap between the Brisbane River beam trawl fishery and the Moreton Bay otter trawl fishery. No *M. macleayi* are caught within Moreton Bay but offshore trawlers catch schools or aggregations of *M. macleayi* outside the ocean bars of southern Moreton Bay and along the ocean beach of Bribie Island. These aggregations are probably associated with a seaward spawning movement as reported by Glaister (1978). The presence of *M. macleayi* in beam trawl catches from the Caboolture and Logan Rivers suggests an overlap between the river and offshore fisheries for this species.

The composition of commercial landings varied considerably river to river. The cause of this is not immediately obvious since a range of factors including catchment areas, dam or weir location, mouth types, agricultural, industrial and urban influences vary from river to river to affect the hydrology and habitat structure in each. Major influences include sewage disposal in all rivers, the volume and location varying with river; dredging in the Bribane and Pine Rivers; a variety of industrial effluents in the Brisbane River; a paper pulp mill in the Pine River; agricultural runoff in the upper reaches and increasing urbanisation in the lower reaches of all rivers.

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Preliminary results of a study of commercial catches, spawning and recruitment of *Penaeus esculentus* and *P. semisulcatus* in the western Gulf of Carpentaria

Abstract: Commercial catch samples and catch per unit effort (CPUE) patterns for the western Gulf of Carpentaria tiger prawn fishery were examined for the period 1979 to 1982. *Penaeus esculentus* made up around 93% of tiger prawn catches in the southern part of the study area. In the northern part a second species, *P. semisulcatus,* made up between 41 and 65% of the overall tiger prawn catch. Minimum size at first maturity of *P. esculentus* was 26mm carapace length (CL) and for *P. semisulcatus* 30mm CL. *Penaeus esculentus* had a protracted spawning period with between 34 and 69% of females having visible ovaries throughout the year. Spawning in *P. semisulcatus* was limited to the period August to December. The main recruitment of *P. esculentus* was between November and February as shown by the presence of prawns smaller than 25 mm CL in the commercial catch. Recruitment for *P. semisculcatus* was from January to April. CPUE in all areas showed two annual peaks, one between February and May and a second between August and November with a minimum in June and July. The first peak is assumed to be due to recruitment of juvenile prawns into the fishery. The winter minimum may be explained by a number of factors including the effects of low temperatures on catchability or depletion and dispersal of the stock. The August to November peak could reflect increased catchability as temperatures rise in spring, or local concentrations that result from stock movements.

Introduction

The western Gulf of Carpentaria is one of the most important areas of the Northern Prawn Fishery (NPF), producing approximately 65% (mean for 1970 to 1982, range 46% to 82%) of annual catches of tiger prawns, *Penaeus esculentus* and *P. semisulcatus,* from the Declared Management Zone (DMZ) of this fishery (AFC 1982). The mean of tiger prawn landings from the DMZ for 1979 to 1982 is 4583t (AFC 1982; Ryan and McNamara 1983).

A fishermen's logbook program (Somers and Taylor 1981) has provided a considerable data base on catch and effort in the fishery. These logbooks do not differentiate between the two species of tiger prawns. To provide information on species and size composition and other biological parameters of the fished populations, a catch sampling program directed at the fisheries in the Groote Eylandt area was conducted between 1979 and 1984.

This paper presents a preliminary examination of trends in catch per unit effort (CPUE) in tiger prawn catches (as recorded in logbooks) in the Groote Eylandt area for the period 1979 to 1982 and investigates the relationships between these trends and spawning and recruitment of the two tiger prawn species. Investigations of the relationships between catch patterns and biology of the fished species may explain, and enable prediction of, catch patterns, and provide a basis on which appropriate management measures may be formed.

Methods

Catch and effort data

Tiger prawn catch and effort data for the period 1979 to 1982 were derived from daily catches and boat-days recorded in fishermen's logbooks. (Data from Commonwealth Department of Primary Industry, Canberra). Fishing locations were recorded in these logs to

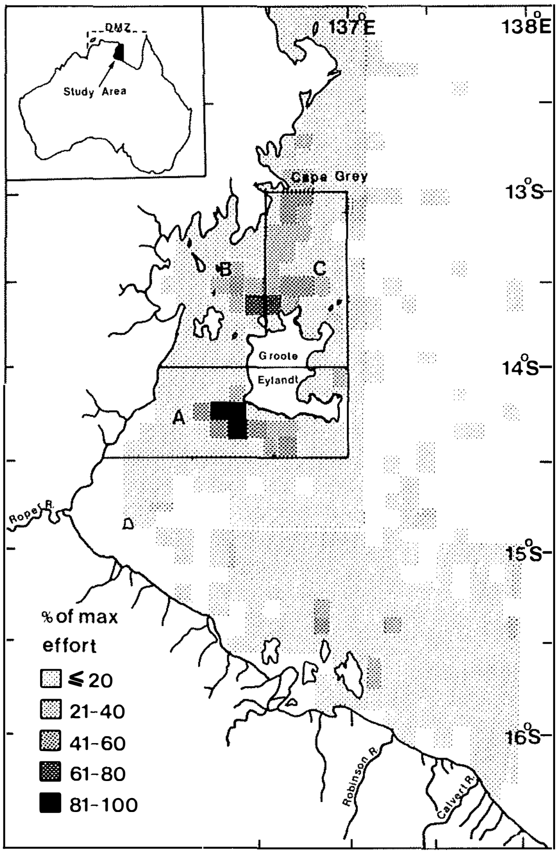

Figure 1. The western Gulf of Carpentaria study area indicating the major statistical areas in the Groote Eylandt region **A.** South Groote **B.** Blue Mud Bay **C.** North Groote. The six minute grids show the relative effort (boat-days) from logbooks for the 1980 to 1982 period.

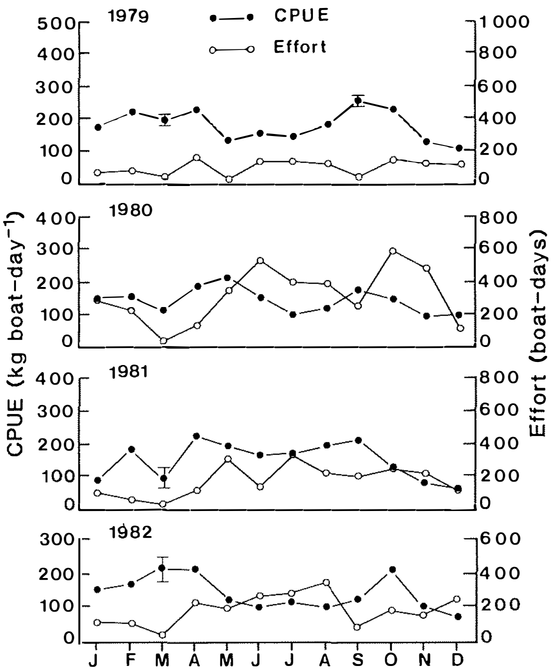

Figure 2. South Groote area, western Gulf of Carpentaria: monthly means of tiger prawn, *Penaeus esculentus* and *P. semisulcatus*, catch per unit of effort and effort, 1979 to 1982. Errors in CPUE are plus and minus one standard error. Where they are not shown, errors were smaller than the symbols used.

different levels of precision. The most precise data included location in six minute square grids. However, many records indicated only more general fishing grounds (Somers and Taylor 1981) and so were ascribed to larger statistical areas. In order to examine all catch and effort data and to conveniently examine CPUE trends, the logbook data for the Groote Eylandt area were divided into these larger areas (termed South Groote, Blue Mud Bay and North Groote, as shown on Fig.1). CPUEs were established by dividing monthly tiger prawn catches (kg) by the monthly effort (boat-days), as declared in logbooks. CPUEs given are thus the means of daily catches for the months and areas under consideration.

Logbook catches do not represent the total landings from the fishery. The proportions of annual DMZ tiger prawn landings accounted for by logbooks (logbook coverage) were 48.7, 62.2, 64.6 and 38.6% in 1979, 1980, 1981 and 1982 respectively. Logbook data are not yet available for 1983 and 1984.

Catch sampling

Two types of samples were collected by NT Fisheries Division personnel: first, from February 1979 to June 1984, prawns were taken from trawlers during fishing operations; secondly (in 1979 to 1981), prawns were removed from ungraded product landed at Groote Eylandt for processing. In addition, data accumulated from a 1982-83 trawl survey in the western Gulf of Carpentaria (Grey and Buckworth 1983) have been incorporated.

Prawns were identified to species, sexed and measured. Carapace length (CL) was chosen as the most convenient and reliable measure of size and was measured to the nearest mm with dial calipers. Females were examined for visible ovaries, stages 3 and 4 defined by Tuma (1967).

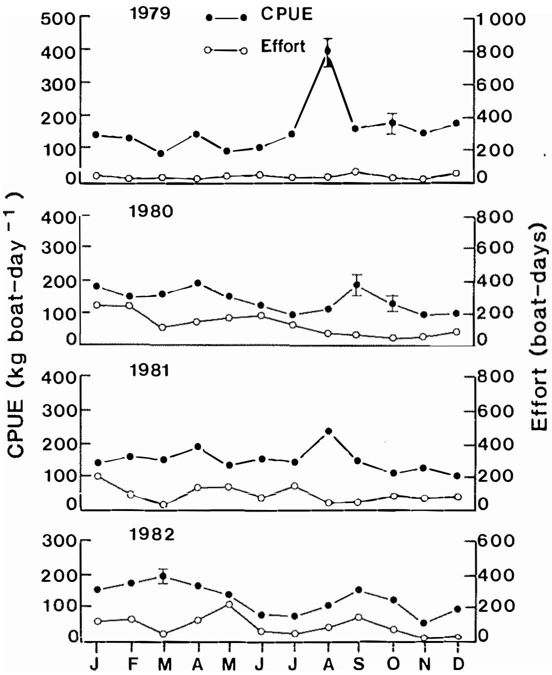

Figure 3. Blue Mud Bay area, western Gulf of Carpentaria: monthly means of tiger prawn, *Penaeus esculentus* and *P. semisulcatus,* catch per unit of effort and effort, 1979 to 1982. Errors in CPUE are plus and minus one standard error. Where they are not shown, errors were smaller than the symbols used.

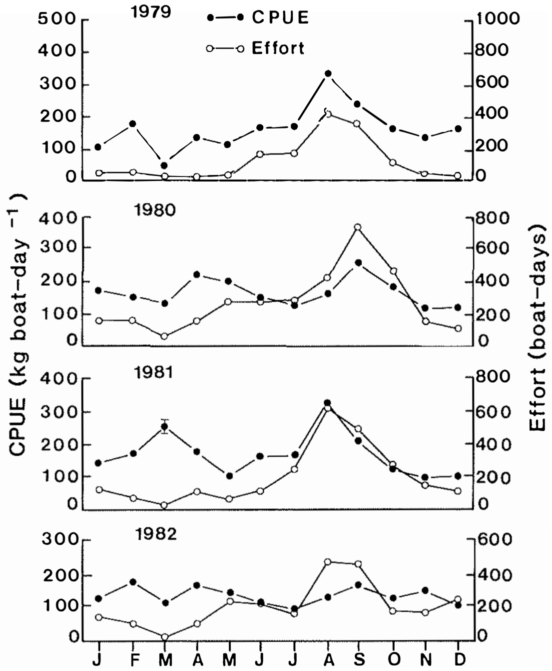

Figure 4. North Groote area, western Gulf of Carpentaria: monthly means of tiger prawn, *Penaeus esculentus* and *P. semisulcatus,* catch per unit of effort and effort, 1979 to 1982. Errors in CPUE are plus and minus one standard error. Where they are not shown, errors were smaller than the symbols used.

During some trawling operations in 1982 to 1984, sea surface temperatures were measured to the nearest 0.1° C, with a mercury thermometer. Satellite derived sea surface temperature data, in the form of weekly charts marked in isotherms (to the nearest 1° C) were obtained for 1980 to 1984 (National Earth Satellite Service, National Oceanic and Atmospheric Administration, United States Department of Commerce).

Recruitment

Prawns $\leq$ 25mmCL (approximately 30 count per pound) were regarded as recruits. The proportion of recruits for each month was calculated to indicate the general pattern of recruitment of *P. esculentus* and *P. semisulcatus.* Because of low sample numbers it was necessary to pool all data from 1979 to 1984.

Reproduction

The proportion of females with visible ovaries was plotted against CL to establish the size of female first maturity in each species. This was estimated as the smallest size at which 1% or more of female prawns had developed ovaries (Rao 1967; Thomas 1974; Crocos and Kerr 1983). To reduce sampling error, size intervals in which the sample size was less than 100 were excluded from this analysis. This removed individuals which were outside the size range 20 to 48 mm CL for *P. esculentus,* and 23 to 50 mm CL for *P. semisulcatus.*

The reproductive status of the fished populations was investigated by calculating the proportion with developed ovaries for each month. For this purpose, all samples from 1979 to 1982 were pooled. It was assumed that females with developed ovaries could be expected to spawn within one intermoult period (Crocos and Kerr 1983), which is of the order of one month or less for *P. esculentus* (Barclay et al 1983; Hill and Wassenberg in press).

Results

Catch and effort

The most heavily fished areas in the western Gulf of Carpentaria, from 1980 to 1982 were

Table 1. Summary of annual logbook catch (kg) effort (boat-days), and mean CPUE for mixed tiger prawns, *Penaeus esculentus* and *P. semisulcatus*, in three areas of the western Gulf of Carpentaria, 1979 to 1982.

Year	Catch	Effort	CPUE	SE
South Groote				
1979	213175	1195	178.4	3.4
1980	533859	3816	140.0	1.5
1981	334923	2213	158.5	2.1
1982	302225	2314	130.6	2.0
Blue Mud Bay				
1979	72249	458	157.7	5.5
1980	233271	1582	147.5	2.2
1981	177919	1191	149.4	2.5
1982	151859	1057	143.7	2.6
North Groote				
1979	347106	1560	222.5	4.2
1980	628465	3370	189.3	2.2
1981	506033	2467	205.1	2.9
1982	358808	2539	141.3	1.7

Table 2. Percentage of *Penaeus esculentus* in tiger prawn catch samples in three areas of the western Gulf of Carpentaria for 1979 to 1982. (Total number of prawns sampled each year indicated in parentheses).

Year	1979	1980	1981	1982	Average
South Groote	93.0 (1754)	82.1 (1898)	85.7 (1278)	95.6 (11244)	92.9 (16174)
Blue Mud Bay	69.1 (1964)	55.2 (1986)	70.7 (1123)	57.2 (12723)	66.7 (17796)
North Groote	50.4 (2269)	27.7 (1710)	55.5 (532)	29.5 (5221)	35.5 (9732)

southwest and north of Groote Eylandt and in the vicinity of Cape Grey (Fig.1).

The monthly tiger prawn logbook effort and CPUE data for the years 1979 to 1982 from the South Groote, Blue Mud Bay and North Groote areas were examined (Figs. 2,3 and 4). A summary of the annual logbook catch, effort and mean CPUE is provided in Table 1.

In the South Groote area, a peak in monthly CPUE occurred between March and May each year (Fig.2). This ranged between 203.0kg boat-day^{-1} in May 1980 to 227.0kg boat-day^{-1} in April 1979. Another peak was apparent in September or October (between 171.9 and 253.4kg boat-day^{-1} in September of 1980 and 1979 respectively. Intervening periods of lower CPUEs had minima between May and August and again in November-December. Effort in the South Groote area increased from April to an annual maximum between May and October.

Two annual peaks in CPUE were apparent in the Blue Mud Bay area (Fig.3). A small peak in CPUE occurred in March or April each year. This varied between 156.2kg boat-day^{-1} in April 1979 to almost 200kg boat-day^{-1} in March 1982. The second peak for this area occurred in August or September and varied greatly in size between years, from 161.0kg boat-day^{-1} in September 1982 to more than 400kg boat-day^{-1} in August 1979. Mid-year lows in CPUE occurred from May to July and were as low as 75.0kg boat-day^{-1} in July 1982. Fishing effort was generally lower in this area than in South Groote or North Groote (Fig.3 and Table 1). High levels of effort occurred in January and February as well as between April and September. Low levels occurred in May and again between October and December.

Two peaks in CPUE were also seen in the North Groote area (Fig.4). A slight peak occurred between February and April each year. The second peak was in August or September and was very pronounced in 1979, 1980 and 1981 but less apparent in 1982. In 1979 a minimum occurred in March (54.3kg boat-day^{-1}) but in 1980 and 1982 it was in July and in 1981 in May. A second minimum in CPUE occurred in November or December each year. Marked seasonal changes in effort were apparent for this area. The annual minimum occurred in March each year and effort subsequently increased steadily to very high levels between July and October, coincident with the large annual increases in CPUE. Effort dropped rapidly after this peak until March.

Species composition

In the period 1979 to 1982, *P. esculentus* was consistently the dominant tiger prawn in the South Groote catches. It comprised between 82.1% (in 1980) and 95.6% (in 1982) of tiger prawns in catch samples (92.9% overall) (Table 2). Catch sample data from the Blue Mud Bay area also showed a predominance of *P. esculentus* (comprising 66.7% overall), but varied between 55.2% (1980) and 70.7% (1981). *Penaeus semisulcatus* was the overall dominant in catches from the North Groote area (64.5%). The proportion of *P. esculentus* varied between 27.7% (1980) and 55.5% (1981).

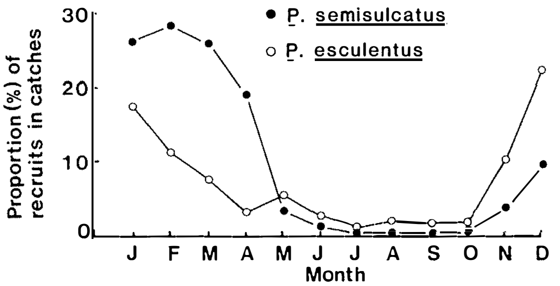

Figure 5. Monthly percentage of recruits (≤ 25mm carapace length) in catch samples in the western Gulf of Carpentaria (pooled data 1979 to 1984) for two species of tiger prawns.

Recruitment

The main recruitment of *P. esculentus* occurred during November to February (Fig.5). During this period the proportion of recruits exceeded 10%. Low levels of small prawns were present during the remaining months. Recruitment in *P. semisulcatus* was delayed one to two months relative to that for *P. esculentus* (Fig.5). The proportion of new recruits present in samples exceeded 10% from January to April, then decreased during July to October and increased again from November.

Reproduction

The smallest female *P. esculentus* with visible ovaries was 21mm CL (a in Fig.6), minimum size at first maturity was 26mm CL, and more

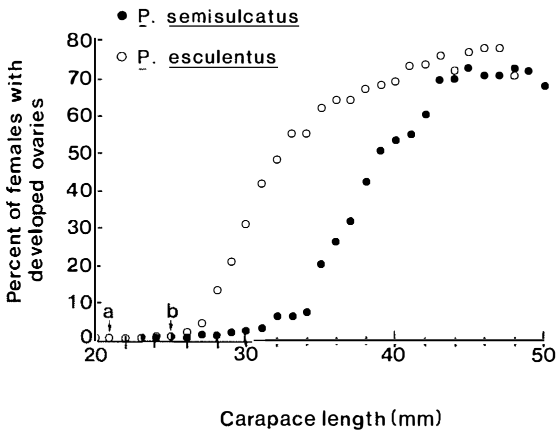

Figure 6. Percentage of females with developed ovaries at each carapace length in the western Gulf of Carpentaria fishery for two species of tiger prawns. Arrows indicate smallest females found with visible ovaries for *Penaeus esculentus* (a) and *P. semisulcatus* (b).

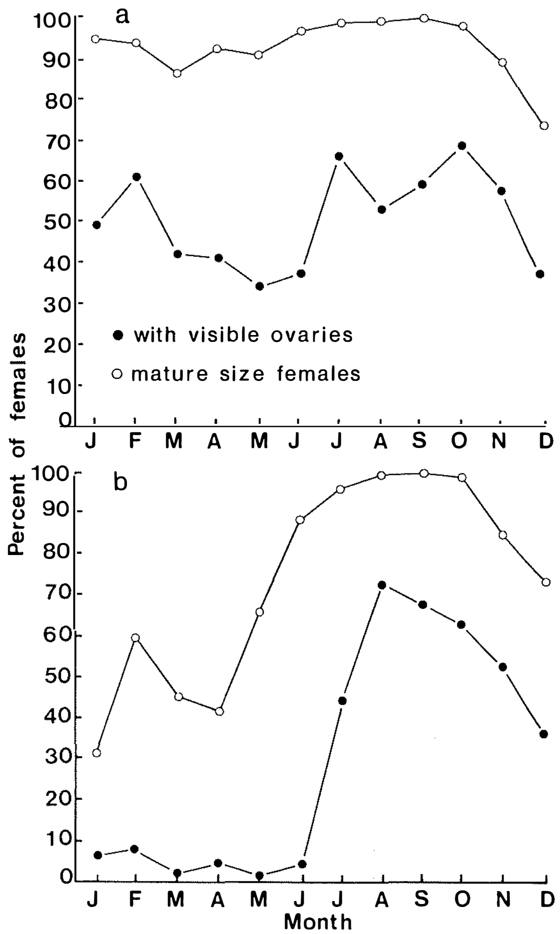

Figure 7. Monthly percentage of mature size females and females with visible ovaries from catch samples in the western Gulf of Carpentaria (pooled data 1979 to 1982) for two species of tiger prawns **a.** *Penaeus esculentus* **b.** *P. semisulcatus.*

than 50% of prawns 33mm CL or larger had visible ovaries. Maturity in *P. semisulcatus* females occurred at a slightly larger size. The smallest individuals with visible ovaries were 25mm CL (b in Fig.6), minimum size at first maturity was 30mm CL and the majority had visible ovaries at 39mm CL.

Between 33.6 and 68.5% of *P. esculentus* females had visible ovaries throughout the year suggesting a protracted spawning period for this species in the Groote Eylandt area (Fig.7a). Nearly 70% of females had visible ovaries in July and October. There were minima in May and December. More than 70% of females in samples of the fished population were of

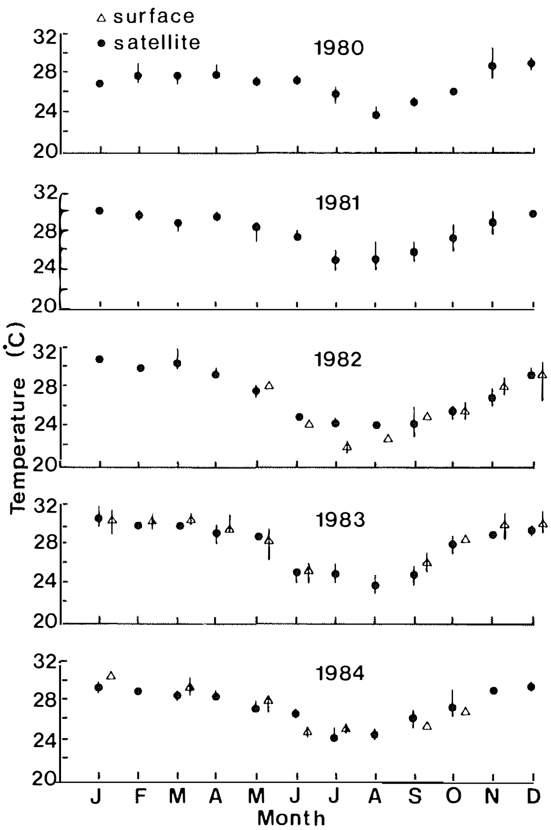

Figure 8. Monthly mean sea surface temperatures from the western Gulf of Carpentaria, 1980 to 1984. Data were obtained from satellite measurements and from trawl records. Vertical lines indicate range.

mature size (≥ 26mm CL) in all months. Between June and August the proportion of female *P. semisculcatus* with visible ovaries increased from 4 to 72%. It remained high to December but was less than 10% throughout January to June (Fig. 7b). This pattern reflected the size of prawns within samples. During the January to June period, the proportion of mature size females (≥ 30mmCL) was reduced and there was consequently a low level with developed ovaries. During January to June, the proportion of mature size females increased from 30 to 87% but there was no corresponding increase in the proportion with visible ovaries.

Temperature

The annual cycle of sea surface temperatures in the Groote Eylandt region for 1980 to 1984 is shown in Fig. 8. Annual maxima in mean temperature (of approximately 30° C) occurred between November and April. Temperatures declined slowly to about 28° C in April-May, then to the annual minimum of about 24° C in July or August. Warming to the annual maximum proceeded over the next four months.

Discussion

Commercial catch sampling showed that the tiger prawn fishery south of Groote Eylandt was based mainly (93%) on *P. esculentus.* In the areas north of Groote Eylandt, however, *P. semisculcatus* was far more common and made on average 34 to 64% of the catch of tiger prawns. The tiger prawn fisheries all showed a basic pattern of two peaks in catch each year, one in summer to autumn between February and May, and one usually in spring between August and November. The summer to autumn peak appears to be the result of recruitment of young prawns into the fishery. Both species of tiger prawns recruit in summer but *P. esculentus* recruits earlier on average (November to February) than does *P. semisulcatus* (January to April). It would be reasonable to expect a difference in the timing of the summer to autumn peak in the single species fishery south of Groote as compared to the two species fishery north of Groote Eylandt. However, no marked difference was seen in the commercial catch data. The cause of this discrepancy is not known but could be related to the low fishing effort at this time. In all these areas, there was a decline in CPUE from April to June which may have been caused by a number of factors.

Several factors may contribute to the decline in CPUEs from April to July. The close correspondence between this decline and decreasing water temperatures between April and July, suggest that catchability changes related to temperature may contribute to the CPUE trends. Variations in the catchability of penaeids with temperature have been noted by several authors, eg Fuss and Ogren (1966), and Penn (1976). Changes in duration of emergence were related to temperature in *P. latisulcatus* by Penn (1976) and in *P. esculentus* by Hill (1985). Some reduction in CPUE would also have been caused by fishing depleting the stock. Movement of the prawns progressively from their nursery areas to the offshore adult habitat could also have been a contributing factor. Somers and Kirkwood's (1984) observation that prawns (*P. esculentus* and *P. semisulcatus*) tagged in March, soon after recruitment, showed more extensive movement and species separation than those tagged in June, supports the dispersal hypothesis.

The August to October peak in CPUE occurred in all three areas. Rapid increases in CPUE from the winter low period corresponded to the spring rise in water temperature. Thus a catchability change associated with temperature may have contributed to the elevated spring CPUE.

Somers and Kirkwood (1984) formed two hypotheses about differences in the migration patterns between *P. esculentus* and *P. semisulcatus.* Firstly that movements may be associated with separate spawning strategies for the two species relative to the transport of larvae to nursery grounds or, secondly, that adults of the two species merely have different habitat preferences. It is possible that movements related to either hypothesis might lead to enhanced CPUEs due to local concentrations of the stock. Schooling of *P. semisulcatus* has been noted for the Kuwait fishery for this species (Van Zalinge et al 1981).

The spring increase in CPUE also corresponded to the periods of major spawning activity for *P. esculentus* and *P. semisulcatus.* Peaks in the proportions of females with visible ovaries and of recruits, are clearly related in *P. semisculcatus,* and both spawning and recruitment are strongly seasonal. In *P. esculentus,* however, although a continuously high proportion of females had visible ovaries, major recruitment was restricted to a relatively short period (November to February). Thus recruitment in this species may be more dependent upon factors affecting larval transport and subsequent juvenile growth and migration processes rather than a spawning peak alone. The impact of environmental perturbations on the protracted spawning of *P. esculentus* is likely to be less dramatic than on the closely defined pattern of *P. semisulcatus.*

It is important to consider the impact of fishing effort on the CPUE and life history patterns described above. Increased fishing effort early in the year would affect survival to the spring spawning season for both species. However its impact would be greatest on *P. semisulcatus* which has the more restricted spawning season. In addition to reducing the number of prawns surviving to the species' major spawning period, there would also be a concomitant reduction in the average size of the individuals that survive to spawn. The result of these two effects is to reduce population fecundity at a time critical for synchronisation with the period when conditions lead to the highest recruitment success.

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Deepwater prawn resources off southern and central Queensland

Abstract: Trawl surveys off southern and central Queensland between 1982 and 1984 found deepwater prawn resources. In the survey off southern Queensland small productive areas of trawlable ground were found on the upper continental slope. Echo soundings and trawls off central Queensland indicated that there was an area of several thousand nautical miles² of trawlable ground on the outer shelf and upper slope. Catch rates greater than 8 kg h^{-1} were recorded for five species of prawns. On the continental slope off both southern and central Queensland, three commercial species—the scarlet or giant scarlet prawn, *Plesiopenaeus edwardsianus,* the red prawn, *Aristeomorpha foliacea,* and the royal red prawn, *Haliporoides sibogae*—were caught in depths from 380 to 740 m. A smaller undescribed species of *Haliporoides* was also abundant in these depths. Off central Queensland, eastern king prawns, *Penaeus plebejus,* were taken on the outer shelf east of the Swain Reefs in depths of 150 to 225 m.

A number of trawlers have worked the new king prawn grounds east of the Swain Reefs since their discovery. Apart from a brief period in late 1982 and early 1983, the deepwater species have remained unfished. Future utilisation of the deepwater resources is however uncertain, as logistic and economic factors may prevent development of these resources.

Introduction

Deepwater trawl surveys conducted off the New South Wales coast have found resources of deepwater prawns (Gorman and Graham 1975). The recording of small catches of prawns from depths of 370 to 740 m off Point Danger (Fig. 1) (Gorman and Graham 1978) indicated that deepwater prawns may also occur off the southern Queensland coast. Marshall (1978) described the depth of the shelf break, off southern Qld and northern NSW, as varying between 210 and 450 m, with gradients on the upper continental slope varying between 7° and 25°. An area with these characteristics could be expected to include trawlable grounds. Previous survey work off the southern part of the Great Barrier Reef (Hughes 1981) indicated that future survey work aimed at prawn resources might locate king prawns, *Penaeus plebejus,* and other deepwater prawn species off the central Qld coast.

Deepwater trawl surveys for prawn resources were conducted off the southern Qld coastline in 1982-83 and off central Qld in 1983-84. The main aims of both surveys were to locate unexploited stocks of prawns in waters of the outer continental shelf and slope; to identify species with commercial potential; and to evaluate the economic potential of the stocks.

The major justification for the surveys was the expectation that if new grounds and resources were discovered, then some fishing effort might be diverted from the adjacent continental shelf trawl fisheries. Although some components of the Queensland east coast trawler fleet have maintained good returns to capital (Hundloe 1981), there is a general belief that the east coast prawn fishery is over capitalised with too many vessels working on the established grounds (Anon. 1982). The exploitation of new resources by the fleet would disperse these vessels over a greater working area and should result in improved catches and an enhanced

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ratio of return to capital invested. Existing management regulations allow vessels permitted to fish off the Queensland east coast direct and unimpeded access to such newly discovered resources.

In this paper, results of the two surveys are summarised and limitations on the development of deepwater trawl fisheries off the southern and central Qld coasts are discussed. Some survey results have previously been published (Dredge and Gardiner 1984; Potter 1984).

Methods

Trawl surveys

The area surveyed off southern Qld, approximately between 26° S and 28° S (Fig. 1), is a relatively narrow strip parallel to the coastline. Gorman and Graham (1978), suggested that the trawlable area south of 27° 35′ S was restricted. Therefore selected depths were surveyed by echo sounder to chart bottom conditions. Initially the whole area between the 200 and 600 m depth contours was broadly surveyed and then later examined in more detail. Position fixes were made with both radar and satellite navigator. Trawls were attempted, where possible, with a single 27 m headrope, 40 mm mesh Siebenhausen prawn trawl. On some occasions, when areas became better known, triple 27 m trawl gear was used to improve catches. Five cruises with an average duration of three days were undertaken between July and September 1982 and another four cruises were completed in November and December of 1982. In 1983, four more cruises were undertaken between March and June. A total of 67 trawls was completed.

The area off central Qld in which the survey was carried out was between approximately 22° S and 24° S, 152° E and 154° E, and exceeded 14000 nautical mile² (Fig. 1). Because of the area's extent, five transects which covered grounds either in depths of 180 to 240 m, or grounds with a wide range of depth contours, were selected to be surveyed. The shallower transects were in the known depth range of adult king prawns. The deeper transects were chosen to give an extensive coverage of both depth range and area within the geographic limits of the survey. Bottom

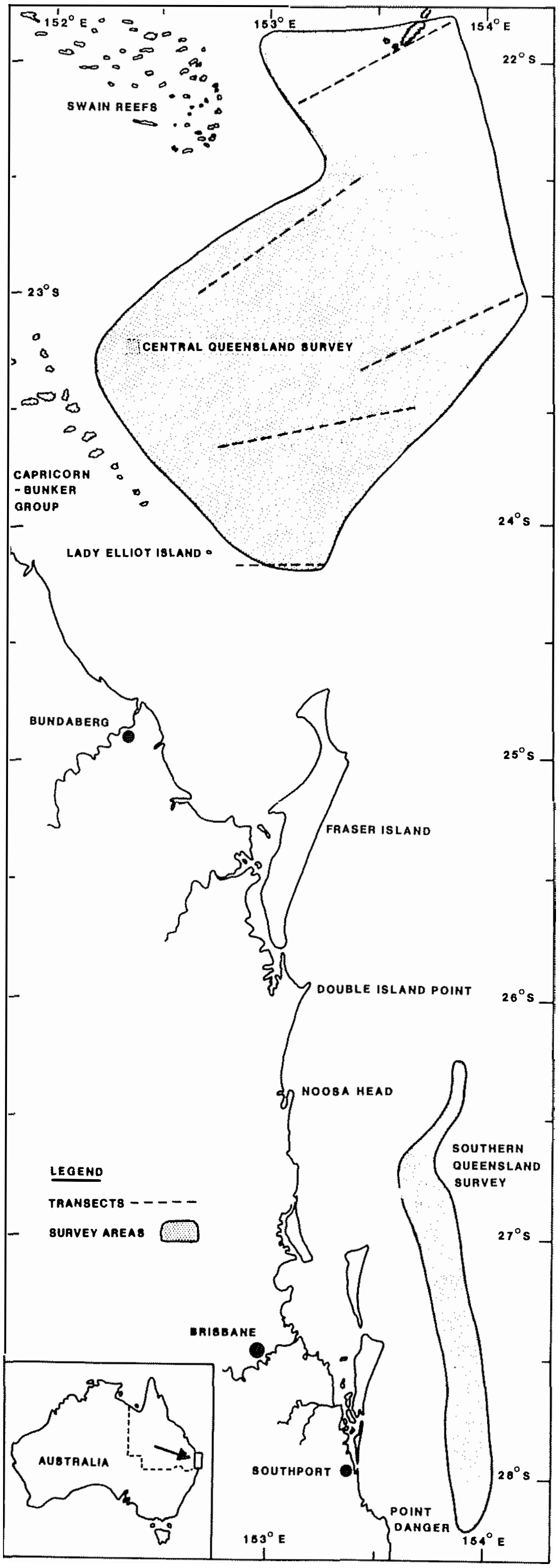

Figure 1. Survey areas for deepwater prawn resources off southern and central Queensland.

conditions on these five transects were examined by echo sounding. Trawls were conducted at predetermined depth intervals, where possible using a single 27 m headrope and 50 mm stretched mesh Siebenhausen trawl.

During a two-month period commencing in August 1983 transects were surveyed, 26 trawls were completed, and grounds suited for trawling were plotted. In the following ten months, another 23 trawl samples were taken either at predetermined depth intervals along the original transect lines, or adjacent to those areas where promising prawn catches were taken during the first two months of the survey.

In both surveys, when trawls were completed, prawns were separated from trawl bycatch and segregated into species or species-complex groupings. Catch weights of prawns were estimated by vessel crews using a volumetric conversion. Subsamples of up to 20 kg of prawns were retained for laboratory examination of meat recovery, length-weight relationships and size distribution.

Economic survey

Data on costs and earnings of central Qld trawlers longer than 18 m were obtained by personal interviews with vessel owners in order to estimate returns to capital for this component of the fleet. Tax return data were not used in this survey. The vessel size constraint was set because smaller boats could not participate in the potential deepwater fishery. The economic survey covered the 1982-83 and 1983-84 financial years. Estimated cost flows incurred by a new 20 m vesel are based on those of fleet operators in 1983 (D. Carter[2], pers. comm). These two data sets have been used to determine the catch required for a financial break-even point to be achieved for existing 18 m or new 20 m vessels exploiting the deepwater prawn resources. Prices for deepwater prawns have been set on the basis of those received during the trawl surveys.

Results

Trawl surveys

The southern survey area (Fig. 1) was between the 200 m and 700 m depth contours. It varied from 8 to 12 n miles wide, and was approximately 20 to 30 n miles offshore. Trawlable ground was limited to an area of approximately 140 n mile², distributed ENE of

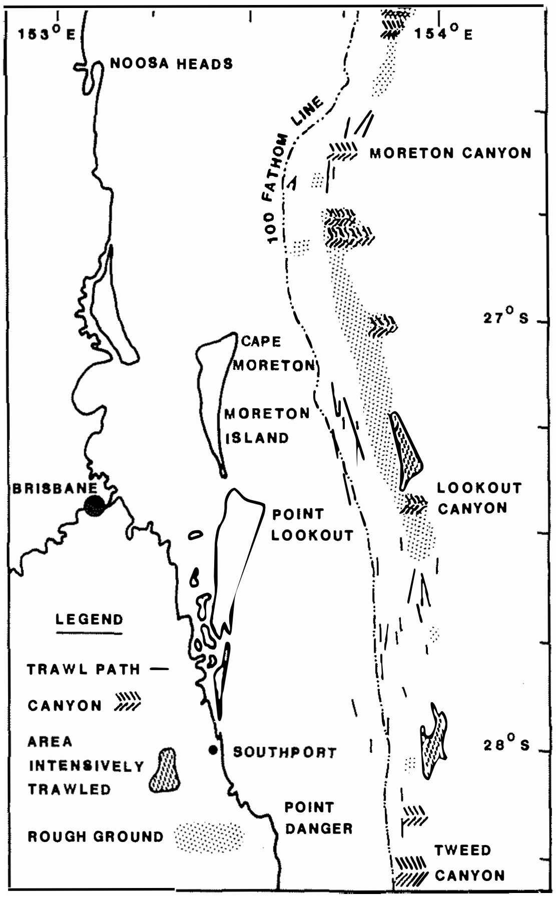

Figure 2. Trawl sites and trawl grounds for the southern Queensland survey of deepwater prawn resources. The 100 fathom line (185 m) is shown.

Point Lookout, NE and E of Southport (Fig. 2). A number of submarine canyons were encountered in depths greater than 300 m, similar to those off the NSW coast. North of Cape Moreton most of the continental slope deeper than 400 m was considered to be too steep for conventional otter trawling. Some sections of the continental slope between Cape Moreton and Point Danger (Fig. 2) were also deemed untrawlable for this reason.

By contrast, off central Qld the survey covered more than 14 000 n mile² with much of the area in the 200 to 700 m depth range (Fig. 3). Soundings and trawls indicated that most of the area surveyed was trawlable. Submarine canyons were encountered in the southeastern sector of the survey area, and a series of gravel beds was found between 150 and 220 m near

[2] David Carter, KFV Fisheries, Townsville, Qld.

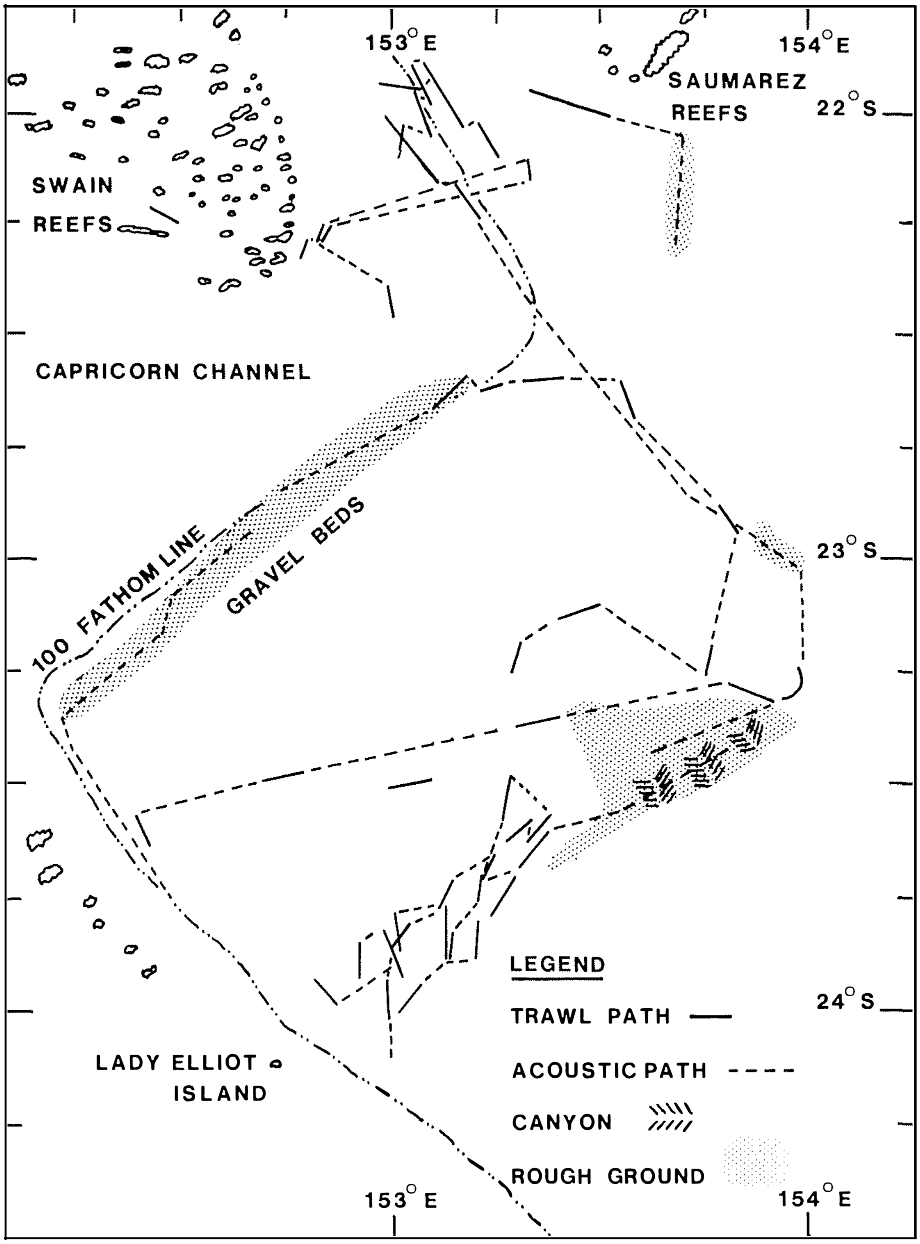

Figure 3. Trawl sites and acoustic survey paths in the central Queensland survey of deepwater prawn resources. The 100 fathom line (185 m) is shown.

the Capricorn Channel. These untrawlable areas represented less than 10% of the total area surveyed (Fig. 3).

During the two surveys 15 to 20 species of penaeid prawns were collected. The identity of several of these species has yet to be confirmed. Of the known species, eastern king prawns, *Penaeus plebejus,* are a valuable commercial species off the Qld coast. Another four species were sufficiently abundant to be of commercial interest. These were the scarlet or

Table 1. Depth distribution and mean catch rates of deepwater prawn species taken by a single 27 m headrope trawl during the southern and central Queensland surveys. Ranges of catch rates are shown in parentheses.

Depth range	No. of trawls	Mean catch rates (kg h^{-1}) Scarlet prawn	Red prawn	Royal red spp.	Eastern king prawn	Total prawns
Southern Qld						
210 to 250	15	0	0	0		0
251 to 300	5	0	0	0		0
301 to 350	0			no data		
351 to 400	6	0	1.5 (0-9)	3.5 (0-11)		5 (0-20)
401 to 450	0			no data		
451 to 500	2	0	5.0 (0,10)	0		5 (0,10)
501 to 550	18	5.0 (0-38)	5.7 (0-27)	6.3 (0-28)		15 (0-70)
551 to 600	15	3.9 (0-14)	4.8 (0-19)	5.5 (0-20)		14 (0-28)
601 to 620	2	11.1 (8,15)	2.7 (2,4)	2.7 (2,4)		16 (15,18)
Central Qld						
150 to 200	6	0	0	0	5.2 (1-9)	5
201 to 250	5	0	0	0	2.1 (0-4)	2
251 to 300	2	0	0	0	0	0
301 to 350	5	0	0	0	0	0
351 to 400	4	0	0	0.4 (0-0.5)	0	0.4 (0-1)
401 to 450	5	0	0	2.9 (0-13)	0	3 (0-13)
451 to 500	5	0	0.1 (0-0.7)	2.9 (0-10)	0	3 (0.5-10)
501 to 550	2	0.3 (0,0.5)	7.0 (2,13)	0.3 (0,0.5)	0	8 (2,13)
551 to 600	3	0.5 (0-1)	13.8 (2-35)	5.0 (0-10)	0	19 (10-36)
601 to 650	4	5.4 (0-8)	10.4 (0-28)	2.5 (0-6)	0	18 (2-35)
651 to 700	2	1.3 (0.5,2)	7.5 (4,11)	2.9 (0.8,5)	0	12 (7,17)
701 to 740	1	1.0	5.0	1.0	0	7

giant scarlet prawn, *Plesiopenaeus edwardsianus,* the red prawn, *Aristeomorpha foliacea,* and two species of the genus *Haliporoides,* commonly known as royal red prawns. These latter four species are deepwater species which complete their entire life cycle in offshore waters. They were found in water depths greater than 380 m, whereas the maximum depth for commercial catches of eastern king prawns was 240 m. Mean catch rates for each of these species are given in Table 1. There is some indication of individual species having preferred depth ranges which overlapped and thus gave mixed catches. Off the southern Qld coast the highest catch rates for mixed deepwater prawns were taken in the depth range 501 to 620 m but off central Qld the highest catch rates were in the 551 to 700 m depth range (Table 1). Red and royal red prawns generally constituted two thirds to three quarters of the prawn catch in these depths.

Scarlet prawn

The scarlet prawn, *Plesiopenaeus edwardsianus,* is a large species with bright red coloration and long legs and pleopods. They were taken in water depths of 530 to 740 m, with a maximum catch rate of 38 kg h^{-1} taken in 530 m off southern Qld (Table 1). By comparison, the maximum catch rate achieved off central Qld was 8 kg h^{-1} taken in 650 m. Individual scarlet prawns weighed between 7 and 180 g. Samples generally had a wide size distribution. Scarlet prawns caught off southern Qld in November 1982 had a mean size of 62 g (range 22 to 146 g) and in June 1983 a mean size of 40 g (range 7 to 112 g). Off central Qld in April 1984, the mean size was 58 g (range 10 to 178 g).

Tail and meat recovery rates averaged 47% and 35% respectively. By comparison, most *Penaeus* species have tail recovery rates of approximately 60% (P. Kelly[3], pers. comm.) The low recovery rates for scarlet prawns are a consequence of the relatively large cephalothorax, slim abdomen and long abdominal appendages.

Red prawn

The red prawn, *Aristeomorpha foliacea,* was an important component of deepwater catches in

[3] Pat Kelly, Sandgate Fishermen's Cooperative, Sandgate, Qld.

both surveys (Table 1). It was found in water depths of 380 to 740 m, but was most abundant in the depth range 530 to 700 m. The best catch rate recorded was 35 kg h^{-1} with single trawl gear in 590 m off central Qld. Red prawns share some of the morphological features of scarlet prawns in having a relatively large cephalothorax and long abdominal appendages. However it is not as large as the scarlet prawn. The mean weight from a sample of red prawns taken off southern Qld in June 1983 from 380 m was 21 g (range 12 to 34 g) and from 520 m was 18 g (range 12 to 35 g).

Royal red prawn

Two species of *Haliporoides* were taken in both surveys. In the southern area, *Haliporoides sibogae* was abundant in depths from 380 to 600 m (Table 1). In June 1983 it comprised approximately 50% of survey catches by weight. The mean weights from three samples taken in 380, 520 and 560 m off southern Qld ranged from 10.5 to 15 g. Off central Qld this species was rare with catch rates less than 1 kg h^{-1}. Generally the few caught were relatively large specimens with individual weights above 25 g.

The second *Haliporoides* species taken in these surveys has not yet been described, although it has also been found off the NSW coast (Graham and Gorman 1985). It is separated from *H. sibogae* by its yellowish hue, the greater curvature of the rostrum, and the distinctive white stripe on the distal portion of the uropod.

This species was not separated from *H. sibogae* until the southern survey was partially completed. Data from June 1983 samples indicate that it was a minor component of those catches, comprising between 0 and 43% of the royal red prawn catch. Off the central Qld coast this species was considerably more abundant than *H. sibogae,* comprising more than 90% of the royal red prawn catch. However the mean weight (8 g) is too small for the species to be of commercial value at this time.

Eastern king prawn

In the central Qld survey, eastern king prawns, *Penaeus plebejus,* were found east of the Swain Reefs (Fig.3) in depths of 150 to 225 m. Catch rates in this area ranged from 1 to 9 kg h^{-1} with maximum catch rates in depths from 150 to 190 m (Table 1). The king prawns taken on these grounds were large adults. In two May 1984 samples, king prawns averaged 54 g (range 30 to 87 g). All females in the sample had visible golden yellow ovaries.

Table 2. Average costs and earnings for five central Queensland trawlers >18 m in 1982-83. Values in $ thousands.

Average capital investment	300
Average annual costs	
Imputed interest	33.5
Depreciation	30
Insurance	9
Licences, etc.	2
Wharfage, slippage	8.5
Wages (skipper, crew)	96
Fuel	56
Repairs	27
Hardware, equipment	24
Processing costs	15
Total	301
Income (190 fishing days)	
Average gross annual income	323
Average gross daily income	1.7
Average net annual earnings	22
Average net return to capital	7.3%

Economic analyses

Trawlers in the central Qld region participate in fisheries for king prawns, banana prawns and scallops. Processing costs are incurred in scallop fishing when scallops are shucked on board the vessels (Table 2). Average net return to capital for the five vessels sampled was 7.33%. In order for these vessels to participate in a deepwater fishery, changes to the cost structure of the fishing plant would be needed. Upgrading costs for existing trawlers were estimated to be $50 000, and some variable costs, particularly those for fuel, would be greater in a deepwater fishery than for the present coastal fishery (Table 3). Crew wages, which were set on the basis of percentage sharing of the gross income to the vessel (35%), were greater in the deepwater fishery because an additional crew member was required to handle the larger catch volume. Fishing time (days at sea each year) was assumed to be the same for both fisheries. Prices for mixed red and royal red prawns varied between $1.50 and $2.60 kg^{-1} according to season and port of landing. Scarlet prawn prices ranged from $2.80 to $4.00, and on one occasion $9.50 kg^{-1}. For the purpose of economic assessment, average prices for these two groups of prawns were set at $1.80 kg^{-1} and $3.60 kg^{-1} respectively, giving an overall average of $2.25 kg^{-1} for a mixed catch. Implied costs were established with wages being determined at break-even point where total cost equals gross return (Table 3). An average daily catch rate of 812 kg of mixed

Table 3. Estimated costs and break-even catches for vessels operating in potential deepwater prawn fisheries. Values in $thousands.

	Existing east coast trawler >18m	New 20m vessel
Capital investment	350	600
Annual costs		
Imputed interest	39	67.5
Depreciation	35	60
Insurance	9	15
Licences, etc.	2	1
Wharfage, slippage	8.5	5
Wages (skipper, crew)	121.5	108
Fuel	70	125
Repairs, refitting	27	35
Hardware, equipment	35	50
Administration costs	—	50
Total	347	516.5
Annual income to break even	347	516.5
Days fished	190	240
Average daily catch required (kg)	812	956

deepwater prawns, at the prices set, would be required to achieve the break-even point.

A possible alternative strategy was to introduce new capital by considering the potential costs and earnings of a new 20m vessel to fish the presently unexploited deepwater prawn stocks (Table 3). A larger vessel would be better suited to work in offshore areas than existing east coast trawlers. Capital and running costs for such a strategy have been based upon those incurred by company operated vessels and include an administration cost which is not a component of private vessel's costs. Yearly fishing time for this vessel was set at 240 days based on the average number of days in the year for which wind speed is less than Beaufort scale 6 at Lady Elliot Island (Australian Bureau of Meteorology, unpublished data). A break-even analysis has been used to consider the economic consequences of this strategy (Table3). An average daily catch rate of 956kg of mixed deepwater prawns would be required to achieve the break-even point for this vessel.

Discussion

Penaeus plebejus is the principal component of the southern Qld and NSW ocean prawn trawl fisheries and is commonly taken in depths of 100 to 180m off southern Qld. The new grounds off central Qld which are now being fished for king prawns cover an area of some 450n mile². They represent a northward extension to the fishery for eastern king prawns to approximately 21° S and are now being fished regularly, and can be regarded as an established part of the Qld east coast trawl fleet's resources.

The three deepwater prawn species which were considered to have commercial potential have wide geographical distributions. Scarlet prawns, *Plesiopenaeus edwardsianus,* are found in the Atlantic, Indian and Pacific oceans, and are caught most frequently in depths of 400 to 900m on mud bottoms. They support a commercial fishery in this depth range off west Africa (Holthuis 1980). The species was not previously known to occur in commercial quantities in Australian waters (Grey et al 1983). Burukovskii (1980) postulated that the species had a life span of three to four years in its southeast Atlantic distribution. Red prawns, *A. foliacea,* are also found in the Atlantic, Indian and Pacific Oceans, and the Mediterranean Sea where they are fished commercially. They are known to occur in the depth range of 250 to 1300m, on mud bottom (Holthuis 1980). Of the two royal red species taken, one is undescribed. The other, *H. sibogae* is known from the Indo-West Pacific region where it occurs in depths of 350 to 600m (Holthuis 1980).

The northern limits of grounds which support commercial quantities of the deepwater prawns species have yet to be defined. Small quantities of scarlet prawns were taken off Mackay, at 21° 07′ S, 153° 33′ E in a depth of approximately 600m (King[4], pers. comm.). Bathymetric charts indicate that north of 22° S there is a large area in the 200 to 700m depth range east of the Great Barrier Reef. This area has received little attention from exploratory surveys to this time (Hughes 1981).

The deepwater trawl grounds discovered off Point Lookout (approx. 27° 25′ S, 153° 50′ E) in the southern area were fished by commercial vessels in November 1982 and several daily catches in excess of 1000kg were reported (Hodge[5], pers. comm.). Even so, no commercial fishing has taken place on these grounds since early 1983. Little attempt has been made to develop the deepwater prawn resources

[4] Michael King, Australian Maritime College, Launceston, Tas.
[5] John Hodge, Central St., Southport, Qld.

discovered off central Qld in water depths greater than 300 m.

We have attempted to identify operational and economic factors which appear to be hindering the development of these potential fisheries. There are some fairly obvious operational factors making the areas and the target product less attractive to fishermen than fishing for eastern king prawns. In the southern survey area, the grounds are smaller and further offshore, and are exposed to rougher sea conditions than king prawn grounds on the adjacent continental shelf. In the central Qld survey area, the 380 to 740 m depth zone, which has the greatest potential, is 12 h travelling time from the nearest port and 6 h from the nearest sheltered anchorage. Most existing vessels are too small to work in these conditions with an adequate safety margin.

The product is caught in larger volumes than eastern king prawns and hence is more time-consuming to handle. Although scarlet prawns do not appear to suffer from black spot, both royal red and red prawns do, which make them more difficult to handle than king prawns.

There are also important economic factors that hamper the development of a fishery for deepwater prawns by fishermen participating in the existing east coast trawl fishery. The prices quoted previously for royal red and red prawns sold in the survey period were poor. Scarlet prawn prices were considerably better but averaged less than half of the king prawn prices.

The return to capital for vessels >18 m reflects costs and earnings of experienced and well established operators whose boats have the capacity to move to the deepwater grounds. Hundloe (1981) gave returns to capital of 8 to 12% for the central Qld trawl fleet. To upgrade 15 to 18 m east coast trawlers to work in the deepwater fishery, most existing vessels would require expenditure of about $50000 for additional warp wire and a satellite navigator, and to upgrade sounders and winches.

To examine the economics further we have considered two strategies. The first is to upgrade a vessel from the existing east coast fleet (which fish in water depths less than 225 m) to work in the deepwater fishery. A break-even analysis was used to estimate the average daily catch from the deepwater grounds needed to cover all actual and imputed costs (Table 3). Dredge and Gardiner (1984) suggested that a daily catch rate of 800 kg could be achieved on the deepwater grounds between Saumarez Reef and Lady Elliot Island. We estimate that an average daily catch rate of 812 kg of the deepwater species would be required to achieve the break-even point without return to capital. While this average daily catch rate is high compared with the king prawn fishery (approximately 200 kg) it compares favourably with catch rates attained by commercial vessels that worked off Point Lookout in November 1982. The data from the surveys are not adequate to judge whether such catch rates could be sustained throughout the year.

An alternative strategy is to bring in new vessels to work the unexploited deepwater prawn stocks. A break-even analysis was also used to consider the economic consequences of this strategy. Costs incurred by such a vessel are obviously much greater than those of an existing vessel, particularly for fuel and imputed finance costs. These greater costs are reflected in the larger daily catch (956 kg) which would be required to attain the break-even point, even though such a vessel would be able to work for a greater number of days each year than existing east coast trawlers.

In summary, it would appear that there is little incentive for existing vessels in the east coast trawl fishery to move into the potential deepwater fishery. The catch rates required to match their present economic performances are high; the grounds are new and more difficult to work; the product is more difficult to handle; and the market is less certain. For new vessels to enter the fishery and maintain economic viability a long term average daily catch rate of almost one tonne would be required. Before such an investment could be made, exploratory work concentrated on optimising catch rates for these stocks would be advisable.

It seems unlikely that the deepwater resources will be developed by the existing fleet while vessels have unlimited access to the eastern king prawn stock. The new king prawn grounds are being extended by the fleet and should be treated as an integral part of the king prawn fishery for management purposes. If the deepwater prawn resources (defined as those in waters deeper than 300 m) are to be developed, they should not be included in any restricted entry plan for the existing east coast trawl fleet.

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New South Wales deepwater prawn fishery research and development

Abstract: Between 1971 and 1982 exploratory fishing and stock assessment programs were conducted by the New South Wales state government fisheries research vessel Kapala for deepwater prawns. The New South Wales continental slope between depths of 200 and 800 m was surveyed acoustically and trawlable bottom delineated. Effective prawn trawling gear was developed and standardised. Royal red prawns, *Haliporoides sibogae,* were found in commercial quantities off the Clarence River and between Crowdy Head and Jervis Bay in depths between 350 and 550 m. They were available both day and night, but daytime catch rates were usually higher. Using the swept area method, a minimum indicated stock of 1410 t of royal red prawns was calculated for the Crowdy Head to Jervis Bay area. Length frequency data of royal red prawns from all areas north of Jervis Bay showed little variation with time. The heads-on counts ranged from 60 to 75 kg^{-1} and the meat yield was about 50% of their total weight. Breeding was observed twice annually, during March-April and July-August. Development of the fishery has been slow. However, total landings increased from 76t in 1976-77 to 494t in 1982-83.

Introduction

Investigations during 1971-72 of the New South Wales (NSW) continental slope prawn stocks gave a first estimate of the total stock size for the ground off Sydney, and discussed some of the problems of handling and processing the catch (Gorman and Graham 1975). In 1975 an assessment of the deepwater trawl-fish stocks off NSW was begun and further exploratory trawling and investigations into the prawn stocks were also carried out. By 1979 detailed charting off the upper continental slope trawling grounds was completed and the extent of the deepwater prawn grounds off NSW was delineated. The prawn trawling conducted between 1975 and 1982 provided additional information on the distribution and size of the stocks; biological and morphometric data were also collected.

Commercial fishing for royal red prawns began in 1975 and annual landings increased steadily. This paper updates the earlier report and includes recent research data and information on the commercial fishery.

Methods

Survey procedures

A reconnaissance of the upper slope between the Clarence River and northeastern Bass Strait was carried out during 1971. The bottom was surveyed by echosounder and where suitable, trawls were conducted. In 1972 a stratified sampling program on the ground between Port Stephens and Sydney was completed. Between 1975 and 1982, 151 trawls for prawns were conducted on the continental slope between southern Queensland and northeastern Bass Strait. These included exploratory trawls made during more detailed charting of the slope, and directed trawls for deepwater prawns on previously charted grounds.

Catch weights of prawns and fish were recorded for each trawl, and length frequency data for the important species collected. Length-weight data and some biological observations were also recorded.

Fishing gear

Nets

The design of the prawn nets used during the surveys allowed for easy repair of damage during exploratory trawling on new grounds and coped with the high incidental fish catches experienced. The four seam design included long tapered panels and extension sections to give good water flow and easy passage of fish and prawns into the codend.

The headrope lengths of the nets used during the early surveys were between 19.5 m and 22.6 m. This range was selected to relate the survey to existing prawn trawling practice, as nets of this size were suitable for most NSW trawlers. More recently, nets of basically the same design but with extended wings were constructed. The headline lengths of these nets were 24.6 m and 27.1 m (Fig.1).

The footropes of the first nets were rigged with chain hung in bights but this arrangement lacked versatility and could not cope with the various bottom types and fishing conditions encountered during the surveys. As a result, a rubber disc and spacer bobbin assembly was developed (Fig. 1) and it proved to be very satisfactory. Underwater observations on the net showed the footrope to be lightly skimming the seabed, and during subsequent survey work, net damage near the footrope was negligible and catches contained little bottom debris.

Otter doors and accessories

The otter doors used with all nets were 1.8 m steel vee doors. The standard design was modified by enlarging the ballast plate to increase the weight of each door from 172kg to 308 kg. This gave the doors a faster sinking rate and ensured good bottom contact when using low warp-length to depth ratios. Their performance was very satisfactory on the varying substrates and conditions encountered. During both prawn and fish trawling operations, 45 m sweep wires and 30 m bridles were employed between the doors and net. This allowed for easy switching of prawn and fish trawls during multi-purpose cruises but also increased the incidental fish catches when trawling for prawns.

Warps

The main warps were either 1 450 m x 14 mm diameter or 1 830m x 12 mm diameter steel wire rope. A warp-length to depth ratio of 3:1 was maintained where possible but for the very deep trawls this ratio was progressively decreased to about 2:1. The length of warp paid out was measured by two Olympic FM 750 trawl meters which remained accurate throughout all surveys.

Warp-tension meters

Dynamic warp tension meters were fitted during the initial survey. As a result the number of ineffective trawls caused by incorrect trawling speeds was greatly reduced and the warp tension system became an integral part of Kapala's trawling operations. Varying surface currents were frequently encountered but by keeping to established warp tensions the correct ground speed for the trawl was maintained irrespective of surface speed. When trawling on the slope, the normal operating load per warp was about 1 050 kg, which gave a ground speed of between 2.5 and 3.0 knots.

Gear measurements

The Kapala prawn trawls were observed and measured in action by divers using scuba (Gorman and Graham 1977, 1980). Measurements were taken of the headline height, door and wing spread for each net, and many of the detailed design improvements were based on observations of the nets in action. Wing spread, measured at the footrope, was 15.5 m for a 20 m headline trawl, and 19.0 m for a 27 m net. These measurements were used for calculating the swept area of each trawl. Later, wing spread and headline heights of Kapala prawn trawls were made in deep water using a trawl instrumentation system. For the 27 m net, wing spread measured across the headline was 17 m and the headline height was 1.4 m (Gorman and Graham 1982).

Standing stock estimation

The swept area method was used to calculate the size of the standing stock of royal red prawns. This method assumes that the catch per unit effort is proportional to the stock density within an area. Indicated stock density, d, for each trawl is—

$$d = \text{catch in kg} / (\text{swept area in ha} \times C)$$

where C = catchability coefficient. Thus, the estimated standing stock (SS) is

$$SS = D \times A,$$

where D = d / n, A = total area of the ground for which the estimate is made, and n is the total

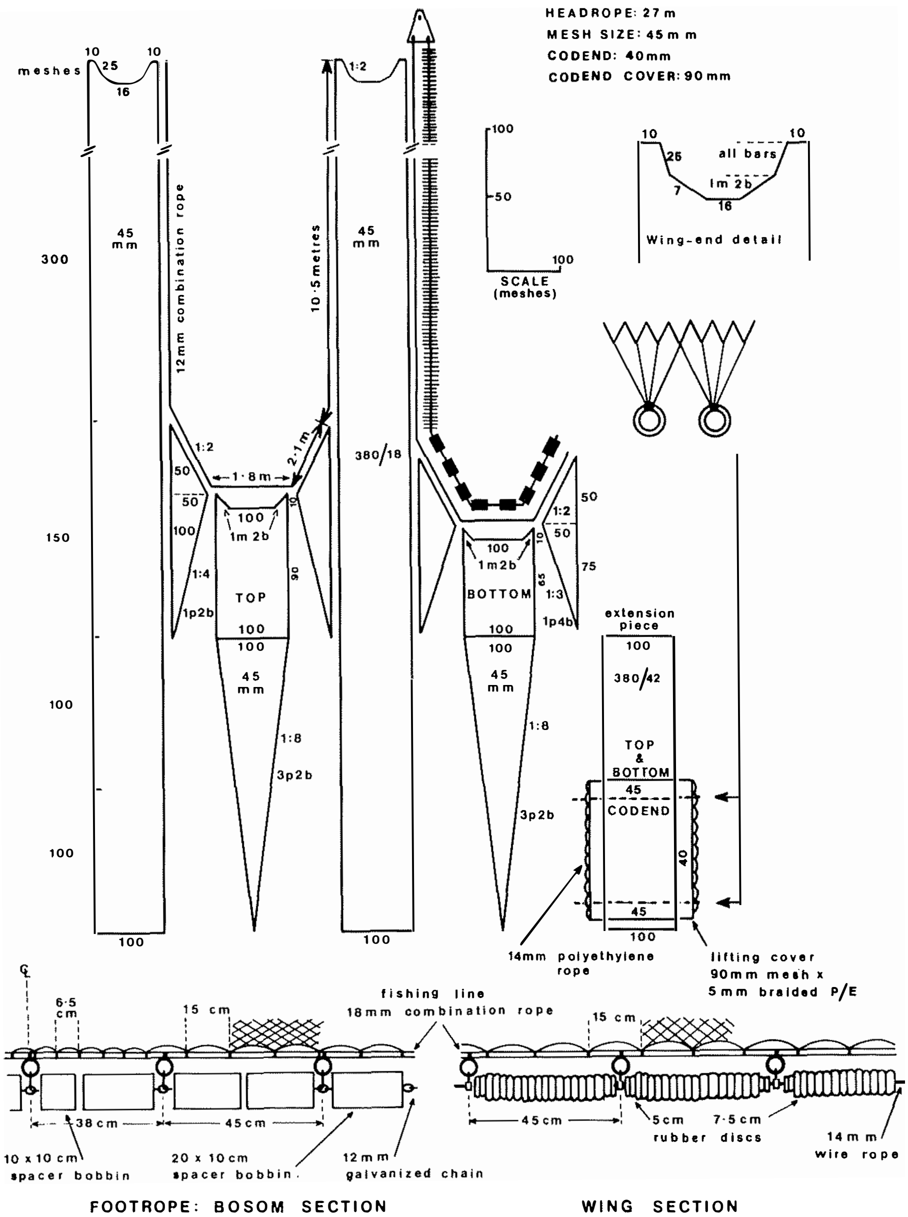

Figure 1. Net plan and footrope assembly for the Kapala 27 m headline prawn trawl

number of trawls. Because the catch rates fluctuated widely, the data showed a high degree of skewness, and a log transformation of the data was used to calculate the mean indicated stock density (D). Francis (1981) states that where the catch-rate is lognormally distributed (where the transformed variable has mean μ and variance σ^2) the true mean catch rate is exp $(\mu + \sigma^2/2)$. This relationship was used to calculate D.

Results and discussion

Continental slope trawling grounds

The NSW coast is approximately 750 nautical miles long and runs from Tweed Heads in the north (28° 10′S) to Cape Howe in the south (37° 30′S) (Fig. 2). Detailed charting of the trawl grounds of the NSW upper slope zone was completed by 1979. The grounds can be divided into six areas which are described below.

Tweed Heads to Point Lookout

The slope between Tweed Heads and Point Lookout, Queensland, was surveyed during 1978 but very limited areas of trawlable bottom were found. Successful trawls were conducted in 365, 410, 550 and 730m. (Coastal charts of NSW offshore waters show depths in fathoms and in practice all soundings were recorded in fathoms; 1 fathom = 1.85m.). Effective trawling was difficult because of strong surface currents, the problems of accurately fixing positions by radar, and the very small area of trawlable ground that was located.

Clarence River to North Solitary Island

This ground was the only extensive area of deepwater trawlable bottom found off the NSW north coast. It is approximately 40n miles long and is smooth between the 180 and 550m depth contours along most of its length. The trawlable area is about 545 km^2 and about one third of this area is between depths of 400 and 550m, the most productive depth range for royal red prawns. A strong south-setting current was often encountered when trawling on this ground. Between North Solitary Islands and Crowdy Head, most of the slope was found to be rough and untrawlable although some small isolated areas of flat bottom were located.

Crowdy Head to Jervis Bay

This is the most extensive deepwater trawling ground off NSW. The area of trawlable bottom is approximately 3500 km^2. Good bottom extends from the continental shelf edge (about 185m) to about 550m along most of its length; between Port Stephens and Sydney, and between Wollongong and Jervis Bay it is trawlable to below 700m. Kapala has carried out successful exploratory trawls off Sydney and Greenwell Point as deep as 1200m (Gorman and Graham 1984). Three significant areas of untrawlable bottom are in 180 to 365m of water between Crowdy Head and Cape Hawke, the designated dumping ground off Sydney, and an area of rough ground between 180 and 475m off Kiama. Canyons were located off Sugarloaf Point, Newcastle, Norah Head, Wollongong, and Jervis Bay.

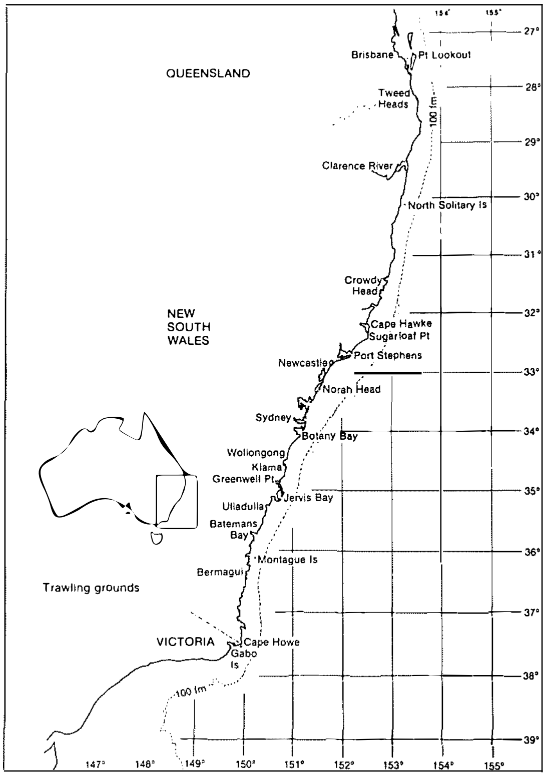

Figure 2. The New South Wales coast showing the continental slope trawling grounds, main fishing ports and the 100 fathom isobath (185m)

Jervis Bay to Montague Island

A small ground between Ulladulla and Batemans Bay is trawlable to deeper than 550m. This ground has several small areas of foul bottom, especially between 365 and 550m, and has a trawlable area of about 260 km^2.

Montague Island to Cape Howe

There is approximately 410 km^2 of trawling ground south of Montague Island, mainly between 220 and 400m; below this depth most of the bottom is very rough with many canyons.

Cape Howe to eastern Bass Strait

A large deepwater ground of about 515 km^2 extends south into eastern Bass Strait off the Victorian coast. The northern and southern areas are trawlable to about 700m.

Areas of deepwater prawning grounds

The areas of the NSW slope trawling grounds

Table 1. Approximate areas (km^2) of each depth zone of the main upper slope prawn trawling grounds off New South Wales.

	Clarence River	Crowdy Head to Newcastle	Newcastle to Botany Bay	Botany Bay to Jervis Bay
Latitudes:	29° 18′ to 29° 58′	32° 00′ to 33° 00′	33° 00′ to 34° 00′	34° 00′ to 35° 00′
Depth zone (m)				
180 to 365 m	340	445	515	670
365 to 550 m	205	335	385	460
550 to 730 m	—	220	250	205

between the Clarence River and Jervis Bay were calculated (Table 1) from Australian east coast navigation charts (Aus 808, 809, 810, 812). The areas are approximate because of the difficulties in precisely fixing positions by radar during some trawling and charting operations, and the paucity of bathymetric data on the charts. Small areas of untrawlable bottom are included in the area estimates.

Prawn survey catches

During the 1971 reconnaisance cruises the full extent of the deepwater trawling grounds off the Clarence River and between Port Stephens and Crowdy Head was not discovered. Two trawls in 320 and 365 m off the Clarence River caught few prawns and no trawling was conducted between Port Stephens and Crowdy Head. The full results were reported by Gorman and Graham (1975). The results for the 1975 to 1982 period are summarised for each area.

Tweed Heads to Point Lookout

During 1978, seven trawls for prawns were conducted off Tweed Heads in depths of 410, 550 and 730 m. Royal red prawns, *Haliporoides sibogae,* were caught in all trawls but the maximum catch rate was only 25 kg h^{-1}. In the 730 m trawl, the small prawn catch included several specimens of scarlet prawns, *Plesiopenaeus edwardsianus,* and red prawns, *Aristeomorpha foliacea.* Although the catches were small the 1978 survey did extend the known geographical range of the main deepwater prawn species into waters off southern Queensland.

Clarence River to North Solitary Island

The mean catch rate for royal red prawns from 11 trawls southeast of Clarence River, between 365 and 500 m was 55 kg h^{-1}. Carid prawns, principally *Plesionika martia,* were common in the trawls deeper than 450 m. Rough bottom prevented trawling at depths greater than 500 m.

Crowdy Head to Jervis Bay

Crowdy Head to Newcastle: Nine trawls between 365 and 550 m averaged a high 149 kg h^{-1} of royal red prawns, but this included a single catch of 900 kg taken off Cape Hawke in 450 m during August 1977. Some trawls conducted during daytime in 365 to 400 m caught few prawns but very large quantities of small non-commercial fish, mainly cucumber fish (*Chlorophthalmus nigripinnis*) and three-spined cardinal fish (*Apogonops anomalus*).

Newcastle to Botany Bay: For 51 trawls between 365 and 550 m, the mean catch rate for royal red prawns was 56 kg h^{-1}; 29 daytime trawls (06.00 to 18.00 h) averaged 69 kg h^{-1} and 22 night trawls averaged 39 kg h^{-1}. Few royal reds were caught deeper than 550 m: between 550 and 820 m, 12 trawls averaged 12 kg h^{-1}; trawls in 900 and 1 000 m caught none. Carid prawns were commonly caught between 450 and 640 m; the highest catch rate was 150 kg h^{-1}. Scarlet prawns were taken in small numbers between 640 and 900 m and several purple coloured prawns identified by the Australian Museum as *Aristeus semidentatus* were caught in 900 and 1 000 m.

Botany Bay to Jervis Bay: A total of 22 trawls was carried out in this area for an average royal red catch of 47 kg h^{-1}; daytime trawls averaged 59 kg h^{-1}. The largest catches were taken north of Wollongong where the bottom conditions appeared to be harder than the other grounds. Quantities of sponges and other sessile invertebrates were often picked up by the net and frequently the footrope bobbins and the bases of the trawl doors were heavily scratched. South of Wollongong the bottom conditions seemed soft and similar to those north of Sydney. However, catches in this area were consistently small.

Ulladulla to Batemans Bay

Four daytime trawls in 400 to 550 m off Batemans during November 1977 averaged 101 kg h^{-1} of royal red prawns, whereas two night trawls in 400 and 440 m in December 1975 caught respectively 25 kg h^{-1} and 8 kg h^{-1}. The large catches taken in 1977 were badly contaminated with hagfish (*Eptatretus cirrhatus*) mucus which covered both the net and catch.

Montague Island to Cape Howe

No trawling for prawns was attempted off Bermagui as very little trawlable bottom was found below 365m.

Cape Howe to eastern Bass Strait

During November 1977, trawls for prawns were conducted at 90m depth intervals from 370 to 730m off Gabo Island; royal red prawns were taken in 460 and 550m only, with respective catches of 10 kg h^{-1} and 1 kg h^{-1}. Few carids were caught in the area.

Incidental fish catches

In the early surveys, incidental fish catches were frequently very large. During the 1971-72 survey, catches in excess of one tonne were common and the mean catch rate for all fish was 490 kg h^{-1}.

Between 1975 and 1982, during which time the grounds were fished heavily by commercial trawlers for both fish and prawns, the mean fish catch rate for prawn trawling operations by Kapala on the Crowdy Head to Jervis Bay ground declined from 519 kg h^{-1} to 180 kg h^{-1}. Of the principal species, the catch rates of dogfishes (family Squalidae) declined from 137 kg h^{-1} to 40 kg h^{-1}, and ocean perch (*Helicolenus papillosus*) from 57 kg h^{-1} to 14 kg h^{-1}. In later catches, small uncommercial species such as cucumber fish and rat-tails (family Macrouridae) made up most of the fish component, with only a small proportion of the total catch comprising marketable fish.

Summary of distribution and availability

Royal red prawns

Royal red prawns were caught on all the grounds between southern Queensland and northeastern Bass Strait. The catches taken off Tweed Heads by Kapala were low. However during 1982-83, more exploratory trawling was conducted in the area by the Queensland Department of Primary Industries (Potter 1984). The results of this survey led to some commercial vessels fishing the area and catching substantial quantities of royal red prawns.

Royal red prawns have been reported by fishermen in fish trawling operations farther south than surveyed by Kapala but no positive identification of the prawns was made. Exploratory trawling by the chartered vessel Wendy Bell in 1981 failed to catch any royal red prawns in deepwater off southwestern Victoria (Walkear 1981).

Commercial catch rates were achieved by Kapala on the Clarence River ground, between Crowdy Head and Jervis Bay, and between Ulladulla and Batemans Bay. Catches from the last area were badly contaminated with hagfish mucus. However, in 1983 and 1984 commercial trawlers successfully fished on this ground but it was reported that trawling was confined to daytime because the hagfish contamination was particularly acute at night. Royal red prawns were caught between the depths of 275 and 820m, but were concentrated between 365 and 550m. A seasonal variation in their main depth distribution was evident. During winter and spring some large catches were taken in depths as shallow as 320m, but during summer and autumn, few prawns were caught in water shallower than 400m. This variation is possibly a response to changes in bottom temperature: Bullis (1956) found that a similar movement by the Gulf of Mexico royal red prawn, *Pleoticus (=Hymenopenaeus) robustus*, could be related to changes in bottom temperature. Prawns were caught during both day and night, but on average the daytime catches were larger.

Carid prawns

Carids, *Plesionika* spp., were caught in quantity between the Clarence River and Jervis Bay, in depths from 450 to 640m. The proportion of carids to royal red prawns increased with depth. Large catches of royal red prawns seldom included many carids and in practice the presence of a significant proportion (>20%) of carids was an indication that the trawl was too deep for royal red prawns. Specimens of the carid prawn, *Heterocarpus sibogae,* were caught regularly in 360 to 550m of water but were never taken in commercial quantities. Carids seem to occur in large quantities off central NSW and experiments with smaller mesh codends and separator trawls may lead to them becoming a valuable resource.

Other species

A small undescribed species of *Haliporoides* was common in many catches in 365 to 550m north of Jervis Bay. It is distinguished by its light yellow markings on the carapace and tail and the prominent white areas on the uropods. This prawn was also reported from Queensland (Potter 1984, Dredge and Gardiner 1984). Small catches of red prawns, *Aristeomorpha foliacea,* were taken between 180 and 650m from southern Queensland to Batemans Bay. Red prawns are semi-pelagic, and in July 1974, several were taken by midwater trawl at the edge of the shelf off Ulladulla (Gorman and Graham 1974).

Scarlet prawns were caught in small numbers in trawls between 550 and 900 m off Tweed Heads and between Sydney and Newcastle, and several specimens of *Aristeus semidentatus* were caught in 900 and 1 000m off Sydney.

Standing stock estimation

Stock estimates were calculated for two survey periods. It is assumed when using the swept area method that the trawl stations are distributed randomly through the area (A). During the 1972 survey a stratified sampling procedure was adopted to most efficiently utilise the available sea time. The 1976 to 1978 trawls were conducted for a variety of reasons such as procuring samples, exploration, gear trials, and demonstration. During both survey periods, trawls were conducted along the whole length and across the total depth range of the ground. It was considered that although not strictly random, the distributions of the trawls did not introduce any significant bias in the stock estimates.

Stock estimates are usually made from trawls conducted over a short period of time. During 1976, 1977 and 1978, 30 daytime trawls were conducted between Crowdy Head and Jervis Bay. An analysis of variance for the catch data indicated there were no significant differences between the mean indicated stock densities (D) for each year ($F_{2,27}$=0.41, P=0.67). The data for these years were combined to estimate a total standing stock of royal red prawns for the area.

Swept area of the trawl: For each trawl, swept area is the product of the distance trawled and the net spread. Most trawls were conducted outside effective radar range, which prevented accurate position fixing. Therefore, an average trawling speed of 2.75 knots was used to calculate the distance trawled. Net spreads were measured underwater by scuba divers and with a trawl telemetry system. The distance between the wing tips ranged from 63.0 to 77.5% of the headline length of the net. For stock estimate calculations, the effective width of the net was taken as 0.75 x headline length.

Catchability coefficient: The catchability coefficient (C) is, as defined by Patchell (1981), a measure of the effectiveness of the trawl gear at catching the target species. It may be expressed as the product of the two variables: availability (C_A) and vulnerability (C_V). For royal red prawns, C_A is the proportion of prawns in and above the substrate that are available to the net as it passes over the seabed and C_V is the proportion of these prawns that are actually caught. The catchability coefficient for royal red prawns was not known, so for the standing stock calculations, C was taken to be 1.

Table 2. Minimum royal red prawn, *Haliporoides sibogae,* stock estimates for the 1972 (Port Stephens to Sydney) and 1976 to 1978 (Crowdy Head to Jervis Bay) survey areas.

Survey period	No. of trawls	D ($kg\,ha^{-1}$)	Area of ground (ha)	Stock estimate (t)
1972	16	6.73±3.86	58525	394±224
1976 to 1978	30	11.92±2.53	118300	1410±299

Estimated stocks of royal red prawns

The minimum indicated stock sizes of royal red prawns were calculated for the Sydney to Port Stephens ground from the 1972 survey data, and for the Crowdy Head to Jervis Bay ground from the 1976 to 1978 catch data.

Daytime trawls during the 1972 survey of the Sydney to Port Stephens area produced a mean indicated stock density (D) for royal red prawns of 6.73 $hg\,ha^{-1}$ and an indicated minimum stock of 394t. The original stock estimate for all species of prawns, calculated from all trawls on this ground during 1972, was 407t (Gorman and Graham 1975).

The mean indicated stock density for daytime trawls during 1976 to 1978 of 11.92 $kg\,ha^{-1}$ was much higher than for the 1972 survey. This increase was probably in part attributable to improved gear and greater fishing experience. The estimated minimum stock of royal red prawns for the Crowdy Head to Jervis Bay ground between 365 m and 595 m depth was 1 410t.

The catchability coefficient for royal red prawns during this study was probably very low. The availability of royal red prawns will be reduced if they buried in the bottom sediments and/or if they moved off the seabed into the water column higher than the headline opening of the net. It is not known if this species buries itself in the substrate, but the much higher catch rates experienced during daytime trawls may indicate some nocturnal burying behaviour. The anatomy of royal red prawns does not suggest that they actively swim far off the sea bottom. Recent night and daytime experimental trawls for deepwater prawns with a second net mounted on top of a standard net, caught very

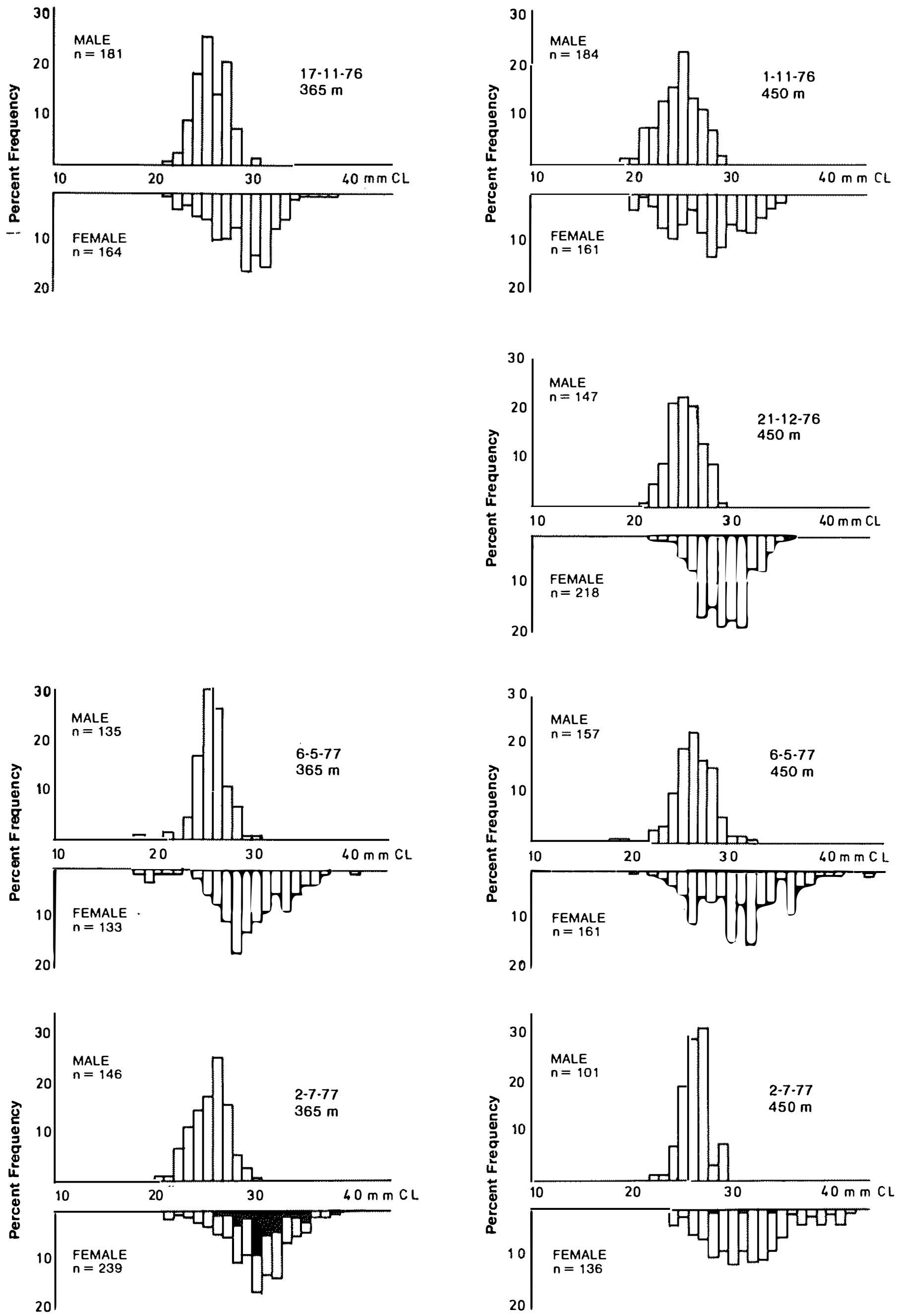

Figure 3. Length frequency histograms for royal red prawns, *Haliporoides sibogae,* caught in 365 and 450 m (200 and 250 fathoms) off Sydney between November 1976 and March 1978. Females with visible ovaries are indicated in the samples taken during the breeding seasons, by solid areas in the histograms.

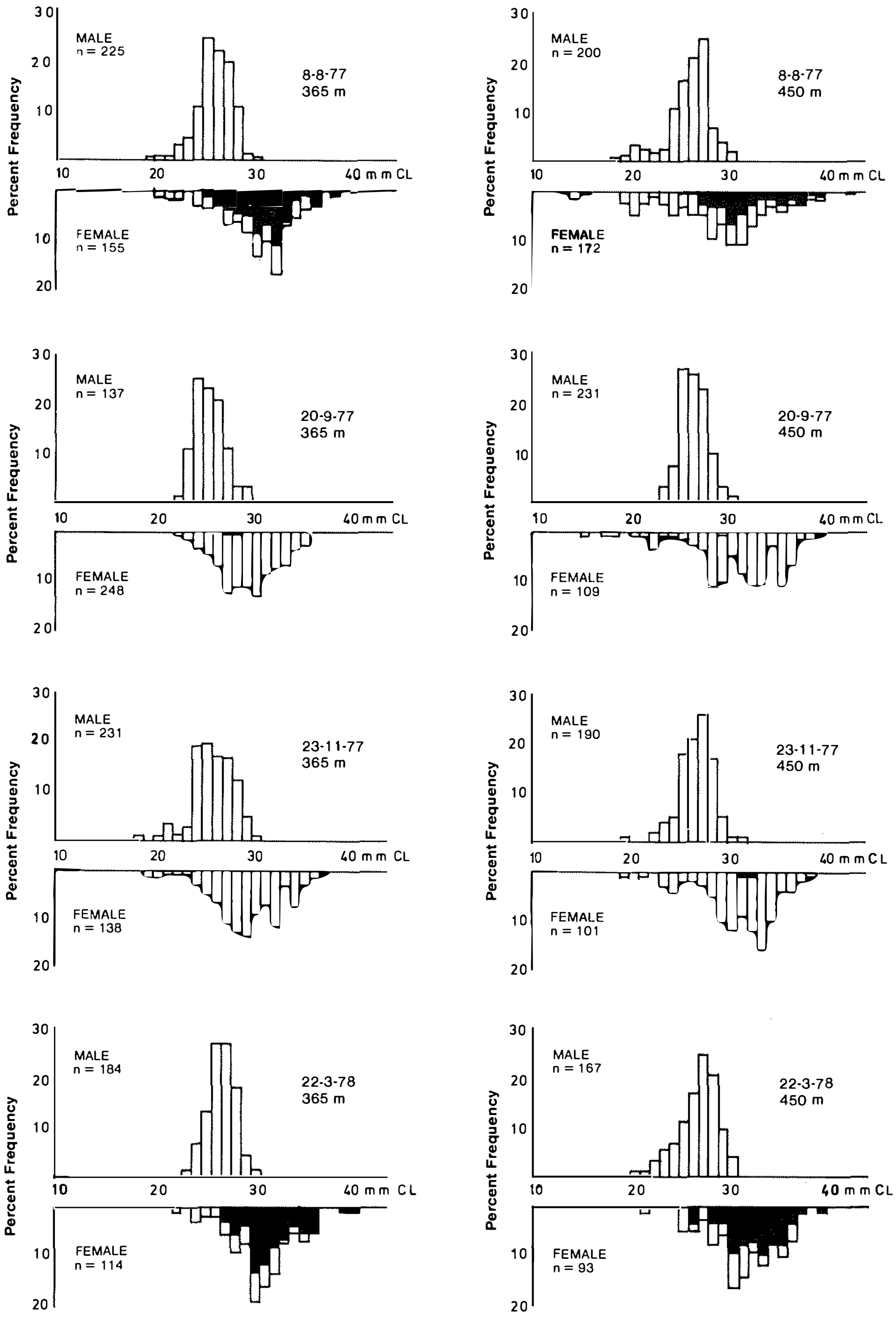

Figure 3. continued

few royal red prawns in the upper net (Gorman and Graham 1985).

To accommodate the seasonal depth movements of royal red prawns, the stock estimates were calculated from catch data for 185 m (100 fathom) depth zones appropriate to the time of the year. The stock estimate for the 1972 survey was calculated for the 320 to 505 m zone; for the period 1976 to 1978, November to March catches in the 420 to 605 m zone, and April to October catches in the 365 to 550 m zone were used for the calculations. The areas of each 185 m zone were equal.

The vulnerability of royal red prawns is a measure of the efficiency of the net at catching the prawns available to it. It is unlikely that many royal red prawns evade capture by actively swimming out of the path of the net. However, by design, prawn trawls lightly skim the seabed to avoid picking up debris, and it is probable that a significant proportion of available prawns pass under the footrope.

Wathne (1977) demonstrated that within and between tows, trawl efficiency can fluctuate widely. His study showed that under tow, the net spread and the amount of effective bottom contact varied significantly, and water currents distorted the shape of the net. The assumed net spread of 0.75 x headline length probably over-estimated the effective spread during most fishing operations as measurements of spread ranged from 63.0 to 77.5% of the headline length. If so, this would introduce a conservative bias to the calculations of indicated stock densities for each trawl. Therefore, the estimated standing stocks of royal red prawns must be regarded as minimum values dependent on catchability.

Size composition of catches

Length frequency data

Length frequency data were recorded for royal red prawns from catches taken in all areas. Irrespective of the time of the year, samples taken between 365 and 550 m on all the grounds between Tweed Heads and Jervis Bay showed similar size compositions. Most males were around 25 mm carapace length (CL) with an overall size range of 20 to 30 mm CL; females were on average larger with most in the 27 to 33 mm CL size range.

Regular samples of royal red prawns were taken from 365 and 450 m off Sydney during 1976 to 1978. The length frequencies of these samples varied only slightly throughout the year, and no obvious modal progressions were evident (Fig. 3). The absence of small prawns in the catches is unexplained. Small prawns were either unavailable or not vulnerable to the trawl. The occasional capture of large numbers of the smaller undescribed species of *Haliporoides,* and the differences between the sexes in the size distributions of royal red prawns suggest that their absence of small prawns was not a function of mesh selectivity.

The largest royal red prawns came from the small catches taken deeper than 640 m. These catches consisted mainly of females between 30 and 40 mm CL, with the largest female measuring 49 mm CL; the few males were mostly 27 to 30 mm CL, and to a maximum of 33 mm CL.

Heads-on counts and yields

The heads-on counts of royal red prawns from the main grounds ranged between 60 and 75 kg^{-1}. Prawns from south of Jervis Bay were small and counts ranged from 67 to 164 kg^{-1}. In contrast two small catches in 700 and 820 m off Kiama and Sydney gave counts of 38 and 34 kg^{-1}. The carid prawn count averaged about 200 kg^{-1}. Royal red prawn tail weight was found to be about 58% total weight, and meat yield about 50% total weight.

Length-weight data

Regression lines for male, non-breeding female, and breeding female royal red prawns (Fig. 4) were fitted for—

(1) log (total weight) on log (carapace length)
(2) log (tail weight) on log (carapace length)

For each of the data sets (1) and (2), analysis of covariance showed the three regression lines to have significantly different slopes from each other ($P<0.001$).

Biological observations

No systematic biological study of deepwater prawns was undertaken. However, some aspects of the biology of royal reds were noted.

Sex ratio

Sex ratios of samples varied widely and no pattern was obvious. The proportion of females in the 365 m samples ranged from 30 to 65%; the 450 m samples were more consistent, with most between 45 and 60% female (Table 3). More than 90% of all royal red prawns caught below 640 m were large females.

Table 3. *Haliporoides sibogae:* Percentage of females in the catch and percentage of females with visible ovaries caught off Sydney between November 1976 and March 1978.

	365m		450m	
Sample date	% female	% with visible ovaries (>24mm CL)	% female	% with visible ovaries (>24mm CL)
1976 Nov 1	—	—	46.8	0
Nov 17	47.5	0	—	—
Dec 21	*	*	59.7	0
1977 May 6	38.7	5.0	50.6	5.0
Jul 2	62.1	30.5	57.4	2.2
Aug 8	30.3	61.3	46.1	40.9
Sep 20	64.4	0.8	31.7	1.0
Nov 21	37.4	0	34.8	2.1
1978 Mar 22	38.3	66.4	34.4	65.2

* no prawns caught

Breeding

Royal red prawn breeding was indicated in the females by the development of the ovaries which are distinctly blue in colour and clearly visible through the dorsal surfaces of the carapace and tail. In the Crowdy Head to Jervis Bay area two breeding seasons for royal red prawns were observed. Females with developing ovaries were evident almost exclusively in the periods March-April and July-August; during the sampling period 1976 to 1978, up to 66% of mature sized females had visible ovaries during these months. A larger proportion of breeding females were found in the 365m samples than in the 450m samples during the winter season. The smallest observed female royal red with developing ovaries was 25mm CL (Fig. 3); the minimum size of sexually mature males was not determined in this survey.

Commercial fishery

Development

Commercial exploitation of royal red prawns began in 1975 but development of the fishery has been slow. Until 1980, there were seldom more than three trawlers operating in the fishery at any one time. Since 1980, up to 10 trawlers have fished for royal red prawns during

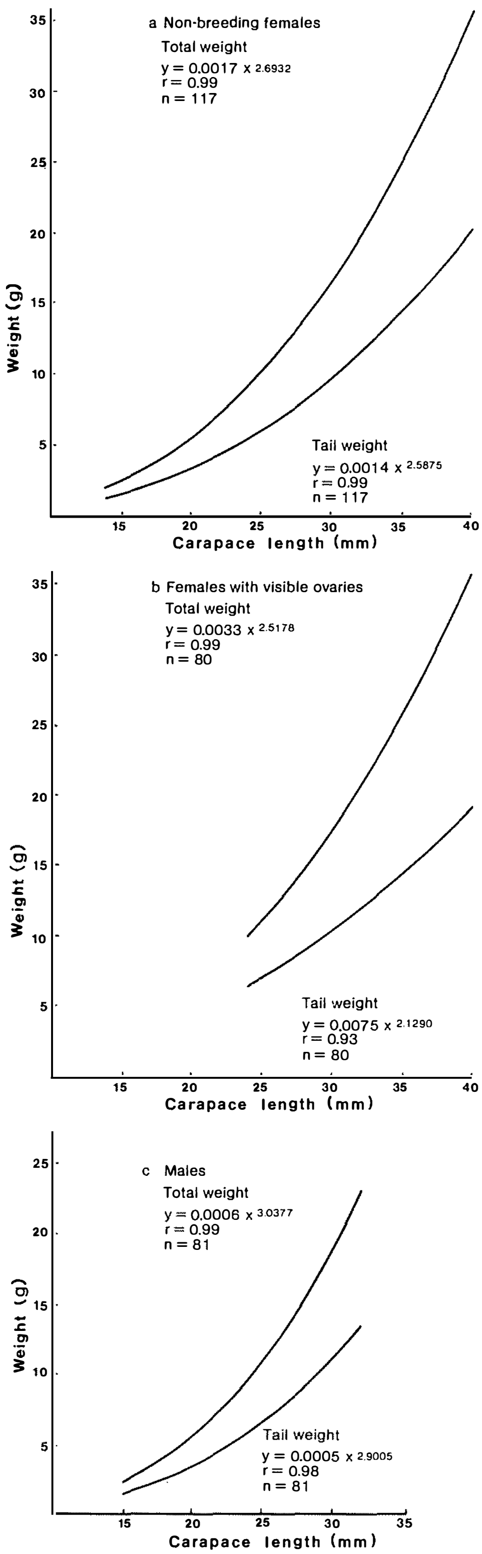

Figure 4. Graphs of carapace length to total weight and carapace length to tail weight regressions for male, breeding female, and non-breeding female royal red prawns, *Haliporoides sibogae*

the summer, with most operating in the fishery on a part-time basis.

Royal red prawns have been landed in most NSW ports. Trawlers operate principally from the Clarence River, Port Stephens, Sydney and Wollongong. Significant landings have also been made at Tweed Heads, Crowdy Head, Greenwell Point, Ulladulla and Bermagui. Since its inception, there has been a progressive expansion of the fishery southwards from Sydney, and in 1984 several trawlers fished off Ulladulla and Bermagui.

Most vessels operating from central and southern NSW ports are purpose-built fish trawlers 15 to 20m length overall, powered by 150 to 300kW engines, and fitted with winches which carry about 1 500m of warp each side. They tow a single 50 to 80m headline prawn net. The Clarence River trawlers are also 15 to 20m in length but are designed and triple-rigged for prawn trawling. The three nets have a total headline length up to 90m. These trawlers fish for royal red prawns when inshore prawn catches are low. Most of the central and south coast boats trawl for royal red prawns mainly during the summer and revert to fish trawling in winter.

Catch rates

Commercial vessels use large gear and fish on the most productive depths and normally achieve catch rates between 200 and 500kg h^{-1}; rates above 1 000kg h^{-1} have been reported.

Vessels operating from central and southern NSW ports land between 500 and 1 000 kg day^{-1}, while the Clarence River trawlers average about 1 000kg for a 24-hour trip. Table 4 shows the annual landings of royal red prawns at the main ports. The figures are derived from Fishermen's Co-operative data, Sydney Fish Market sales and fishermen's catch returns.

Handling on board

Royal red prawns are thin shelled and fragile and require more careful handling than shallow water species. They quickly develop melanosis (black-spot) when they are removed from the sea. Melanosis is caused by enzyme reactions which produce the black pigment, melanin, and this process occurs rapidly in dead prawns particularly at high temperatures (Anon. 1972). Prawns are caught in bottom temperatures around 10°C and are hauled through surface waters of about 20°C; on deck the air temperature is frequently greater than 20°C.

Table 4. Annual landings (tonnes) of royal red prawns, *Haliporoides sibogae,* at NSW prawn landing ports.

	1976 -77	1977 -78	1978 -79	1979 -80	1980 -81	1981 -82	1982 -83
Tweed Heads	—	—	—	—	—	—	8
Clarence River	—	2	27	—	—	39	53
Crowdy Head	—	—	—	—	—	8	31
Port Stephens and Newcastle	62	38	82	42	89	72	98
Sydney	—	45	66	61	70	100*	110*
Wollongong	14	45	70	211	112	225	165
Greenwell Pt	—	—	—	—	4	6	29
Total	76	130	245	314	275	450	494

*estimated from Sydney Fish Market sales

Fast sorting and storage of the prawns is essential to prevent the development of melanosis and off-flavours, and microbial spoilage (Freeman et al 1981). The most appropriate medium for storage is either refrigerated seawater (RSW) or chilled seawater (CSW)—an ice and seawater mixture. As few vessels in the fishery have provisions for RSW, most hold their prawns in CSW. Use of sodium metabisulphite in the water is common but no study has been undertaken to ascertain the appropriate concentration. Addition of salt (sodium chloride) to lower CSW temperature was discouraged by processors because royal red prawns were found to readily absorb salt.

Processing and marketing

Royal red prawns landed in Sydney are sold mainly through the NSW Fish Marketing Authority's auction market for local consumption. Initial consignments to the Sydney Fish Market were presented for sale in a very blackened state, and they therefore met considerable buyer resistance. Later, prawns kept in CSW have attracted higher prices. Table 5 shows the quantities and average prices of royal reds sold through the Sydney Fish Market since 1976.

Most of the catch from other ports is processed and packed by local fishermen's co-operatives or independent buyers for both the domestic and export markets. When the fishery started, processing of royal red prawns involved the production of frozen blocks of peeled meat. More recently, packs of IQF (individually quick frozen) meat have been more successful at the domestic wholesale level. Attempts to produce an acceptable boiled-prawn product, either as meat or whole prawns, have not been a success. During 1984, the Clarence River Fishermen's Co-operative exported to Japan

Table 5. Sales of royal red prawns, *Haliporoides sibogae,* through the Sydney Fish Market from 1976 to 1983 (source: New South Wales Fish Marketing Authority).

Year	Whole Prawns (kg)	Average Price (ckg^{-1})	Royal red meat (kg)	Average price (ckg^{-1})
1976-77	33449	133	—	—
1977-78	56742	164	—	—
1978-79	99141	185	2696	682
1979-80	97245	193	—	—
1980-81	81084	191	—	—
1981-82	100594	167	3054	663
1982-83	122000	244	—	—

whole royal reds blast dry frozen in 12 to 14kg packs.

Consumer demand in NSW for royal red prawn meat is mainly at the retail level. Seafood shops sell uncooked royal red prawn meat usually much cheaper (on a meat-yield basis) than the traditional boiled prawns. There is still a high resistance to royal red prawn meat in the catering sector based mainly on its characteristic high moisture content and its comparatively small size (Anon. 1983).

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Management, economics and marketing

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Review of penaeid prawn fishery management regimes in Australia

Abstract: Apart from the long established prawn fisheries of New South Wales, significant exploitation of penaeid prawns has been practised elsewhere in Australia for only the past two decades. Fishing may be directed at one species (South Australia) ranging to many (up to 10 in the Gulf of Carpentaria). During this time prawn fisheries have become arbitrarily separated into zones, each of which has independently acquired a set of rules dependent on the management authority. At different stages of development each has become subject to some form of limited entry regulations. Supporting regulations vary from zone to zone but usually include closed seasons, net restrictions, protection of nursery areas and vessel size.

The prime objective of management controls is resource maintenance although controls may be directed at reducing the excess fishing capacity which is a common feature in most Australian prawn fisheries. Despite these management measures and the cautious expansion of fishing effort, some fisheries have experienced recruitment overfishing which has necessitated drastic effort controls. While stock production models are a basic tool, more serious consideration will need to be given to stock recruitment relationships. Management strategies include planning of opening dates from nursery surveys and prediction of optimum catch levels from nursery studies and preseason trawl surveys. All major Australian prawn stocks now appear to be fully or excessively exploited, and face the problems of reducing fishing effort.

Introduction

This paper reviews and compares the management regimes which have been developed in the penaeid prawn fisheries of Australia. The fisheries have been described by Haysom (1985) and Ruello (1975b). The review includes a brief description of the areas managed and species fished, the management authorities, their history, objectives and current status of the fisheries, a discussion of management measures used, the scientific basis for management, and problems perceived in controlling fishing effort and catches in prawn fisheries. Subjects which will not be covered include: costs of management, including the high cost of an effective logbook program, problems of management of overlapping resources (eg scallops with prawns), management consequences to other fisheries resulting from limiting entry to one or more of them, management of prawn habitats and the long-term effects of repeated trawling, and problems of enforcement.

Management areas

The choice of management authority, operating either independently or jointly, is a function of the Australian constitution. Where a fishery is confined to state territorial or inland waters ie inside three nautical miles (5.6 km) from high water mark, it is managed independently under appropriate state legislation. Where all or part of the prawn stock is in Commonwealth waters (outside of three miles) it is managed jointly between the Commonwealth (Department of Primary Industry) and the state or territory involved.

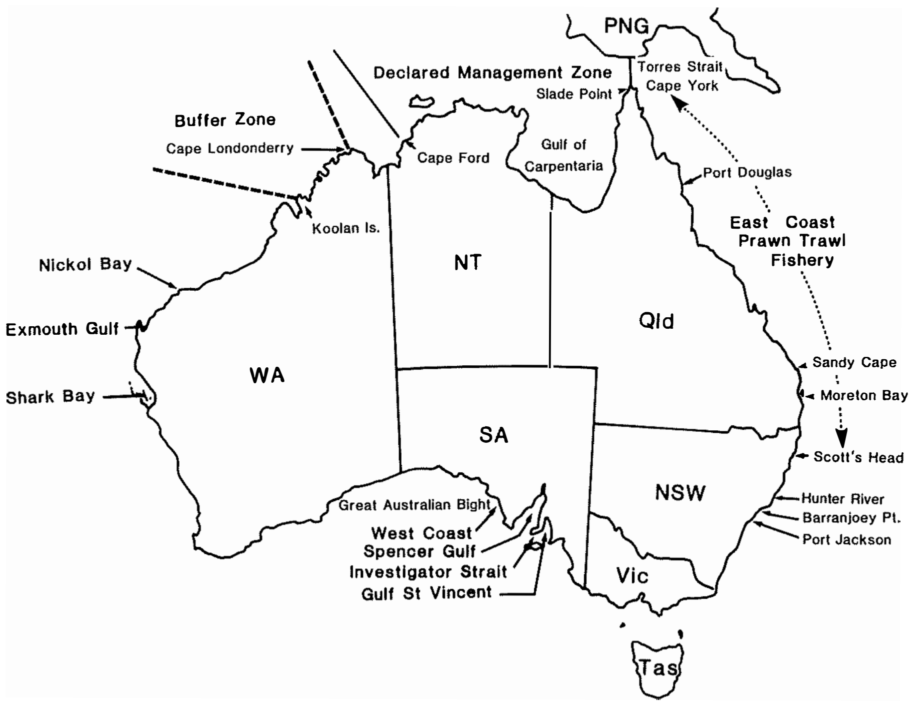

Figure 1. Australia showing locations referred to in the text

Any state or territory may have fisheries managed independently or jointly. Certain waters off northeastern Australia are subject to international control involving Commonwealth, state and Papua New Guinea.

The major management areas (Fig. 1) and a brief description of the fisheries and their major species follow.

Individual state

New South Wales

Estuarine prawning in NSW uses five methods: hauling, running, pocket netting, otter trawling and seining for school prawn, *Metapenaeus macleayi;* eastern king, *Penaeus plebejus,* and greentail prawns, *M. bennettae.* Otter trawling is used offshore for school ana eastern king prawns.

Northern Territory

There is a local trawl fishery in NT waters west of Cape Ford for banana prawns, *P. merguiensis* and brown tiger prawns, *P. esculentus.*

Queensland

Beam trawl fisheries operate in state waters and river systems of Qld from Port Douglas to the southern border for banana prawns, greentail and school prawns as for NSW. Offshore trawl fisheries operate in state waters for eastern king, greentail, brown tiger, banana, coral prawns, *Metapenaeopsis* spp., and red spot king prawns, *P. longistylus.*

South Australia

Otter trawl fisheries in SA state waters of Spencer Gulf, Gulf St Vincent and Investigator Strait, fish for western king prawns, *P. latisulcatus.*

Western Australia

There are otter trawl fisheries in WA state waters of Shark Bay and Exmouth Gulf for western king and brown tiger prawns; Nickol Bay mainly for banana prawns and the Kimberley and various inshore and embayment fisheries for a variety of species.

Joint management areas

Northern Prawn Fishery

The declared management zone (DMZ) of the NPF covers the Gulf of Carpentaria and waters adjacent to the NT coastline between Slade Point (Qld) and Cape Ford (NT) (Fig.1). The catch comprises: banana; Indian banana, *P. indicus;* brown tiger; grooved tiger, *P. semisulcatus;* endeavour, *M. endeavouri* and *M. ensis;* greentail and western king prawns. The principle, to extend the western boundary to Cape Londonderry (WA), with a buffer zone extending to Koolan Island, has been endorsed by the Australian Fisheries Council. Both WA and DMZ licensed boats will be permitted to operate in the buffer zone.

East Coast Prawn Trawl Fishery

An area covering all Commonwealth waters from the eastern boundary of the DMZ of the NPF to Scott's Head, NSW (Fig. 1) has been designated the East Coast Prawn Trawl Fishery (ECPTF). The southern boundary will be changed to Barranjoey Point under the proposed management plan. It is fished for school, eastern king and greentail prawns in estuaries, for school, greentail and royal red prawns, *Haliporoides sibogae,* inshore, and for school and eastern king prawns offshore. It involves the Torres Strait Fishery which is expected to be managed jointly by the Commonwealth, Qld and Papua New Guinea. Both Commonwealth and state waters from the tip of Cape York to Sandy Cape (24° 30′S) (Fig. 1) are subject to the Commonwealth Act under which the Great Barrier Reef Marine Park Authority (GBRMPA) is administered. GBRMPA determines the zones where trawls may or may not operate but does not control boat licensing, gear restrictions etc. Fisheries in Torres Strait and the northern Great Barrier Reef are based mainly on brown tiger and red spot king prawns.

South Australian West Coast Prawn Fishery

Complementary Commonwealth and SA state legislation covers two major grounds, Anxious Bay and Ceduna, in the eastern Great Australian Bight. Western king prawns are caught in both areas.

Management authorities

The research and data base for prawn fisheries confined to a single state or its territorial waters is provided by the responsible management authority. These are: NSW Department of Agriculture, Division of Fisheries; NT Department of Ports and Fisheries (NTPF); Qld Department of Primary Industries (Qld DPI) and Qld Fish Management Authority (QFMA); South Australian Department of Fisheries; Western Australian Fisheries Department.

Each of these organisations has its own research branch. Long-term research on prawns has also been undertaken by the Commonwealth Scientific and Industrial Organization (CSIRO) Division of Fisheries Research on the NPF, the East Coast Prawn Fishery and on banana prawns in northwest WA.

Joint management arrangements are:

Northern Prawn Fishery

In 1983 the Northern Prawn Fishery Management Committee (NORMAC) was set up to give advice directly to the Australian Fisheries Council (AFC), which comprises Commonwealth and state ministers responsible for fisheries, together with the Commonwealth minister responsible for CSIRO. NORMAC has five government (Commonwealth, Qld, NT, WA and CSIRO) and seven industry representatives.

Data gathering has been by the Commonwealth Department of Primary Industry (Commonwealth DPI) and CSIRO, together with research and data collection by NT and Qld. Sources of data are vessel logbooks, processors' returns, licensing records, biological research and economic research.

East Coast Prawn Trawl Fishery

Interim management arrangements were reached in May 1983 between Qld, NSW and the Commonwealth to limit new entry and restrict the size of replacement boats. A government and industry task force was established in 1984 to develop longer term management arrangements. The task force will report to the AFC. Management will be required to acknowledge and complement management requirements in adjoining territorial waters of NSW and Qld, of the GBRMPA and of the Torres Straits. The last mentioned fishery is developing towards joint international management by the Commonwealth, Qld and Papua New Guinea (PNG).

Research and data requirements for the east coast fisheries are maintained by the QFMA, Commonwealth DPI, NSW Department of Agriculture and GBRMPA, together with the Qld DPI and CSIRO. Input to the Torres Strait research and data base will be made by PNG Department of Primary Industry.

SA West Coast Prawn Trawl Fishery

Three vessels operate in the Great Australian Bight under Commonwealth licence and state ministerial exemption and the fishery is regulated under complementary state and Commonwealth legislation. Ministerial exemptions are issued to allow developmental fishing. Licences are not issued until the long-term viability of the resources is determined.

Management objectives

Individual state

New South Wales
NSW aims to maintain its resources at a level approaching their biological maximum sustainable yield but at the same time acknowledges that the economic viability of the industry must be considered. A 1982 freeze on numbers of prawn licences reflected concern for the worsening economics of this fishery.

Northern Territory
Emphasis on development of NT prawning fleets and processing plants has given way latterly to the concerns expressed for the NPF.

Queensland
Priorities in management in Qld of the east coast beam trawl prawn fishery are basically social and economic. They take into consideration the role of bait supply, usage of juvenile prawns from stocks fished by otter trawlers, recreational fishermen and concerns of the general public. Priorities in management of the overall east coast trawl fishery have in the past been mainly biological and social, reflecting speculation about the effects of capture of younger age groups in inshore areas on availability of prawns to offshore trawlers. In the late 1970s the main priority became economic as the size of the fleet escalated without restriction to a number exceeding 1000 vessels until a freeze was introduced in 1979.

South Australia
Prawn fisheries in SA are managed with four major objectives: to maintain and improve the stocks; to ensure a fair and reasonable sharing of access to the resource between the various sectors of the community; to optimise the economic return from commercial exploitation; to achieve equitable distribution from the benefits of management to the community.

Western Australia
In WA the prime objective must be the maintenance of the resource at a level approaching the maximum sustainable yield, while giving proper attention to the economic viability of the fishing units with a view to maintaining a profitable industry (Bowen and Hancock 1984).

Joint management areas

Northern Prawn Fishery
A management plan for the NPF DMZ is based primarily on input controls to contain and reduce total fleet fishing capacity in order to improve economic returns to the fishery (Wesney et al in press).

East Coast Prawn Trawl Fishery
A report on the east coast prawn trawl fishery (Anon. 1984) set out the broad objectives of any fisheries management plan as: 'to ensure the resource is protected and maintained at a sustainable level . . . to utilise the resource in an economically efficient manner for the benefit of the community and the user and be consistent with national, social and political objectives.'

Great Barrier Reef Marine Park Authority
GBRMPA's management priorities focus on conservation of the reef environment, and social aspects of different user groups. They will determine, through its zoning plans for various sections of the marine park, where trawlers may legitimately operate.

South Australian West Coast Prawn Fishery
The objectives of the management regime for the fishery off SA's west coast are the same as those for the state fisheries.

Management regimes

The history, evolution and current status of management regimes is summarised for each authority.

New South Wales

Commercial prawn fishing in Australia probably commenced in Port Jackson, Sydney, for school, eastern king and greentail prawns in the early 1800s but was not formally controlled until the NSW Fisheries Act was passed in 1865 (Ruello 1975a, b). A new Fisheries Act in 1881 reflected concern about the state of local (river and inshore) prawn stocks by prescribing closed seasons, closed areas, a minimum size for prawns, and gear restrictions. The oceanic fishery for eastern king prawns developed along the NSW coast in the late 1940s. Exploratory surveys by the NSW Fisheries Department's research vessel Kapala in the early 1970s showed the presence of commercial quantities of deepwater prawns mainly royal red prawns in depths of 275 to 685 m (Gorman and Graham 1975).

By 1983 the number of prawn vessels in NSW had risen to 373, giving a fluctuating but generally increasing total catch, which included increasing fishing for juvenile prawns. However, the small rise in catch shared amongst more boats with increasing costs, caused marked deterioration in the economic position of east coast prawn trawl fishermen. A freeze was applied by the NSW government in 1982 to stop further entry of offshore prawn trawlers, followed in January 1984, by a freeze on any additional boats entering the prawn fishery. It is expected 300 NSW boats will qualify for licences to fish for prawns in Commonwealth waters within the boundaries of the East Coast Prawn Trawl Fishery.

Northern Territory

In the NT, serious fishing for prawns commenced with the exploratory surveys of the Gulf of Carpentaria in the late 1960s. Emphasis was given by the Commonwealth government to development of processing establishments and fishing fleets. By about 1974 concern was being expressed about the growing capacity of the fleet and in January 1977 vessel numbers were frozen under arrangements for the NPF DMZ. The only remaining stocks under direct NT control are the territorial waters west of Cape Ford (Fig. 1), where no additional licences are being issued for the present.

Queensland

Commercial prawn fishing by beam trawlers in Qld probably started in the 1840s (Ruello 1975b) for greentail and school prawns in the Brisbane River and spread to nearby rivers, and in 1941-42 produced 46t. Development of trawling in more open waters for eastern king and brown tiger prawns may have been delayed compared with NSW as a consequence of the prohibition until 1950 of otter trawling. In 1960 the Qld government allowed the introduction of double-rig trawling which was quickly adopted by most of the larger trawlers. Today more than 250 beam trawlers (5 to 9m length) are endorsed to operate in Qld rivers, but not all of these are actively fishing, taking a catch in excess of 500t. The east coast otter trawl fleet has stabilised at approximately 1200 active trawlers, of which about 80 also operate in the NPF. The 1982-83 Bureau of Agricultural Economics (BAE) catch estimate of 4300t is said to be an underestmate (Haysom[1], pers. comm.). Gear and boat size restrictions are designed to reduce competition between inshore beam trawlers and larger offshore trawlers, which are usually wideranging along the coast and operating in a regime where control is shared between state and Commonwealth, and subject not only to GBRMPA jurisdiction and planned Torres Strait international controls but to limited entry arrangements as part of the East Coast Prawn Trawl Fishery.

South Australia

Consistent commercial quantities of prawns were located in SA for the first time in 1968, initially in Spencer Gulf followed by Gulf St Vincent and the west coast. Licence limitation was applied at the beginning of the fishery and the number of vessels was increased to the present 39 in Spencer Gulf, 14 in Gulf St Vincent, three in Investigator Strait and three on the west coast. In Spencer Gulf, catches have stabilised with a yearly average of 2000t but effective effort has been increased significantly through experience and by the use of larger and more efficient vessels. Real effort in the Gulf St Vincent fishery (approx 500t) has likewise increased, in this case through conversion of the whole fleet of 14 licensed vessels from single to triple rig. The Investigator Strait fishery did not commence until 1973 when boats with Commonwealth licences began fishing there. Catches rose to 200t by 1979, taken by five Commonwealth and three state licensed vessels. The fishery is now managed by the state following agreement with the Commonwealth under the baselines of the Sea and Submerged Lands Act 1973. Since 1979, catches and effort in Investigator Strait have declined dramatically, to 38t by two boats in 1983, but it is not known whether this is the result of recruitment overfishing or of increased fishing effort in the Gulf St Vincent fishery from which tagging has shown that most of the stock originates. There are two vessels operating under ministerial exemption in Investigator Strait. The west coast fishery increased from 7t in 1968 to 290t in 1973 but then collapsed, due, it was strongly believed, to recruitment overfishing. Currently only three boats are permitted to fish, and their greatly improved catch rates produced 218t in 1983. Present management strategies reflect government and industry agreement to promote optimal harvesting based on a prawn crop model and detailed preseason monitoring. Harvesting strategy includes permanent closures (major nursery areas), temporary area closures (to allow growth to optimum size), moon closures

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(to reduce fishing effort at times of poor return in quantity and/or quality), and seasonal closures (to contain fishing effort).

Western Australia

The management of WA prawn fisheries was described by Bowen and Hancock (1984). Limited entry was introduced to Shark Bay in 1963, Exmouth Gulf in 1965 and Nickol Bay in 1971 as a consequence of relatively recently discovered stocks of prawns and the threat of rapid development which would preclude orderly expansion. As a result of regular reassessments, licences in Shark Bay were increased stepwise from 25 to a maximum of 35 by 1975, from 15 to 23 in Exmouth Gulf by 1981, and from 13 to 16 in Nickol Bay by 1975. Licences are transferable and attract a resale value. The current situation is of full or excessive exploitation through gradually increasing effective fishing effort, which in Shark Bay has, for western king prawns, exceeded the optimum required for maximum sustainable yield and, for brown tiger prawns, begun to affect recruitment. The brown tiger prawn stock in Exmouth Gulf suffered a severe decline in production in 1981 (Fig.6) due to reduced recruitment resulting from excessive fishing effort. Reduced fishing has been accompanied by phased recovery of spawning stock and subsequent recruitment (Penn and Caputi 1985). Seasonal closure of nursery areas has allowed protection of prawns to desirable market size in Shark Bay and Exmouth Gulf.

Other management strategies include seasonal closures to protect breeding stock, area closures both permanent and seasonal (to protect major nursery areas), moon closures (by agreement with the industry) and (in Exmouth Gulf only) reduction of fishing effort by roster fishing (to allow stocks to recover from recruit overfishing) (Penn and Caputi 1985).

Northern Prawn Fishery

Commercial trawling operations in the NPF were commenced in the Gulf of Carpentaria on a trial basis in 1965 and 1966 following an exploratory survey by CSIRO, Commonwealth DPI and the Qld government. By 1970-71 annual catches had exceeded 7000 t by which time 252 boats were operating and prawn processing plants were established (Anon. 1982). In 1971 and 1972 following concern by industry, seasonal closures were introduced to protect pre-spawning adults. The biological justification for this was later questioned and, from 1973 to 1975, 1 January to 15 March closures of the eastern Gulf were maintained on economic rather than biological grounds. The entire Gulf was closed early in 1977, but the area closed was reduced in 1978 to defined eastern and southeastern Gulf waters closures for the same period.

From 1 January 1977 there was a freeze on further entry of boats into the DMZ for a trial three-year period. This resulted from concern about growing overcapitalisation, and the economic and possible biologial effects of the increase in size and number of large freezer trawlers. The interim regime provided criteria for eligibility of entry of vessels together with provisions defining managed area, seasonal closures, vessel replacement, carrier and freighter operations, processing protection zones and a product landing zone. Longer term plans, providing for economic management as the principal objective and applying to both banana prawn and tiger and endeavour prawn stocks, became effective on 1 January 1980. In October 1982 the AFC requested a review of the NPF to consider the early introduction of measures to restrain existing and potential capacity in the fishery. In the following year AFC endorsed a seven point management package which included a Boat Replacement Policy based on under-deck-volume and engine power, and a Voluntary Licence Entitlement Buy-Back Scheme (VLEBBS), involving a mandatory contributory levy paid by all operators and which varies depending on the size and engine power of the boat. VLEBBS was planned to be fully operational by 1 January 1985. The opening date of the season in recent years has been based on preseason sampling by CSIRO and state research organisations in conjunction with commercial boats from the fishery. CSIRO, NT and Qld have had major research programs in the Northern Prawn Fishery since 1963.

East Coast Prawn Trawl Fishery

The East Coast Prawn Trawl Fishery (ECPTF) has expanded significantly in recent years. Qld licensed otter trawlers increased from 700 in 1976 to 1413 in 1980, but have fallen since. The number of vessels in NSW rose gradually to reach 718 in 1983. The increase in numbers of trawlers was accompanied by increases in fishing capacity through engine power, boat size, electronic sophistication and number of nets towed as well as in total fishing time and greater mobility. Despite this there was only a small increase in total prawn catch, and with increasing costs the economic

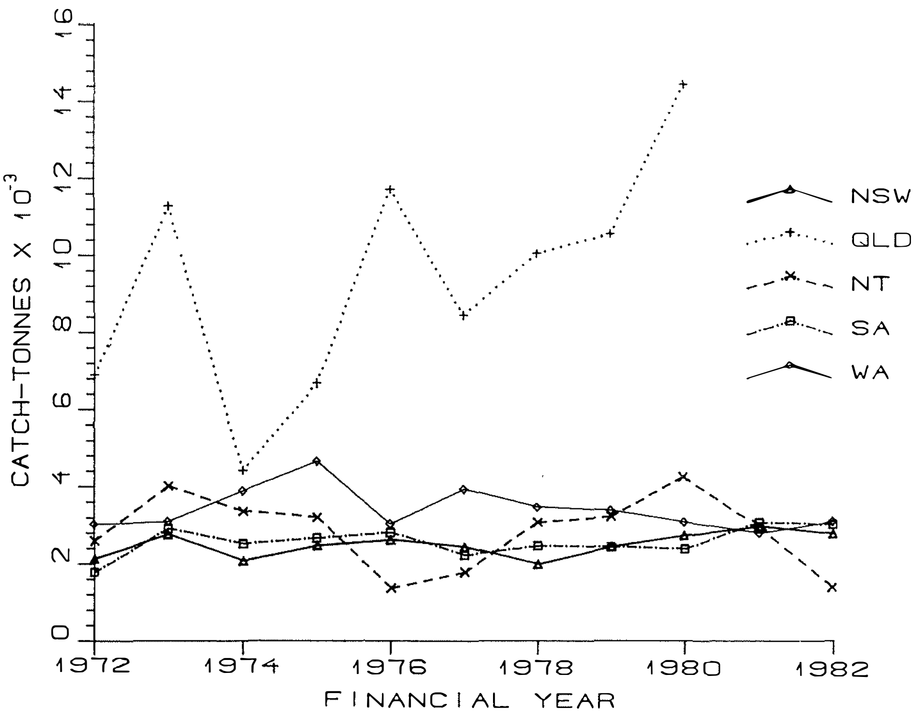

Figure 2. Annual landings of prawns (all species) recorded for individual states and the Northern Territory 1972 to 1982. Data source: Australian Bureau of Statistics

position of most fishermen deteriorated badly. In September 1979, the Qld government introduced a freeze on the number of state licensed boats followed by positive moves to reduce their number. In December 1982 the NSW government prohibited the entry of any new licensed fishing vessels into the prawn fishery but any vessel licensed at that time was permitted to trawl for prawns. On 1 January 1984, a total freeze was introduced. In January 1984, the Commonwealth government introduced, for a 12-month period, a limited entry interim scheme in Commonwealth waters, currently from the eastern boundary of the NPF DMZ to Scott's Head, NSW, with 1023 boats (725 Qld and 298 NSW) with licences endorsed to fish within its boundaries, but a total of 1100 boats is expected to qualify.

Current status of fisheries

Catch data for Australia as a whole are given in Table 1, and in common with the figures for most states, Qld being the exception, have shown little movement over the past decade (Fig. 2). Catch statistics have been related to fishing effort data, for those fisheries where available in Figs 3 to 8. This can only be done with any meaning where data for individual species as well as areas are available. Figs 3 and 4 show fairly stable levels of catch, effort and catch per unit of effort (CPUE) for western king prawns in Spencer Gulf and Shark Bay. Figs 5 and 6 show the lowered catch and CPUE of brown tiger prawns in both Shark Bay and Exmouth Gulf. It was noted above how effective

Table 1. Australian prawn production 1972-73 to 1982-83. Source: Australian Bureau of Statistics. Production figures for Victoria in 1980-81 and for Queensland in 1981-82 and 1982-83 were not available when this table was compiled

Year	Catch (t)
1972-73	16445
1973-74	23999
1974-75	16263
1975-76	19652
1976-77	21565
1977-78	18807
1978-79	21036
1979-80	22059
1980-81	26921
1981-82	11834
1982-83	11364

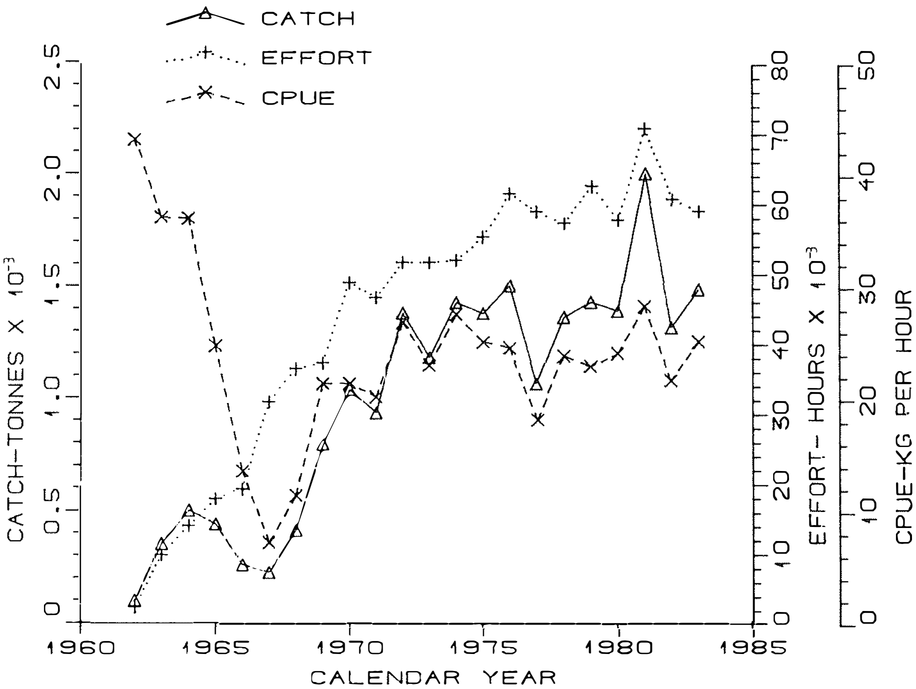

Figure 3. Catch, fishing effort, and catch per unit effort of western king prawns, *Penaeus latisulcatus*, in Spencer Gulf, South Australia. Data source: Carrick 1982

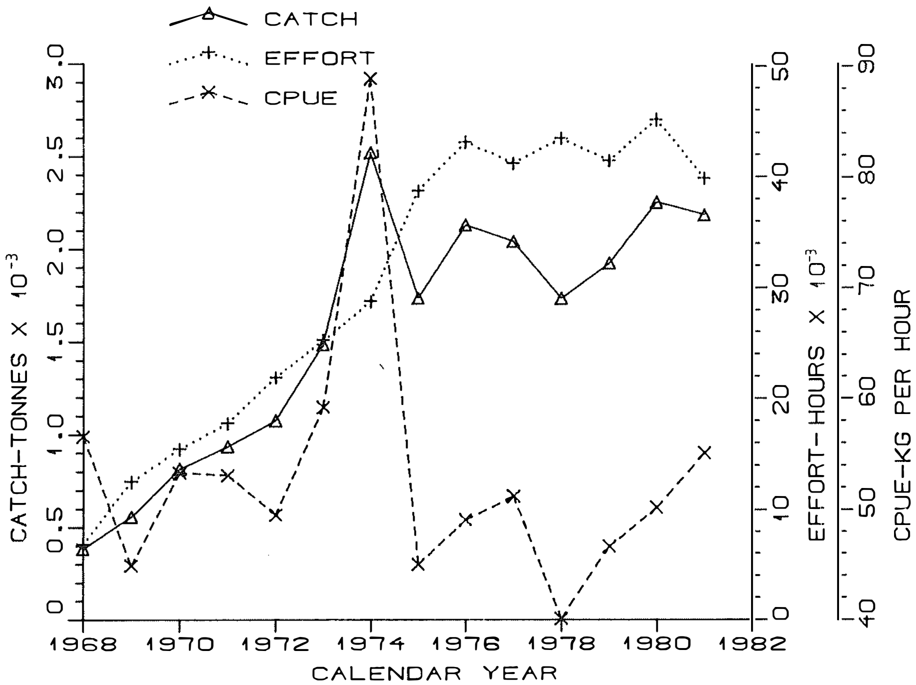

Figure 4. Catch, fishing effort, and catch per unit effort of western king prawns, *Penaeus latisulcatus*, in Shark Bay, Western Australia. Data source: Annual reports of Western Fisheries Research Committee (unpublished)

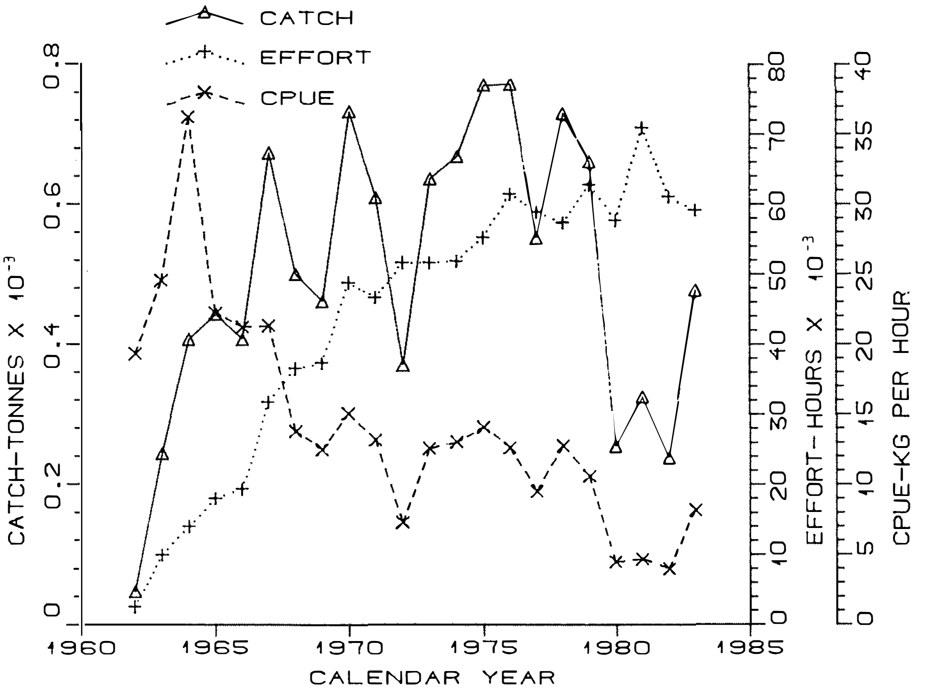

Figure 5: Catch, fishing effort, and catch per unit effort of brown tiger prawns, *Penaeus esculentus,* in Shark Bay, Western Australia. Data source: Annual reports of Western Fisheries Research Committee (unpublished)

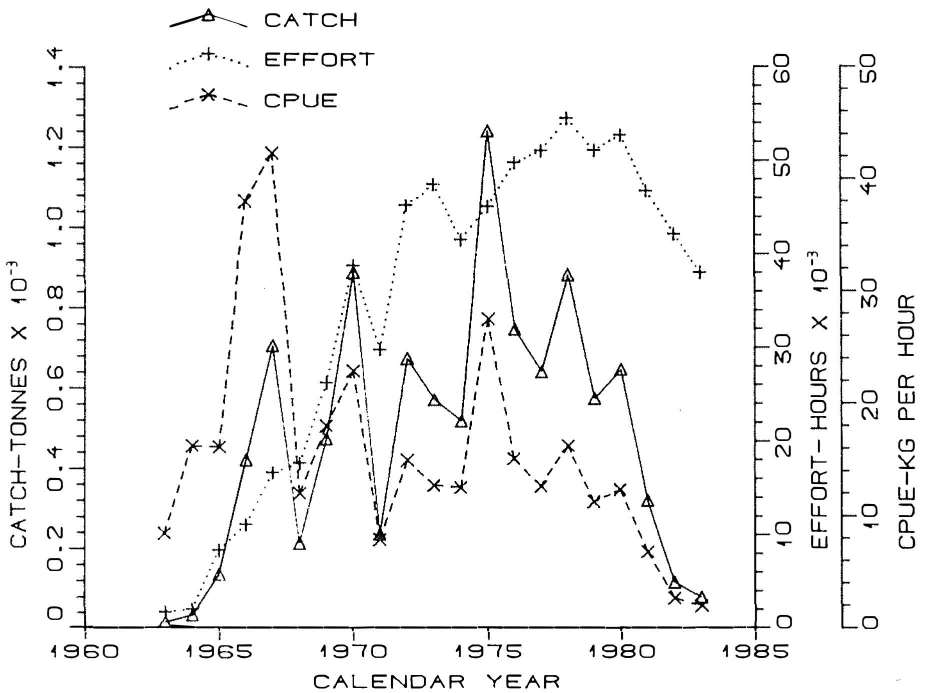

Figure 6. Catch, fishing effort, and catch per unit effort of brown tiger prawns, *Penaeus esculentus,* in Exmouth Gulf, Western Australia. Data source: Annual reports of Western Fisheries Research Committee (unpublished)

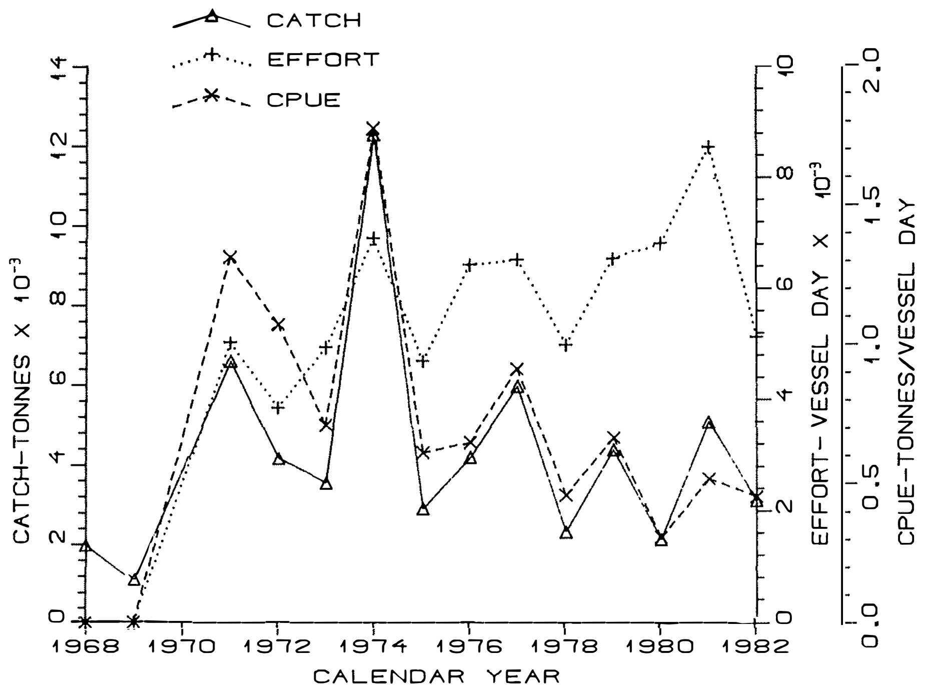

Figure 7. Catch, fishing effort, and catch per unit effort of banana prawns, *Penaeus merguiensis*, in the NPFDMZ. Data source: CSIRO, Cleveland

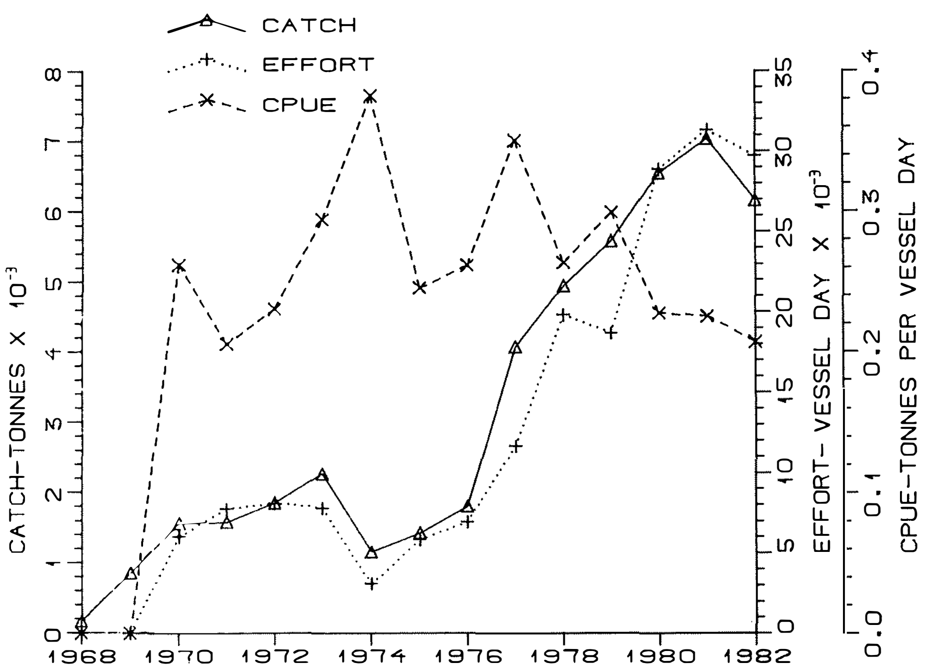

Figure 8. Catch, fishing effort, and catch per unit effort of tiger prawns, *Penaeus esculentus* and *P. semisulcatus*, and endeavour prawns, *Metapenaeus endeavouri*/ *M. ensis*, in the NPFDMZ. Data source: CSIRO, Cleveland

effort had in fact increased in Spencer Gulf for no increase in catch, and how the Investigator Strait fishery had declined and the West Coast fishery had collapsed. Data for banana prawns from the NPF (Fig. 7) show somewhat increasing effort for fluctuating and slightly declining catch and CPUE. Fishing effort for tiger prawns (Fig. 8) has escalated in the NPF during the past decade, accompanied by a decline in CPUE in recent years. The tendency towards an increasing effective fishing effort without associated increase in catch underlines the clear need for corrective management.

Management discussions

In NSW management proposals are discussed with industry through the executive of the NSW Association of Professional Fishermen which meets approximately quarterly with representatives of the Department of Agriculture. The NSW Fish Marketing Authority is the statutory body charged with the marketing of seafood in NSW.

In the NT discussions are held with the NT Fishing Industry Consultative Committee which reports to NORMAC.

The Qld Commercial Fishermen's Organisation (QCFO) to which all licensed Qld fishermen belong has a number of subcommittees dealing with various elements of the prawning industry. Some industry and government communication takes place at this level when government officers are invited to subcommittee meetings. The QCFO as well as processors, wholesalers and co-operatives are represented on the QFMA. The QCFO is also represented on a consultative committee advising GBRMPA, but the main dialogue between the authority and prawning interests takes place between GBRMPA and the QFMA. Two representatives of the QCFO and one from the QFMA are members of the East Coast Prawn Trawl Fishery Task Force.

In SA liaison with the industry is through departmental and industry liaison groups or their equivalent eg Spencer Gulf and West Coast Prawn Management Committee comprising a non-industry participating chairman (retained by the industry), and representatives: five for the boat and licence owners, one for the skippers, one for the processing sector and two for the Department of Fisheries (both from the research branch). In addition, specific officers in the Department of Fisheries are nominated as fisheries manager for individual fisheries—a manager co-ordinates all departmental activity relating to a particular fishery. Following each survey by research staff a summary of the results is sent to industry within a week. Before the major opening periods, November and April, the committee assesses survey results and develops harvesting strategies. The committee has the endorsement of industry to make recommendations if rapid changes in the management strategy are required. Government has the ability to respond within 24 h eg promulgating closures if small prawns recruit to the fishing area. An annual workshop is held (usually in September) to present to industry a summary and interpretation of the year's research data and status of the fishery.

The WA Fisheries Department has regular meetings with holders of prawn licences, usually at the end of the season to review the state of the fisheries, and before the season, when current progress in research is presented and plans for management for the ensuing season discussed. Formalisation of these procedures into, say, an industry advisory committee with industry representatives comparable with that for rock lobsters in WA, was not generally welcomed by the industry as an alternative to full industry participation. Representations may also be made to the department through the Rock Lobster and Prawning Association and the Australian Fishing Industry Council (AFIC).

The composition of NORMAC ensures the full involvement of the fishing industry in management advice on the NPF. Actual decision making is the responsibility of the AFC. The seven industry representatives on NORMAC include two each from Qld and NT (representing catching and processing sectors), one from WA, and one each from the Northern Fishing Companies Association and the United Prawn Trawler Operators Association. Such a wide representation will ensure full participation by the fishing industry Australia-wide. An annual preseason workshop provides a forum for discussion between industry and government, management and research staff.

Four out of seven members of the East Coast Prawn Trawl Fishery Task Force are from the fishing industry (two from QCFO and two from the NSW Association of Professional Fishermen). This group has full involvement in management discussions with the three representatives from Commonwealth (DPI—chairman) and state (Qld and NSW) governments.

Management measures

Limitation on boat numbers

All the known prawn fishing areas, except for Commonwealth waters off WA where no major stocks have been located, are now subject to some form of restricted entry. They include areas where limited entry dates back 21 years, when it was introduced into the then still under-exploited stocks of WA and SA. More recently recognition of over-capacity has led to the limitation of fleets fishing the north and east coasts of Australia ie limited entry in the NPF, and freezes on boat numbers in Qld, NSW and ECPTF. The Moreton Bay prawn fishery area of Qld was the subject of restricted entry in the form of a permit system from 1970, (Haysom 1975) but this was subsequently replaced by a limit on vessel size. Whether introduced in anticipation or in retrospect, all Australian prawn fisheries are now subject to excessive fishing effort. This subject is considered below.

Permanently closed areas

Permanent closures, which are of value in protecting the nursery habitat from physical damage by trawling, have been maintained in SA and WA. In NSW, Ruello (1975a) concluded that the closure of nursery areas was undoubtedly beneficial in view of the direct relationship between the size and market price of prawns. All estuaries in the Qld section of the Gulf of Carpentaria are permanently closed to trawling. In recent years, trawlermen's groups in Qld have become more aware of the role of seagrass meadows and tidal wetlands in maintaining the stocks on which their livelihood depends, and have become much more vocal in demanding the closure or preservation of nursery areas. Special consideration needs to be given to the conservation of mangroves fringing creeks carrying juvenile (particularly banana and western king) prawns. NORMAC recognises the importance of prawn nursery grounds in the NPF and it is intended that, once identified, recognised nursery areas, in addition to those already closed in NT waters, will be permanently closed to fishing thus ensuring maximum protection.

Temporarily or seasonally closed areas

Areas of concentration of young prawns may be subject to early season closure to allow juvenile prawns to grow undisturbed to a useful market size. This measure may have biological overtones but usually reflects the economic requirements of the industry. Areas are closed temporarily for this purpose in SA, WA and the NPF. Preseason research and commercial trawling provide the basis for opening the closed area to fishing in SA, in Exmouth Gulf and the NPF, where a fixed annual opening date was found not to lend itself to variable environmental conditions and recruitment patterns. The reverse applies in Shark Bay, however, where a number of years of preseason sampling in a much less variable environment focused on the now standard opening date of 15 April. In SA the variability in time of recruitment necessitated variable opening dates in order to prevent recruitment overfishing or growth overfishing.

The winter closure of the Hunter River, NSW, from 1961 was to allow sufficient prawns to breed and so replenish the stock (Ruello 1975a). However this incorrectly assumed that the spawning stock was formerly over-exploited, but Ruello concluded that the closure had some economic justification in protecting juvenile prawns during rapid spring growth.

Closed seasons

Closed seasons differ from the seasonal area closure in that the closed season applies to the whole fishery. Such a closure may be introduced or maintained for more than one reason. In SA seasonal closures are used to restrict the total time available for fishing and therefore to restrict the increasing real effort. Some of these closures may also be for convenience eg during Easter and Christmas, or economic, eg to cut down on the penalty rates paid for processing during holiday periods. The closure of Shark Bay from 1 November to 1 March had its origin in the need to further control the interest of the fleet in juvenile prawns. The juveniles had been mostly protected by the temporary closure between 1 August and 15 April of an extended nursery zone, but juveniles just inside its boundary continued to provide an attraction at a time when catches of adult prawns in the main fishery had been reduced to uneconomic levels. Subsequent information on the need to protect the tiger prawn spawning stock of Shark Bay has provided an additional justification for the seasonal closure of the whole fishery. The whole DMZ was closed from 15 December 1984 to 15 February 1985.

Moon closures

Periodic closures were introduced in SA over the six to 10 nights around the full moon (1) to prevent harvesting a significant proportion of soft newly moulted prawns, (2) to restrict fishing during low catchability periods and (3) to restrict the total number of nights (hours) available to the industry for fishing, again as a response to the increase in real effort being expended in the fisheries. Moon closures have also been applied recently in Exmouth Gulf as part of the management package to further control fishing effort by the roster – reduced fleet. These have the advantage of eliminating competitive fishing between companies at a time when catch rates reach uneconomic levels.

Minimum legal size

Size restriction has not been found to be a measure of practical value in prawn fisheries due to the low survival rate of captured prawns. Restrictions on net meshes have traditionally been the preferred alternative for controlling size, with more recently nursery closures and seasonal closures. Ruello (1975a) summed up a typical experience with his comment on the abolition of a minimum legal length for prawns in NSW estuaries. In his view the recommendation that the minimum legal length of prawns should be rescinded was certainly most timely because thousands of pounds of dead prawns were being discarded weekly in northern NSW in the early 1950s. Ruello concluded that if the cost of enforcing regulations was taken into account it would represent a most costly regulatory measure with negative value to the industry. The minimum mesh size of trawl net was increased to raise the average size of prawns caught, giving not only a more valuable product but better escapement of bycatch of small finfish.

Net mesh regulations

NSW otter trawls must have a mesh no less than 40 mm and no greater than 60 mm (codend 40 to 45 mm). Regulations in the NT are complementary to those of the NPF which has no controls on mesh size. Qld prohibits a mesh of less than 38 mm, but mesh size is not regulated in Commonwealth waters off Qld. SA has a mesh size restriction of 45 mm in the codend and 50 mm in the wings. WA has minimum mesh size regulations relating only to estuarine fisheries but the marine sector has standardised on 50 mm (codend 47 mm) as a workable mesh.

Vessel characteristics

In SA replacement vessels may not exceed an overall length of 19.8 m and an engine power of 365 continuous bhp. WA has had discussions with industry on the need for additional controls on trawling capacity in recognition of continually increasing fishing effort within the limited entry framework. Traditionally gear has been selected as the controlling mechanism in contrast to a boat replacement policy which directly restricts vessel dimensions. Vessels over 20 m in length are currently prohibited in territorial waters off the Qld east coast. Arrangements for the NPF focus heavily on a boat replacement policy which is the main management tool for containing total fleet fishing capacity. This is based on a unitisation concept involving a combination of under-deck-volume and main engine power. Units (which are transferable) have been allocated to the total NPF fleet based on current boat dimensions and main engine specifications. Boats under 375 boat units, which is approximately equivalent to a 21 m bounty size vessel, can upgrade to 375 boat units without having to acquire additional units from within the fishery. This contains the potential for an expansion of fishing capacity, but which the industry maintained would, in practice, be minimal and would be more than offset by the introduction of a Voluntary Licence Entitlement Buy-back Scheme to remove boats from the fishery. The boat replacement policy for the East Coast Prawn Trawl Fishery was to allow for a replacement boat of up to one metre longer than the original one. [This was subsequently changed to allow small vessels to upgrade to 9 m but a larger vessel can be replaced only by one of the same size. Ed.] The East Coast Task Force favours a unitisation scheme, involving units based on the vessel's share of the fishing effort applied by the fleet, which may be sold and transferred. This is intended to provide flexibility in vessel replacement while containing fleet capacity.

Gear regulations

In NSW estuaries prawn trawl nets are limited to a total length of 11 m and each vessel is permitted to tow a maximum of two nets. Nets are measured along the headrope of the net. Offshore and inshore prawn trawl sweeps are limited to 5 m in length. In Qld offshore waters, both otter and beam trawls are restricted to a headrope length of 40 m, while the otter trawls have a further restriction that the combined headrope and footrope length shall not exceed

88 m. Minimum mesh size is 38 mm in each case. Other restrictions apply to certain bay waters, and to rivers, creeks and lakes. In SA vessels are limited to triple-rig in Gulf St Vincent, and double-rig in the other fisheries. Additional restrictions of total headline length are also in force in Spencer Gulf (29.26 m) and Gulf St Vincent (27.45 m). In WA licensed trawlers have, from 1976, been restricted to two nets and a total headline length of 29.26 m, as a measure to place an upper limit on the unit of effort, and in order to discourage the building of larger replacement vessels qualifying for the shipbuilding bounty, which had proven uneconomic in both Shark Bay and Exmouth Gulf. There are no net size regulations in Commonwealth waters in the NPF or off Qld.

Buy-back scheme

Although buy-back schemes have been the subject of considerable discussion with reference to various fisheries around Australia, so far plans have come to fruition only in the NPF. In other situations the main stumbling block has been a source of finance. This is being overcome in the NPF in the form of a compulsory annual levy on licence holders on the number of boat units established according to the DMZ boat replacement policy rules. Arrangements for buying out four of the 23 prawn trawler concessions in Exmouth Gulf were completed in early February 1985, utilising an interest-bearing loan to be repaid by the remaining 19 concession holders.

Bases for management

Data base

Each management authority has its own data base, with varying degrees of longevity, continuity and reliability. Data provided by fishermen on a compulsory monthly basis are screened for inconsistency, analysed and published by local authorities and by the Australian Bureau of Statistics (ABS). Catch data suffer from the usual tendency towards under-reporting, and fishing effort statistics are often too generalised for the sophisticated analytical procedures required for modern management purposes. Research logbooks, where they have been maintained successfully eg in SA and WA, and by NT, Qld, CSIRO and Commonwealth DPI in the NPF, provide a means of validation of ABS data, and more detailed statistics of fishing effort. The ingredients for success of a research logbook system were given by Hancock (1975): (1) sustained personal contact with fishermen; (2) computer validation for spurious logbook entries; (3) validation between fishermen's and processors' returns and logbooks; (4) rapid availability of data for management; and (5) prompt feedback of information to participants.

Ingredients (4) and (5) may place a heavy responsibility on the administrating authority, particularly in the NPF, where a large number of boats land prawns at several ports.

An essential ingredient of any management program is a system of monitoring, not only of catch and effort statistics, but of important biological parameters as well as relevant characteristics of the fleet and its logistics. The amount of detail required will reflect the degree of involvement in management which will be a function of the perceived level of exploitation or the degree of insecurity. Unfortunately, failure to collect the requisite amount of information cannot be rectified at any later date when concern about exploitation levels is likely to be experienced. Increasingly, economic surveys are assuming an important role, with the Commonwealth Bureau of Agricultural Economics (BAE) usually providing the required data base. Monitoring of the size composition of the catch, either on board or at the factory, relative to the season of capture is an essential requirement for detection of any growth overfishing which becomes a possibility when excessive effort is concentrated into times (early season) and areas (near nursery grounds) in which young, small prawns predominate.

Biology and life history

Proper identification of species to be managed is of vital importance, particularly when several occur together. Ruello (1975b) listed the names of prawns of commercial importance which are now well known, and Grey et al (1983) have provided detailed descriptions of each species. Despite this there is still some confusion over identification of three species pairs taken in the NPF. These are tiger prawns, *P. esculentus* and *P. semisulcatus,* banana prawns, *P. merguiensis* and *P. indicus,* and endeavour prawns, *M. ensis* and *M. endeavouri.* SA is perhaps the only fishery with a single major species the western king, *P. latisulcatus.* In Shark Bay western king are dominant to brown tiger prawns, while the reverse is usually the case for Exmouth Gulf where distinctive management problems have occurred. The NPF requires two different fishing strategies for major species groups ie banana and tiger/endeavour prawns. The life history and behaviour of the major species have now been researched, and are vital to the design of management strategies and evaluation of their consequences. A major biological feature of penaeid prawns which is highly significant for management is their short life span of usually only one to two years. The tendency for juveniles to be found in discrete nursery areas justifies the protection of fragile seagrass and mangrove environments.

Population dynamics and modelling

Dynamic pool models (Beverton and Holt 1957) have little practical value in prawn fisheries firstly because of the short life span with its inherent variability in recruitment, and secondly because quantification of natural mortality (M) remains as elusive as in many other fisheries. Lack of knowledge of M is also a fundamental problem in any predictive strategy such as timing of opening of seasons or of temporary closures. In such circumstances the major influence on decision making will usually therefore be the preferred market size and value. Stock production models (Schaefer 1957; Pella and Tomlinson 1969 (Genprod); Fox 1970) can provide a useful description of a fishery (Bowen and Hancock 1984) and their application to short-lived species should give meaningful equilibrium representations. The emphasis with prawns is, however, more reasonably directed towards average expected catch and optimum economic yield than the maximum sustainable yield (MSY). However, stock production models have no value for predictive purposes. Bowen and Hancock (1984) described procedures for calculation of effective effort based on Hall and Penn (1979) and presented data from WA fitted by Schaefer and Genprod models and these are brought up to date in Fig.9.

A multistage recruitment model for banana prawns in the Gulf of Carpentaria has been described by Staples (1985). The development of a prawn crop model by SA is proceeding.

Preseason sampling

The lack of information on M demands a more pragmatic approach when it comes to preseason sampling as practised in SA, WA and the NPF. The major motivation for delaying catching at the beginning of each season has been to achieve a desired market size and value as well as to prevent possible growth overfishing. In SA the preseason sampling concept has been extended to arrange harvesting schedules which attempt to enhance the quality (size count) of catch by directing effort to optimum areas and periods (Anon. 1983). The results are being incorporated into a prawn crop model. In Shark Bay, the standardised opening of temporary nursery closures on 15 April has been found to meet industry's requirements for market sizes of above 15g whole (30 per pound whole). In Exmouth Gulf the objective of optimising size for market purposes has more recently been coupled with a need to reduce fishing mortality and encourage survival to spawning.

In the NPF, preseason surveys of banana prawns have been conducted during recent years by CSIRO and state fishery scientists, in collaboration with the fishing industry, using commercial prawn trawlers. Opening dates are directed towards maximising yield and value per recruit rather than optimising biomass (Somers 1985).

It must be emphasised that although decision making may reflect economic requirements, the underlying advice must have a biological basis without which in the long term there will be no possibility of reducing the intensity of monitoring and study. Long-term forecasting such as that being undertaken by Staples (1985) might eventually be used as a practical basis for quantitative allocation of the banana prawn resource, but would require a much greater investment of time and budgets.

Stock recruitment relationship

Dawson (1980) defined recruitment overfishing as a situation in which the spawning stock has been reduced to a level at which the average recruitment to the stock is significantly reduced. There has been slow acceptance that recruitment overfishing can occur in prawn stocks.

In 1970 at the International Council Symposium on Fish Stocks and Recruitment, Hancock (1973) reported that there was a complete lack of information on stock and recruitment relationships in Crustacea.

Garcia and LeReste (1981) in an FAO review concluded 'There are no shrimp stocks, even those which have been heavily exploited, for which it can be shown with certainty that the recruitment has been affected by the exploitation of adults, except perhaps recently in the Gulf between Iran and the Arabian peninsula. There is more generally a tendency

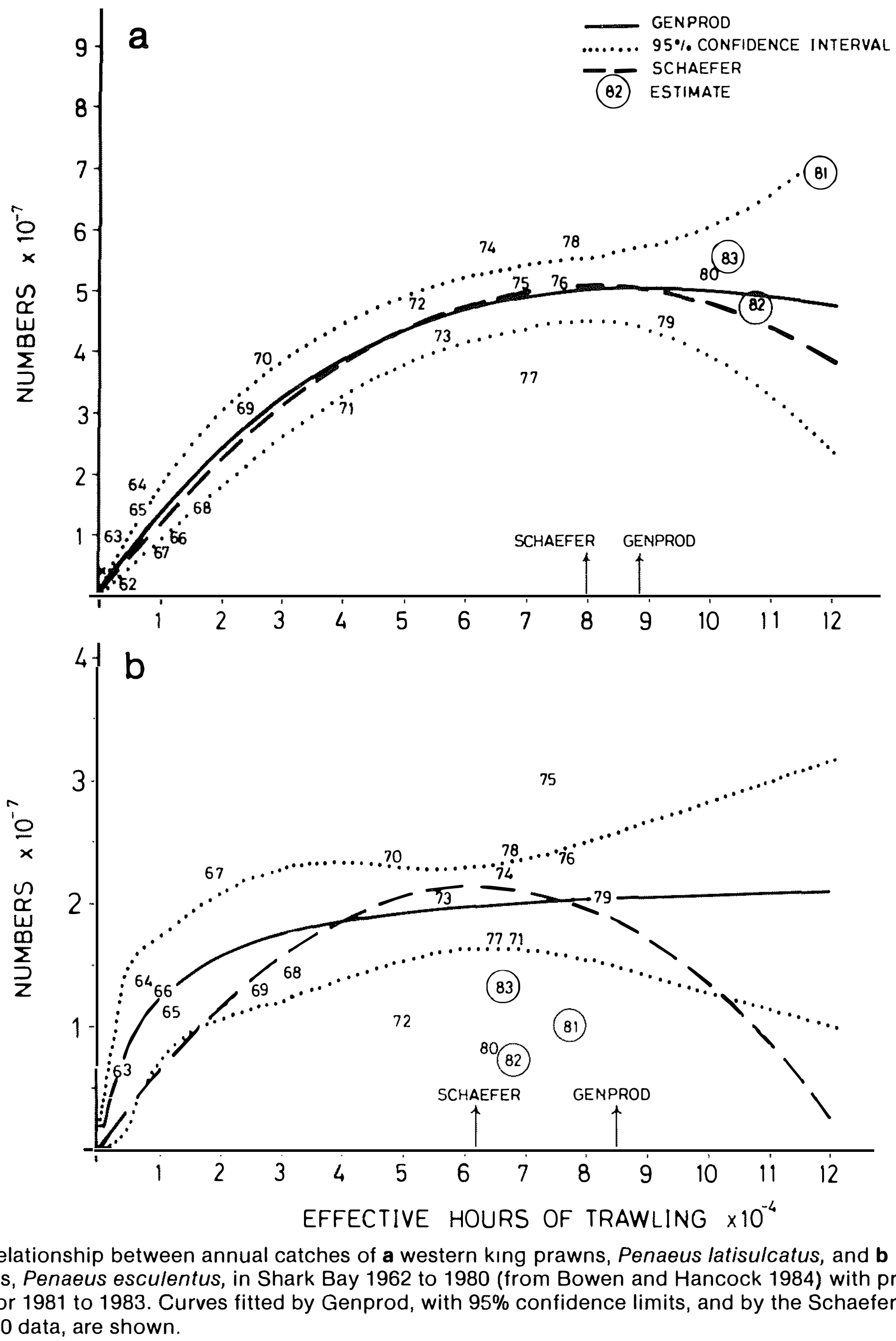

Figure 9. Relationship between annual catches of **a** western king prawns, *Penaeus latisulcatus*, and **b** brown tiger prawns, *Penaeus esculentus*, in Shark Bay 1962 to 1980 (from Bowen and Hancock 1984) with preliminary estimates for 1981 to 1983. Curves fitted by Genprod, with 95% confidence limits, and by the Schaefer model to 1962 to 1980 data, are shown.

to assume that the recruitment is not limited by the abundance of spawners within the normal range of exploitation levels and that it seems to be more influenced by environmental conditions or by the deterioration of the estuarine conditions.'

The Fishery Management Plan for the shrimp fishery of Gulf of Mexico (Anon. 1981) contained the statement 'No scientific data exist to show an advantage from protecting spawning shrimp: there is no relationship between the number of spawners and recruits'.

At the 1981 International Meeting on the Scientific Basis for the Management of Penaeid Shrimp held in Key West, Florida, several countries, including Australia, reported concern that effort levels might be affecting levels of recruitment. Bowen and Hancock (1984) commented to the meeting 'widely held views, which put the emphasis on economic, rather than biological, management, are now being challenged. Only future events will show whether the tiger prawn stocks in Shark Bay are showing recruitment over-fishing as a consequence of excessive fishing effort'.

Garcia (1983), however, in a manuscript based on the meeting concluded 'that the presently available (ie to 1981) relationships do not demonstrate that the recruitment of shrimps is a function of stock size' but in referring to data from Shark Bay and Exmouth Gulf Penn (1984) stated 'These last observations may indicate that there indeed is a level of effort above which recruitment problems are met.'

Gulland (1984) in a manuscript written at about the same time stated 'A possible relation between recruitment and the size of the spawning stock has received remarkably little attention . . . Recently, shrimp scientists have paid more attention to the possibility of average recruitment being affected by adult stock. In view of the serious practical implications of such relation, if it exists, even more attention should be paid in the future'.

Penn and Caputi (1985) have provided convincing evidence that recruitment overfishing can occur, in the specific circumstances of enclosed, relatively small fisheries for brown tiger prawns in WA. Circumstantial evidence has been provided on a similar situation in western king prawns in SA. Perhaps the most heartening feature is that corrective measures have led to recovery of the stocks in WA and SA, but for such collapses to happen is not in the best interests of orderly management. The pity is that the long-held view that prawns are not subject to recruitment overfishing has tended to give managers a false sense of security, and even some scientists seem to have closed their minds against such a possibility. It will be interesting to see whether acceptance of the reality of recruitment overfishing in prawns will lead to the recognition of examples from other fisheries. Clearly a matter of such fundamental importance to management of prawns as the stock recruitment relationship must provide a major challenge to those responsible for research and data collection.

Perceived problems

It must be anticipated that management of prawn fisheries by controls on fishing effort and catch is not likely to provide a simple solution.

Control of fishing effort

The problem of excessive fishing effort has materialised whether limited entry has been introduced or not. Limitation of the number of boats has clearly not been effective as a method of effort control without additional controls on individual catching capacity. All Australian prawn fisheries are now faced with the problem of reducing fishing effort. While the major concern in the smaller fisheries is one of excessive exploitation leading to recruitment overfishing, both they and the larger fisheries have recognised the need to reduce fishing effort in order to return towards optimising economic returns. In the NPF the boat replacement policy, the unitisation arrangements involving transferable units and the Voluntary Licence Entitlement Buy-Back Scheme, are all designed to serve this purpose. Managers of smaller fisheries will watch these developments with interest, but are aware that any tendency, within a small fishery of reduction towards too few surviving vessels could draw public criticism of a privileged group monopolising a common property resource. One well recognised cause of excessive fleet capacity is where, in an effort to establish eligibility criteria, fleet activity has been concentrated on fisheries expected to be managed by limited entry. This has more recently been overcome by initial freezing of boat numbers, followed by selection based on past performance. Shipbuilding bounties payable only on boats built to specifications larger than optimum for a fishery have led to increases in replacement boat sizes. Problems of excessive effort in limited entry fisheries have also been engendered by lack of alternative fisheries, high value of the catch, and the occurrence of mixed species, where the supporting catch of one or more minor species may encourage continued fishing of a species which has been fished down to uneconomic catches (Penn and Caputi 1985).

Total Allowable Catch

The concept of a Total Allowable Catch (TAC) has usually seemed more appropriate for long-lived species. Its use for prawns which have an annual crop would require a precise knowledge of relative year class strength and of the seasonal effects of fishing and natural mortalities, otherwise wastage may occur. On the other hand, in a situation of high exploitation rate, the TAC will need to take cognisance of the minimum requirement of spawning stock to ensure adequate recruitment. In Exmouth Gulf, WA, measures to ensure recruitment have relied on control of boat numbers and a restricted season to ensure an adequate spawning stock. The cost, however, is considerable because it requires virtually daily monitoring of the fishery by research staff, in much the same way as the SA optimum harvesting program. The concept of quotas has not received general support from licensees of the NPF.

With a TAC there will be a tendency towards intense competition early in the season, which will lead to shorter and shorter seasons, probably before maximum yield or value per recruit have been realised.

Summary and conclusions

1. Virtually every Australian prawn stock is the subject of a declared management regime either on a state basis, or jointly with the Commonwealth.

2. Each fishery has become subject to some form of limited entry regulations, ranging from restrictions on further entry, to the issue of special concessional licences.

3. Supporting regulations vary from zone to zone but usually include closed seasons, net restrictions, protection of nursery areas and controls on vessel size.

4. The major objective of prawn fishery management is seen to be resource maintenance although in recent years controls have been directed towards reducing excess fishing capacity in order to improve economic returns.

5. Management by licence limitation has been introduced both early in the development of fisheries to control expansion of fishing effort, and in well established fisheries to reduce fleet fishing capacity and improve economic returns. In both cases licences have become transferable and have attracted a resale value.

6. The potential has been revealed for growth towards overcapacity, even in fisheries in which fishing effort was limited at an early stage of development, leading to recruitment overfishing in certain confined stocks.

7. All major Australian prawn stocks now appear to be fully or excessively exploited.

8. Australian prawn fisheries vary from multispecies to single species fisheries, involving different harvesting strategies.

9. The Australian fishing industry is now fully involved in management discussions and procedures.

10. Management strategies include planning of opening dates to optimise size at first capture from nursery studies and preseason trawl surveys.

11. Research advice for management is dependent on a reliable and timely data base, which can be costly and difficult to provide in fisheries distributed along an extensive coastline.

12. Stock production models continue to provide a useful descriptive but not predictive, basis for management. Recognition of recruitment overfishing at high levels of effort in more than one prawn fishery requires a new philosophic approach which needs to be acknowledged in planning of research and data collection.

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Review of the Gulf of Mexico management plan for shrimp

Abstract: Extended United States jurisdiction for fisheries management was initiated in 1976 with management planning delegated to regional groups or councils, one of which has responsibility in the US territorial waters of the Gulf of Mexico. A plan for managing shrimp in the Gulf, implemented in 1981, has as its principal objective the maximisation of yield of shrimp recruited to the fishery. The technique used is to defer harvest through seasonal and area closures to allow prerecruits to reach a larger, preferred size. The effectiveness of federal regulation is largely dependent on co-ordination of management and enforcement in contiguous inshore state waters. The benefits of federal management are also enhanced by favourable environmental conditions which produce and extend greater numbers of prerecruits into the offshore federal sanctuary.

Seasonal closures in the western Gulf are estimated to have increased Gulf-wide yield of *Penaeus aztecus* by 9% in 1981, and 6% in 1982. Monitoring spring water temperatures and salinities allows some degree of accuracy in predicting annual abundance of this species. Salinities about 10‰ and temperatures above 20° C are favourable. Benefits of management of *P. duorarum* in the eastern Gulf are less clearly defined, and relationships to environmental factors are not clearly understood. Restriction of US vessel access to former foreign fishing grounds and increased imports from mariculture may require a reassessment of the management program.

Introduction

In 1976 the United States extended its jurisdiction over fisheries, exclusive of tuna, to 200 nautical miles (362 km) and provided a program of management. Before that time fisheries in the territorial sea were managed by the states. In the US Gulf of Mexico there are five state jurisdictions which were not changed by the extended federal jurisdiction. Louisiana, Mississippi, and Alabama each have three n miles (5.4 km) of sea and Texas and Florida's west coast have nine n miles (16.3 km) (Fig. 1a).

The US Congress opted for regional management with the US Gulf of Mexico as one of eight jurisdictional regions. Management planning authority was delegated to the Gulf of Mexico Management Council (the Council) composed of appointed members and ex officio representatives from state and federal agencies. Fishery management plans must comply with specified national standards and once approved are implemented by federal regulation.

A fishery management plan for Gulf shrimp was initiated in 1977 under contract by a team of university fishery scientists, economists, social anthropologists, and lawyers. Procedures call for the development of the draft document to be closely monitored by a committee of Council members. An appointed advisory panel of users of the resource (fishermen, processors, dealers, and consumers) reviews the plan to determine the impact. An appointed committee of scientists, of assorted expertise, reviews the document for technical accuracy and to assure that the best available data are utilised. The draft document is presented for review at a series of public hearings and appropriate changes are included before it is submitted for federal approval. Plans may be rejected for not complying with prescribed guidelines during the review process or must be implemented as federal regulation at the end of 140 days.

The principal objective of the shrimp management plan is to optimise the yield of

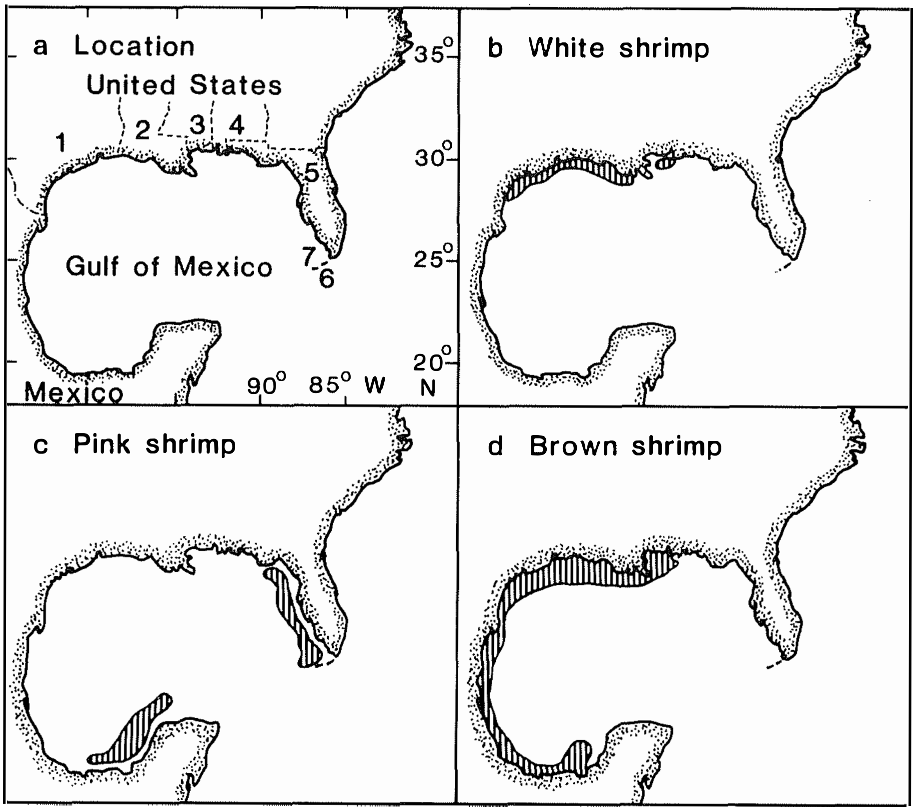

Figure 1. Gulf of Mexico with locations of principal fisheries for white, pink, and brown shrimp. **a.** Locations—1. Texas, 2. Louisiana, 3. Mississippi, 4. Alabama, 5. Florida, 6. Florida Keys, 7. Tortugas shrimp grounds. **b.** White shrimp, *Penaeus setiferus,* fishery. **c.** Pink shrimp, *P. duorarum,* fishery. **d.** Brown shrimp, *P. aztecus,* fishery.

shrimp recruited to the fishery (Anon. 1981). This is done by deferring harvest of small shrimp until they reach a preferred size. Among the many problems encountered was the specification of the preferred sizes of the various species for diverse users, including a large canning industry desiring small shrimp and processors with markets for very large shrimp.

Shrimp provides the United States with its most valuable fishery. The 1983 landings were valued in excess of $500000000 ($500M) with $416M of that from the Gulf of Mexico (National Marine Fisheries Service 1984a). In a year with good environmental conditions, the US Gulf may produce around 120000t of whole shrimp. There are about 10000 full-time commercial vessels and boats in this shrimp fishery and numerous part-time and recreational boats. The principal shrimp species in the Gulf in order of importance are the brown, *Penaeus aztecus;* white, *P. setiferus;* and pink, *P. duorarum.* All three species are estuarine dependent having been spawned offshore, migrated into the estuaries as postlarvae, and returned to offshore waters as subadults, or adults. Although all three species may be found together, there are seasonal, spatial and diurnal variations in distribution and availability.

The management plan

White shrimp

The white shrimp, *P. setiferus,* is most closely associated with the estuarine environment. It is found farthest inland in nearly fresh water, grows to a larger size in inland waters, and remains closer to shore than the other two species, (Fig. 1b). The fishery extends offshore only to a depth of about 27 m. This species is active during daylight, and thus for all of the

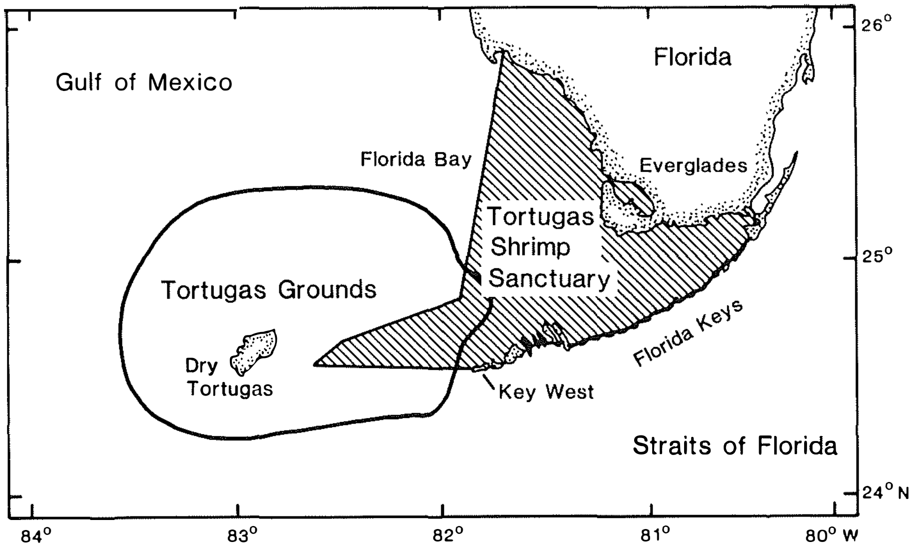

Figure 2. Tortugas pink shrimp, *Penaeus duorarum,* grounds and shrimp sanctuary.

aforementioned characteristics, supported the initial commercial fishery for Gulf shrimp in the early 1900s on beaches with haul seines.

Gunter and Hildebrand (1954) described the direct relationship of Texas white shrimp production with earlier rainfall; however, quantitative sampling of the young of this species has been difficult, and predictions of seasonal abundance are not very accurate. White shrimp are recruited into the bay fishery in August following the primary exodus of juvenile brown shrimp in June. The harvest extends through November. Some large overwintering whites provide a late spring fishery in May and June. Because adult white shrimp are often mixed with the more abundant juvenile brown shrimp at that time, white shrimp provide a management problem to the states. With the inshore distribution of this species, management jurisdiction lies almost entirely with state regulatory agencies. The states employ several techniques to defer harvest of small shrimp. Closed seasons, closed areas, minimum size, trawl mesh size, and daily catch limits are utilised. Because white shrimp are active in daytime, but browns and pinks are more available at night, prohibition of night fishing is used to direct the effort to the larger whites. States may also establish sanctuaries in shallow tributary bays to protect the small shrimp which inhabit them and allow trawling in major bays where larger ones are predominant.

Although there is no evidence of biological overfishing in any of the Gulf shrimp fisheries, recent declines in white shrimp catches in some areas of the northern Gulf have given rise to concern by some fishery scientists. Some feel that overfishing may be expected with this species because of the relatively easy fishing access to the stock throughout its inshore range. The annual commercial catch of white shrimp averages about 16500t of tails. Additionally, there is a largely unreported recreational catch by an estimated 239000 participants. Brown (1981) estimated landings of 4687t by this group in 1979. Probably a major portion consisted of white shrimp.

Pink shrimp

The fishery for pink shrimp, *P. duorarum,* is located in the eastern Gulf near the Florida Keys on the Tortugas shrimp grounds (Figs. 1c, 2). The grounds were discovered in 1949 in an area of rough bottom north and west of Key West. Trawl space is limited by coral rock and loggerhead sponges. Much of the present fishable bottom was cleared by trawling activity. Fishing occurs throughout the year but peak catches are made from October through May. Landings amount to about 4490t of tails annually by 400 to 600 trawlers.

Juveniles migrate from the Florida Everglades, a vast complex of salt and freshwater marsh, passing through a vast shallow, largely unfishable portion of Florida Bay. Florida had earlier established a shrimp sanctuary in Florida Bay and had a minimum size limit of 70 tails to the pound, which provides an animal of an average total length of about 103 mm with a tail weight of about 6.5 g. Sampling programs had shown that pink shrimp taken in that area beyond the 18 m isobath are generally larger than that. The Council's plan adopted a sanctuary in federal waters contiguous to the state sanctuary for a total area of approximately 3400 n miles^2 (11662 km^2). The joint sanctuary lies between the nursery area in the Everglades and the 18 m isobath (Fig. 2).

The plan also recommended, and Florida subsequently adopted, the repeal of the state's minimum size limit. This action discouraged the wasteful practice of culling and discarding small shrimp. Recent sampling has shown continuous recruitment inside and outside the sanctuary (Roberts 1983). Mixed sizes of pink shrimp occur but small shrimp are predominant at most stations within the sanctuary. Sampling has not shown a consistent seasonal size distribution that would allow seasonal closures. Tagging studies showed pink shrimp released inside the sanctuary moved to deeper waters to the north and west and that shrimp in the sanctuary do recruit to the fishery (Klima, Jones et al 1983).

Nichols (1984a) has calculated a theoretical gain of 14 to 20% in weight and 45 to 64% in value from shrimp recruiting to the fishery through the protected area. He used a natural mortality rate of 0.3 per month and fishing mortality rates of 0.3 per month for summer, and 0.5 to 0.7 per month for peak winter fishing. Mortality rates were estimated from mark and recapture studies.

Recruitment probably varies with environmental conditions in the Everglades, but consistent trends between environment and catch have not been identified.

Brown shrimp

The major fishery for the brown shrimp, *P. aztecus* is in the northwestern Gulf (Fig. 1d). Average annual landings are about 30000 t of tails, but recruitment varies with environmental conditions in the bay nursery areas with landings reaching 45000 t in good years.

Postlarval brown shrimp enter the bays in March from offshore spawning grounds beyond the 18 m isobath. The number of postlarvae immigrating is not a reliable prediction index for later recruitment to the fishery because of the overriding influence of dynamic conditions of environment in the estuarine nursery areas.

Favourable estuarine conditions for juvenile brown shrimp include warm water temperatures, well-flooded marshes, and relatively high salinities. In March and April late cold fronts may lower water temperatures in the shallow marsh, and strong north winds accompanied by abnormally low tides may temporarily drain the nurseries. These adverse conditions along with spring flooding may sharply reduce survival of the postlarvae and juveniles. Shrimp researchers in Louisiana using techniques developed by Barrett and Gillespie (1973) can predict the relative recruitment by measuring the number of hours of water temperature below 20° C in April and the total area of Louisiana estuaries with a salinity above 10‰. They also monitor rainfall and the discharge of the Mississippi River, because the latter greatly influences salinity of coastal waters (Perret[1], pers. comm.).

In Texas estuaries National Marine Fisheries Service (NMFS) biologists monitor influx of postlarvae as an early indicator. However, they find the relative magnitude of catches in the bay commercial and bait shrimp fisheries in May and early June, and sampling of juveniles in the marsh habitat to be more reliable in predicting the brown shrimp production in the Gulf waters off Texas for the following 12-month period. Using this procedure, in 1982 the Galveston Laboratory of NMFS predicted landings off Texas of 9800 t for the season and actual landings were 9900 t. In 1983 the prediction was for 8100 t and landings were 8200 t (Klima, Baxter et al 1983).

Juvenile brown shrimp emigrate from the bays en masse in late May and early June at a size below that desirable for harvest. Fishing is delayed by a co-operative closure of Texas and adjacent federal waters for 45 days. Prior to implementation of the fishery management plan for shrimp, Texas had closed its Gulf waters to the extent of its jurisdiction of nine n miles (16.7 km) and had a minimum size limit for shrimp landed in the state. Vessels could fish beyond state jurisdiction; and because this is a night fishery, they could slip into the closed waters with small chance of apprehension.

[1] W.S. Perret, Louisiana Dept. of Wildlife and Fisheries, Baton Rouge, Louisiana.

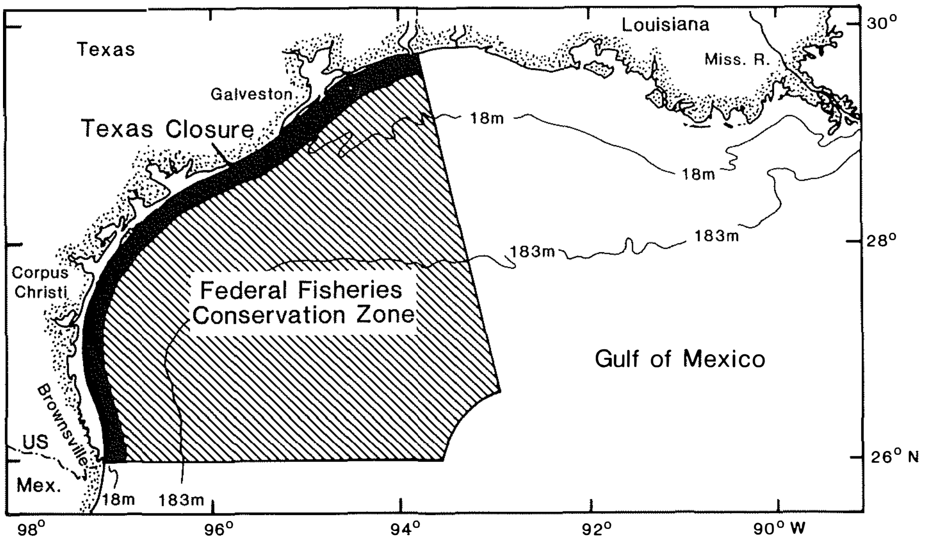

Figure 3. Northwestern Gulf of Mexico with seasonally closed Texas territorial waters (solid) and concurrently closed Federal Fisheries Conservation Zone (striped).

Culling and discarding small shrimp was extensive with losses of about 2200t during June and July.

As with the pink shrimp in the Tortugas fishery, brown shrimp size generally increases with distance from shore. The desirable size for recruits is a minimum total length of about 114mm at a weight of 11.6g. Although most shrimp 48km or more from shore are larger than this size, the Council opted to close the entire 322km fishery conservation zone off Texas because of the difficulty of enforcement that Texas had encountered in its closure (Fig. 3). Indeed, compliance has been improved through the co-operative closure; the number of cases filed for violation of the closure in state waters declined from more than 150 per year in 1980 to 21 per year in 1981 after closure of the federal zone. The Council plan encouraged the repeal of minimum size limits, and Texas changed its law to allow the landing of any size of shrimp. This state provision, however, is contingent on the continuation of the seasonal closure of federal waters to protect the small shrimp.

State biologists monitor the size of juvenile brown shrimp in Texas bays by sampling, and, with use of the Von Bertalanffy growth model from Parrack (1979) estimate the likely date that shrimp will reach a size of 90mm. They then identify the nearest period of extensive ebb tide at night and estimate the peak emigration from bays to Gulf to be at that time. The flexible closure date is then set to commence with the migration. Nichols (1984b) employed simulation modelling techniques to evaluate the effects of the combined closure on harvest of shrimp. He used a virtual population analysis (VPA) to obtain estimates of fishing mortality rates and recruitment under existing conditions. He generated fishing mortality rates and applied them in a scenario simulating fishing without the closed seasons in 1981 and 1982 starting with the recruits estimated by the VPA. He estimated that the actual Gulf-wide yields from the joint closure exceeded the yields projected without the closure by 3973t or a 9% increase for the first closed season in 1981. For 1982, the estimated gain was 1875t or 6%. The difference in estimated gains between the two years resulted from greater recruitment, from favourable environmental conditions in 1981, and the increase of an inshore bay fishery on small shrimp in 1982.

Nichols (1984b) also used yield per recruit models to illustrate the potential for optimum size management and evaluate the existing closures and the trade-offs between inshore and offshore yields. Using a Gulf-wide fishing mortality rate of 0.5 per month, he found a net gain of 17% in weight yield with fishing delayed 1.5 months to permit growth to a size of about 113mm. A maximum value of 94% over nonregulation would be obtained with a three-month delay and harvest at a size of 134mm. This size and delay, however, is not acceptable to the industry.

The seasonal closure of federal waters off Texas did not extend eastward off other states. One reason was that shrimp migrating across Mississippi Sound are of harvestable size when they reach federal waters. Off Louisiana the situation is different because the fishery there is directed at a smaller size shrimp. In Louisiana the predominant catch is made by small boats fishing inshore for small shrimp. A large portion is processed through peeling machines or is canned. This contrasts with Texas, where there are no canneries and where the larger product is targeted to a different market. Because Louisiana does not close its territorial offshore waters for the egress of small shrimp, a unilateral federal closure would cause a further shift of fishing effort to the small shrimp in the inshore, state-controlled waters and would be counterproductive by reducing abundance offshore. Louisiana's vast wetlands complex provides for a greater production in weight and far greater production in numbers of shrimp than Texas; however, the Texas landings have a greater value. There is no doubt that the yield in Louisiana and offshore waters could be increased by deferring harvest to increase the size of shrimp at entry to the fishery. This would require state as well as federal action, and the industry does not currently support such action.

Discussion

The Council recognises that there are shortcomings in the management plan, some inherent and some which develop as conditions change. Annual reviews are used to identify and address the problems by use of technical and user advisory groups and revision of the plan. There are presently several problem issues which need to be resolved.

First is that of overcapitalisation or excessive participation in the fishery. The 10000 boats and vessels in the Gulf shrimp fleet are not needed to maintain production at present levels. The authority given to the Council by the enabling legislation is restricted. One of the national standards provides that conservation and management measures shall, where practicable, promote efficiency in the utilisation of fishery resources, except that no such measure shall have economic allocation as its sole purpose. Another provision is that fees established for permits shall not exceed the administrative cost of issuing them. Thus, entry could be limited, but only for reasons other than economic allocation. Permits could be required but only at a cost of about $10.

The displacement of the fleet from foreign fishing grounds is another concern which has contributed to the excessive entry in the domestic fishery. During the early 1970s, slightly more than 10% of the US Gulf shrimp fleet's effort was expended off Mexico (Griffin and Beattie 1978). For Texas, adjacent to the Mexican border, 17% of its landings and 19% of its shrimp revenue came from waters off Mexico. The Brownsville-Port Isabel port complex at the border had the greatest shrimp landings in the Gulf; a resident fleet of 400 vessels over 15m and numerous processing and freezer plants. These vessels had the option of fishing the productive grounds either off Texas or Mexico. In the late 1970s, Mexico extended its economic zone and phased out all provision for US shrimp fishing by 1980. The exclusion was not strictly enforced, and many US vessels continued to fish illegally off northern Mexico. In 1980 the US Congress amended its Lacey Act (which prohibits interstate traffic of wildlife and wildlife products taken illegally) to include crustaceans. Thus, it became unlawful to land in the US shrimp that were taken unlawfully off Mexico. In 1982, the US launched a massive effort in drug interdiction on the high seas and netted a substantial portion of the shrimp fleet in violation of the Lacey Act. Penalties of up to $10000 may be assessed for each violation. Some south Texas fishermen who had enjoyed the benefits of the seasonal Texas closure and fished off Mexico during that period have become embittered and now object to the management measure because they are idle during the closure. There is also concern by fishermen that shrimp produced in Texas estuaries may migrate to Mexican waters during the closure and thus are unavailable when the season reopens. In fact, earlier tagging studies have shown that shrimp in near equal numbers cross the US and Mexico border in both directions (Nichols 1985). The studies, however, do not provide good indication of migration during the June to July closure. Joint tagging studies with Mexican scientists are planned for the 1985 closed season to address this question.

Another consideration is the increase in the proportionate catch of small shrimp inshore contributing to growth overfishing. The plan defines growth overfishing as a level of effort directed at juveniles which prevents the exploited population from providing its maximum yield, but does not impair the reproductive capacity of the stock.

In 1976 Louisiana had 18000 licensed commercial and recreational shrimp fishermen, and this increased to 37000 in 1983. In Texas inshore landings of brown shrimp had remained below 1360t until 1979, but by 1983 they exceeded 2700t. Klima, Baxter et al (1983) calculated the number of individual brown shrimp caught inshore in Louisiana to be 1.3×10^9 in 1983 which constituted 66% of the state's landings. In Texas they found the inshore catch of brown shrimp to be 0.6×10^9 shrimp or 56% of the total number landed. Most of the Louisiana inshore brown shrimp caught are smaller than 92mm total length, and most of those in Texas are smaller than 97mm. This is well below the target size to achieve for maximum weight and value yield.

A recent and serious problem for Gulf shrimp fishermen is the increase in shrimp imports at competitive sizes and low prices. Although the US processors have long been dependent on foreign shrimp to satisfy the growing market, the level of imports exceeded 152000t in 1983, an increase of 62000t over 1973. World production of shrimp raised in ponds, estimated to be 33036t (tail weight) in 1983, is projected to be more than 234000t by 1990. If one third of that additional production enters the US market, economists estimate a decrease in price of 18% (NMFS 1984b). The size of pond-raised shrimp at harvest in Latin America, particularly Ecuador, has been in the range of 123 to 138mm total length, or individuals which weigh from 14 to 20g. This is the same size range targeted for harvest in the management program in the Gulf. The Council has begun to monitor the sizes of imported shrimp so that it may direct fishing to a size best suited to the economics of the domestic market place. Finally, the introduction and growth of so called analog seafood products provided a totally new competitor in the market for shrimp. The imitation shrimp products manufactured from surimi or low cost fish, are already competitive at the lower end of the shrimp price spectrum and can be expected to have increased impact on that share of the market (NMFS 1984b).

The proposed future course of action for the Council is to continue monitoring and evaluating both the federal and the states' shrimp management regimens to determine how to achieve the goal of optimising the yield of shrimp recruited to the fishery not only in terms of weight but also in terms of the most valuable and marketable size classes. Modifications in seasons, sanctuaries, or directed size at entry may be required to address changes in catch patterns or economic conditions resulting from internal or external factors. The Council will also pursue a co-ordinated program of management in state and federal waters so that the industry and resource may be benefited throughout its range.

Acknowledgements
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Operational strategies, management and marketing of a major Australian prawn fishing company

Abstract: The measures adopted by a fishing company to adjust to the technological advances in fishing techniques and more recently to rapid acquisition and analysis of information are described. The organisation of the company and the development of the company's resource monitoring system, are described and its arrangements for fleet deployment are reported. Finally, an account is given of the company's approach to the marketing of its products.

Introduction

The industrial revolution in fisheries has occurred in three distinct phases. The first phase began last century in Europe and North America with motorisation of boats by steam. It is still in progress in some parts of the world but was generally completed by the beginning of World War II. The period from the end of World War II until about 1975 saw a transformation of fisheries everywhere and in all sectors of the industry. High speed internal combustion engines were adopted, synthetic fibres were introduced, power-blocks, echo-sounders, on-board freezing and processing equipment, reduction plants, new products such as fish-sticks, the growth of distant-water fleets and other innovations have vastly changed fisheries. With this technical power in our hands, the third phase of the revolution takes special significance. This phase in the fisheries industrial revolution, is the industry's participation in the information revolution. This permits rapid transfer of information through the new communication equipment and its processing by computers, leading to major changes in research and management.

Each of these phases, identified chiefly by technological changes, has been characterised by distinct types of research and administrative attitudes. Research during the first two phases was concerned for the most part with life histories, migrations, discovery of racial differences, age determination, stock assessment, and economic theory. In the current phase, a new type of research is emerging with a need for real-time information.

In all this period, which extended from about 1850 until now, the history of fisheries has been marked in many cases by dramatic changes of fortune, e.g. the North Sea herring, the California sardine, and the Peruvian anchoveta. In the 1920s and 1930s various workers noted the recuperation of the stocks of several species of North Sea fishes following the respite from fishing imposed by World War I. From this evidence Michael Graham (1935) argued that catches would be kept up, would be composed of individual fish of greater market value, and could be taken at a reduced cost per kilogram of landed catch, if the size of the fishing fleet, and hence the total amount of fishing effort, could be kept down. Michael Graham's intention was to ease the lot of fishermen; he argued that a stock could yield higher catches if effort was reduced and thus fishermen, as a group, could have an easier life and a better income with a smaller fleet. Not all depleted-stock situations are attributable to excessive fishing, however, and in many of those that are fishery-caused the blame by no means lies wholly with fishermen. The wide occurrence of over-exploited stocks is a feature

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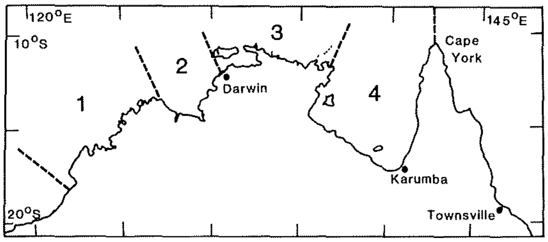

Figure 1. Northern Australia showing area of operations of KFV fisheries. Numbers refer to the fishing grounds: 1. West Coast (Kimberleys), 2. Joseph Bonaparte Gulf, 3. Northern Territory and 4. Gulf of Carpentaria

of the current period, a consequence of technological advances which have made all stocks accessible and all species vulnerable.

Once society embarked on the industrial revolution the reduction of fish stocks became inevitable because the behaviour of fishermen was determined by current social and economic systems. The interpretation of the Michael Graham argument and its projection, as well as the institutional arrangements for the conduct of research and design of management measures has been such as to relieve fishermen of responsibility for major decisions upon which the welfare of their fisheries depended. The responsibility for fisheries management has been assumed, at least theoretically, by fishery administrators relying upon advice furnished by in-house research arrangements. We believe that the decisions that can lead to a company's economic and technical efficiency are based on the same information as that upon which management decisions are based. Therefore there cannot, and should not, be one set of information for industry and another for administration. The required information must be of real-time relevance and availability, that is information should be available within the time span in which decisions are to be made and be relevant to the events of that time span.

KFV Fisheries is a Queensland company operating in the prawn fishery from Cape York peninsula to the Kimberley region of Western Australia (Fig. 1). The company operates 32 steel trawlers with its operational base at Townsville in Queensland, where general administration, fleet engineering, fleet management, and production are handled. Fleet logistics and engineering bases are maintained at Karumba, in the Gulf of Carpentaria, and at Darwin, in the Northern Territory. This paper shows how this company makes use of data with respect to prawn resources, environment, ships, gear, personnel, plant and markets. The use of this information has considerable effect on the day to day conduct of activities and management of this enterprise, and enables the company to assume its share of responsibility for the conservation of the natural resources whilst achieving its own goal of profitability.

Company organisation

Because of its large size, the company is organised into seven divisions operating in close liaison with one another and all under the control of the Administration Division (Fig. 2). The Administration Division is based in Townsville, and is staffed by the general manager, administration manager and chief accountant (Fig. 2). The Karumba base manager reports directly to this division. The Fleet

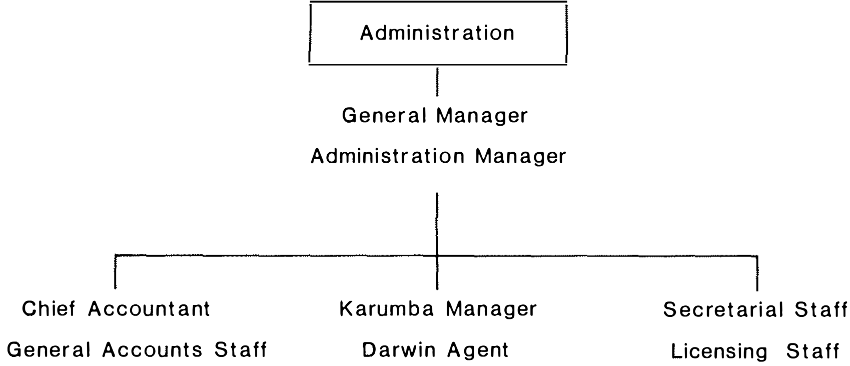

Figure 2. Structure of the Administration Division

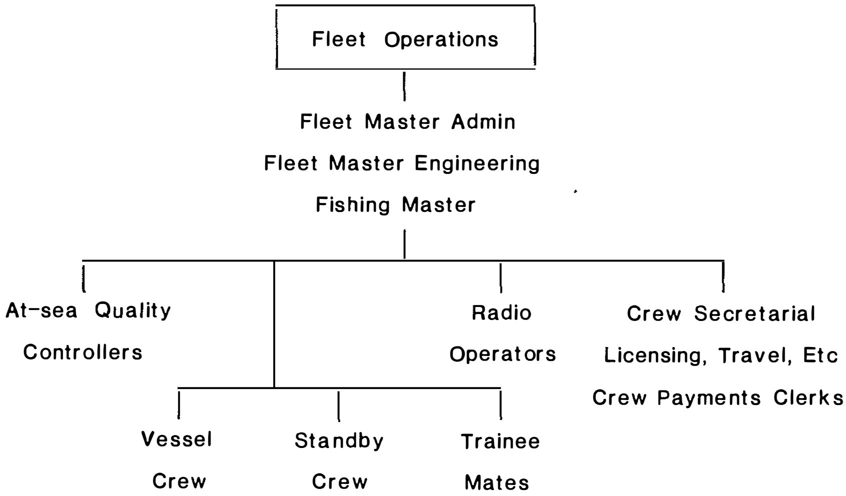

Figure 3. Structure of the Fleet Operations Division

Operations Division is controlled by a senior fleet manager with three fleet managers each with a specific area of responsibility (Fig. 3). These are: at-sea administrative and general fleet control; fishing gear and fishing technology; and vessel engineering assessment and control. All fleet operations personnel spend a significant time at sea to maintain contact with the skippers and crew. The Engineering Division is divided into two parts: one responsible for refits; and one for at-sea maintenance (Fig. 4). The refit subdivision is controlled by a manager and the chief engineer, and uses subcontractors to carry out major refit work at the Townsville base. Vessel classifications and surveys are totally under their control. Refit programing and work schedules are prepared in consultation with the Administration and Fleet Operations divisions. At-sea maintenance is under the control of a managing engineer who is responsible for the maintenance of the vessels while they are fishing. Under him are five at-sea task force engineers each with a particular area of expertise, for example, refrigeration, propulsion or electrical. They move from boat to boat as necessary. We also have a base engineer at Karumba. The Logistics Division is responsible for all supplies to the fleet (Fig. 5). As the company's vessels remain at sea for periods of up to three months—a virtual floating city, the logistics division is the company's lifeline. It is responsible for both the movement of supplies from the bases to the fleet and the movement of product from the vessels to the processing plant. The logistics manager has under his

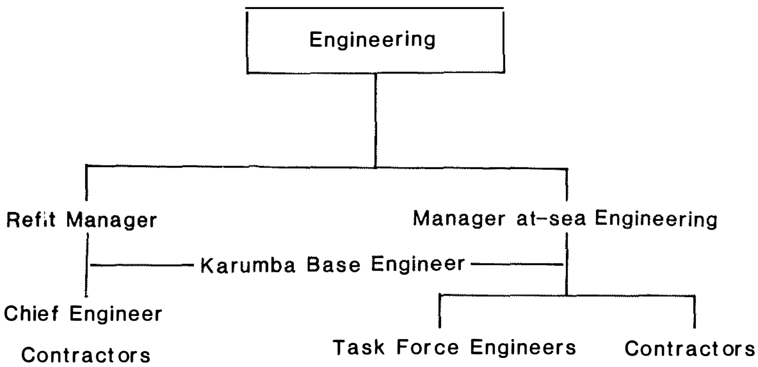

Figure 4. Structure of the Engineering Division

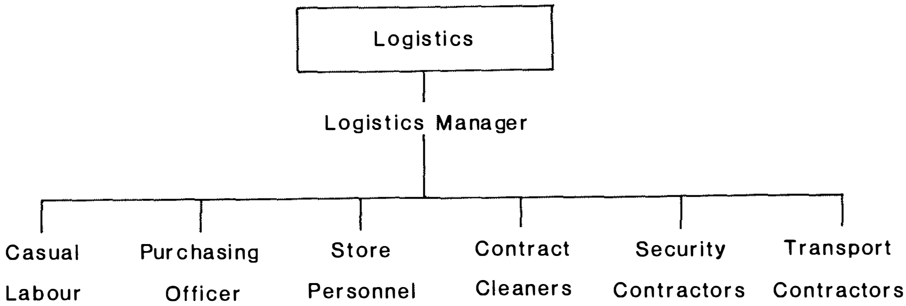

Figure 5. Structure of the Logistics Division

control purchasing officers, storemen, drivers etc. He is also responsible for property and vehicle maintenance. The Production Division is controlled by a production manager under whom are a production foreman, three supervisors, a factory engineer, and the various factory workers (Fig. 6). This division works in close consultation with the fleet operations and sales divisions so that they can program production to best suit catching and sales patterns. All the company's sales are handled from the offices of the parent company, Kailis and France, based in Perth. The Kailis and France sales team is responsible for all of the group's marketing activities. This arrangement provides significant economies of scale and allows for the concentration of sales expertise.

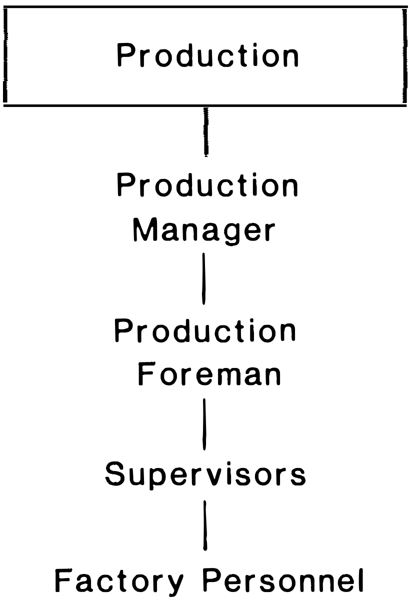

Figure 6. Structure of the Production Division

Because of its importance, marketing is dealt with later in the paper in detail.

Data-processing division

If the Logistics Division is the company's lifeline, the Data-processing Division is the heart. The company lives or dies on its ability to gather information and to make evaluations and decisions in the shortest possible time. This division is responsible for data processing and research and development. It consists of a manager, a computer analyst, a consulting scientist and a marine biologist (Fig. 7). The Data-processing Division provides the following data to the company's divisions—

a. Fleet operations: This covers historic catching patterns on the various fishing grounds for the last several years, size composition of catch on a particular day, month, or year, by boat or by fishing grounds, the current position of each vessel and its present catch, weekly and monthly performance rating for each vessel, and the identity of the crews and their experience.

b. Engineering: Maintains a register of components fitted to each vessel, the maintenance history of components, servicing date on engines and equipment as well as cost estimates of forecast maintenance.

c. Logistics: This includes an inventory of vessel requirements, including fishing gear, spare parts and a historic register of each vessel's fuel consumption. This aids future fleet deployment, planning for mothership operation and projected fuel consumption based on the style of operation planned for each vessel.

d. Administration: Weekly and monthly profit-and-loss reports, and budget information for financial modelling which, provided on the

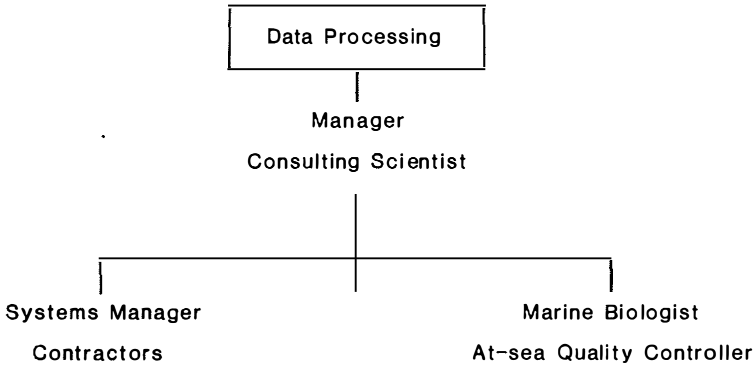

Figure 7. Structure of the Data Processing Division

basis of real-time information enhances our ability to make financial projections.

e. Production: Inventory of unprocessed prawn available including the location, species, size composition and quality. The information is used to plan production and sales.

f. Sales: Provides inventories of stocks of finished product, forward projections of processing output, proposed vessel deployment and catch information related to future market strategy.

Resource monitoring system

The company previously maintained a record of daily reports made by each skipper of the catch he had taken and of the ground he was working. The data from these reports, were analysed manually with a programable calculator and they furnished a description of seasonal cycles of specific catch rates. The information thus assembled on the dynamics of the banana prawn fishery led to successful prediction of size of catch of the 1981 season.

Acquisition of a micro-computer enabled the company to increase the speed of data processing, enlarge the scope of its storage and retrieval of catch-and-effort information and to improve its procedures of statistical analysis. Further we applied these techniques to the tiger/king/endeavour prawn fishery as well as to the banana prawn fishery. Catches in each of these fisheries can vary widely from day to day (Fig. 8). When the banana prawns season opens in March or April, vessels may be switched away from tiger prawns. Consequently at this time there may be large variations in daily catch in this fishery (Fig. 8). The results of analyses of catch-and-effort data soon showed that we needed a more accurate description of population composition. We had, of course, our records of landed catch in each trade category (the count-per-pound classification), but we saw the need to obtain some measure of the composition of the population on each ground. Information of that kind would give us some feeling for the timing and rate of recruitment and lead to a better understanding of the origin of fluctuations in abundance. We therefore initiated a program of regular recording of carapace length by quality-control people at sea. Length frequency data have been accumulated for a period of two years and used for verifications of production returns. They will be further processed in an examination of migrations and recruitment.

The company was becoming aware of factors that affected recruitment, distribution, and other characteristics of the resource which lead to good seasons and bad seasons. Thus the company could make everyday decisions with respect to fleet operations with the benefit of real-time diagnostic reports of the state of the resource and forecasts for the immediate future. Moreover, these size-composition data serve for advance product assessment by providing accurate commercial grading of samples taken from the major fishing areas. These data are conveyed to the marketing and production people who are thus better able to time the unloading of catches and to plan production schedules.

Fleet deployment

All of this equipment, technology and information would be totally useless were it not for those who must use its product. People are

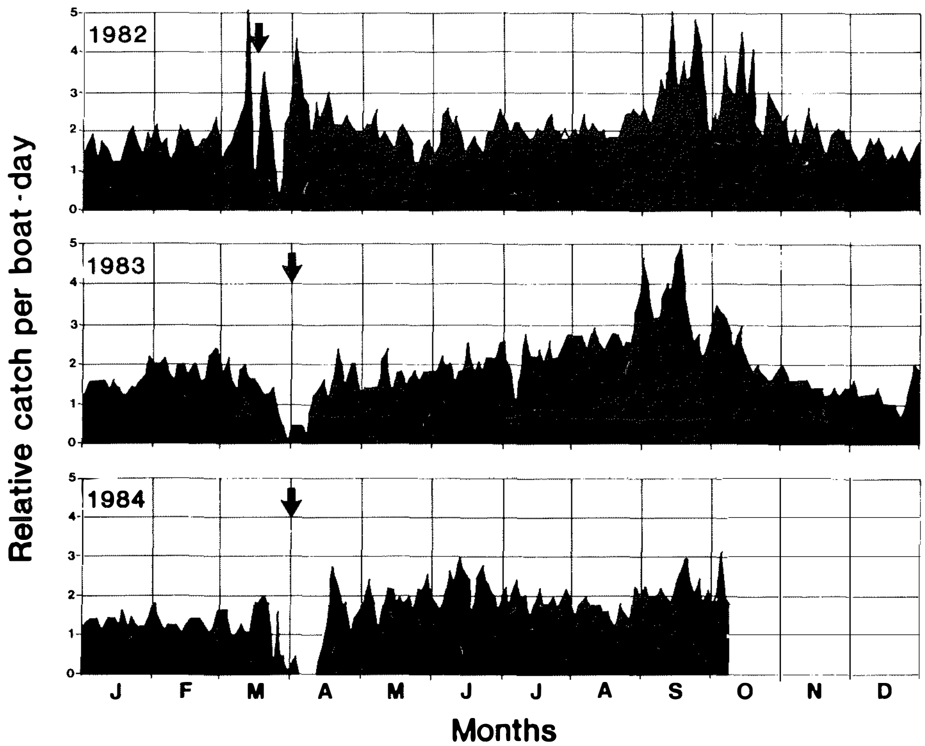

Figure 8. Relative catch of tiger prawns per boat each day by the KFV fleet in the Northern Prawn Fishery. Opening dates for the banana prawn fishery are indicated by arrows.

still the most important resource in an organisation. Without people who can appreciate the message carried by each piece of information our time and money would be wasted in a pursuit of information. Conversely, a good manager can be even better when all the relevant information is available to him in an effective form. Fleet deployment is an example of effective, timely use of information. The fleet operator has one objective in mind, namely to harvest the greatest number of prawns within the total allowable catch while utilising the least effort to provide the greatest economic yield. KFV's fleet deployment is based on long-term, medium-term and short-term strategies.

Long-term strategy

Long-term strategies are often very critical to the fleet owner's final profitability and are designed to maximise the days at sea, the catch and the overall profitability of the fleet. These strategies, with a large fleet, are often totally different from those favoured by the independent single-vessel owner. At the start of each year a broad-based fishing plan is established to determine what the strategy will be on a seasonal basis. Are all vessels to be deployed in the banana prawn season or are some to be maintained in the tiger prawn fishery? How should vessels be deployed between the Kimberley fishery, Joseph Bonaparte Gulf, the Northern Territory, and the Gulf of Carpentaria? How many vessels are to be deployed, where, and at approximately what time? To allow for successful fleet deployment, information relating to catches on other grounds on a real-time basis is essential. Therefore, a strategy is developed which will maintain some vessel presence in all localities for the majority of the fishing period even though some vessels will be unprofitable or less profitable than others for certain periods.

Medium-term strategy

The medium-term relates to seasonal planning, for instance during the banana prawn season we have to decide how many vessels should be deployed to carry out echo-sounder surveys inside closed areas to ascertain abundance and to determine the best deployment of the fleet to take maximum advantage of the first few days of fishing. Simultaneously we have to decide how we will deploy fleet masters to best utilise our fleet. For example before the start of the banana prawn season, senior engineering and fleet personnel are stationed at sea. They take control of small groups of vessels to ensure that on-the-spot changes in tactics can be worked out and immediately initiated.

Short-term strategy

Short-term fishing strategy depends on analysis of vessel performance and the availability of prawns on various grounds on a monthly, weekly, and daily basis. A short reaction time is essential. For example the grounds of Joseph Bonaparte Gulf or the Kimberley coast may not produce prawns for days or weeks on end. Even so a surveillance and searching exercise is carried out by one or two vessels. Should they find prawns it may be necessary to respond rapidly. Decisions have to be made regarding the suitability of particular vessels for the area to be fished. Is their mechanical status such that uninterrupted fishing can be carried out? Do the crews have the expertise required for that particular fishery? If a large segment of fleet is to be re-deployed, consideration must be given to logistics, redirection of motherships and provision of engineering and other services.

Marketing

Attention is directed here on end user instead of on the consumer because the end user has a major influence on what the consumer will accept and occupies a strategic position along the line of movement of supplies to consumers with ability to facilitate or impede the flow, and thus can exercise effective influence on the returns that fishermen will receive. Our definition of an end user is a person who presents our prawns to the consumer. At the retail end of the market the end user is the supermarket or retail shop, in the institutional or food services area the end user is the restaurant or hotel. Clearly there are many other links in the distribution chain, from producer to end user, such as exporter, importer, wholesale distributor, and auctioneer. It is not always possible to sell direct to the end user but we must be aware of his requirements and be ready to take advantage of the service he can offer. Many fishermen cannot or choose not to offer their products to end users and instead supply their catch to processors. However, they should appreciate how the efforts to maximise prices received by seafood processors determine the prices to fishermen.

Australian prawns are already well established on the Australian domestic market and on international export markets, as high quality, high value products. However, the scene is constantly changing and producers must not become complacent. Australian costs, particularly fuel and labour, continue to escalate and on the export market our costs of production bear little resemblance to our selling prices. In other words, the prices we receive for prawns are determined by the competitiveness of our products with prawns offered to the export market by other international suppliers. We must strive to stay ahead of our competitors with unique presentations which make it difficult for our buyers to directly compare our products with those from other suppliers.

For years there had been very little innovation on the part of the Australian producers. Australian prawn producers simply prepared their prawns in 2 kg blocks of raw-headless-shell-on product or 1.5 kg blocks of raw-head-on product. In 1978, our company developed and established the bulk pack prawn market in Japan. This allowed prawns to be sold direct to Japan without the added costs of reprocessing and yet still maintained the pricing levels achieved by the 2 kg block form. The bulk pack is simply the 13 kg ship-to-shore trawler carton (60x30x15 cm) over which is placed a printed plastic overbag. With the bulk pack it is possible to process a large quantity of product in a very short time and therefore it makes it possible for hundreds of tonnes of prawns to be sold soon after the beginning of the season. This fast turn around in production enables the company to convert prawns to cash in the shortest possible time and thereby helps to alleviate a seasonal cash flow problem caused by high vessel refit expenditure and low pre-season catches. Japan and other markets accepted the bulk pack concept which today has become almost a commodity. Bulk packs are however, only one style and certainly not the complete answer. For many years Australia was the exclusive supplier of high quality frozen-at-sea bulk packs and enjoyed a very satisfactory price. Today, however, our competitors such as Indonesia, Mexico and Argentina, offer similar products and hence influence our pricing.

Large quantities of our bulk packs were thawed in Japan and repacked into smaller packs under customer brands with foreign language printing. Australian producers could attempt to prepare these customer branded packs in Australia—which at one time was almost impossible due to the language barriers, packaging problems and Commonwealth Department of Primary Industry (DPI) export regulations (since amended). Alternatively producers could encourage the export customer to purchase a bulk-pack product at a similar price to that being paid for traditional 2 kg packs. This would obviate the need for the Australian producer to incur extra costs of reprocessing.

Value-adding

Demand for value-added seafood is increasing rapidly. Each stage of the value-adding process involves specific amounts of capital, expertise and profit. It therefore follows that the greater the value of each kilogram of prawn leaving Australia the greater is the benefit accruing to the processor and the country. Although Australia is a developed country its seafood producers need to develop a value-adding technology. An example of this is the production of speciality dishes such as Fisherman's Pie in a foil tray, the boil-in-the-bag fish in mushroom sauce, and others. We are developing these production skills to the benefit of the company as a whole. Value-added technology enables producers and processors to gain greater control of the industry and to introduce economies of scale.

Quality-control and brand image

High quality seafoods should be the aim of Australian prawn producers. We must always strive to produce the highest quality seafoods. The quality-control of product starts the moment the prawn is caught and continues until it reaches the end user. Attention must be paid to the rate at which freezing occurs, the temperature at which product is stored, the conditions under which reprocessing occurs and control of preservatives such as anti-oxidants. Hand in hand with top quality is the importance of establishing a brand image. Be proud of your product and work towards promoting your brand. Japan is a particularly brand-conscious market. Establishing a successful brand image requires that the best quality product is sold under this particular brand name. The next step is to present to the buyer an image which shows that you are a reliable and trustworthy trader. This process, in the KFV case with the Japanese market, took several years to accomplish before total confidence was gained from Japanese buyers. The road to a poor brand image is far more rapid. A buyer in Japan need receive only one bad shipment (short weights, black spot or wrong specification) and within a very short time lower bids for further shipments will reflect the market's expectation of your poor performance.

Currency exchange

One area important to exporters is foreign currency management. Although ultimately we are concerned with how many Australian dollars we receive for our prawns we often find we are selling in foreign currencies such as US dollars, Japanese yen, Spanish pesetas etc. Because of the high unit value of prawns, close attention must be paid to rates of exchange of foreign currency. A movement in the US dollar to Australian dollar exchange rate from the time the goods are sold until the time they are shipped or received by the customer, can often turn a profit into a loss. For example if a container of product is sold in US dollars for US$100000.00 and the exchange rate at the time of the sale is US$1.00=A$0.80 then the sale is valued at A$125000.00. If between the time the sale is agreed and the product is packed and shipped, the exchange rate moves against the US dollar and becomes US$1.00=A$0.85 then the value in Australian dollars becomes only $117647.06, a loss of more than A$7000. Expert advice should be sought by Australian exporters from banks or financial consultants to minimise risks and maximise returns. Payment terms should also be closely examined by exporters. Term letters of credit are available, often enabling an exporter to achieve a much higher unit price by insuring himself against fluctuations in the currency market.

Aquaculture

Aquaculture is an important development which is having a significant impact on prawn marketing. Aquaculture, like any source of prawns from other countries, is a competitor. Australia must be ever mindful of any competitor's activities. The size of prawns being harvested from commercial farms in South East Asia and South America ranges between 15 and 25 count-per-pound head on. The increased quantity of prawns of this size from farms, plus the prediction that the quantities will increase, is having a depressing effect on market prices of this size category. To date the farms are not harvesting large quantities of under 15 count-per-pound head on. The Australian prawn catching sector must take notice of these developments and strive to catch only larger prawns.

Conclusion

KFV Fisheries have formulated a philosophy and the strategies outlined in this paper. The personnel involved have a strong commitment to liaison with the various research arms of government. They also see the need for integrated rather than fragmented research programs formulated in negotiation between industry and government to avoid a waste of money and human resources. The company believes it has benefited significantly from its own integrated approach to fisheries management and has had a significant impact on management policies adopted in the Northern Prawn Fishery. That management regime may well prove to be a model for fisheries in Australia. Neither government nor industry can achieve its objectives alone. Information and analysis provided by industry to government is the key to good management.

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Table 1. Statistics of KFV operations showing the number of personnel and trawlers together with annual consumption and production data.

Personnel:		
Landbased	120	
At sea	180	
Trawlers		
KFV class (23m, 340kW main engine)		16
Success class (23m, 410kW main engine)		8
Gove class (25m, 418kW main engine)		4
Miscellaneous (27 to 42m)		4
Fuel usage:		
15 million litres (5 l kg^{-1} of prawns)		
Catch:		
2500 tonnes (Approximately 100 million prawns)		
Gear used:		
500 nets		
15km warp wire		
Food:		
120 tonnes		
Packaging:		
230000 to 250000 cartons		

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Collaboration—an alternative to annihilation by regulation

Abstract: An examination is made of the objectives of various categories of persons engaged in or associated with prawn fisheries, and of the tasks and duties properly attributable to each of these categories. The performance of their tasks and the discharge of their duties entail decision-making for which a common information base should be available. The development of such a common property information base is discussed. The fishing closures from 1983 to 1985 in Exmouth Gulf are examined in the light of the principles enunciated in the paper.

Introduction

This paper was designed to be deliberately provocative to make the reader think. It presents the personal views of the pioneer of the prawn industry in both Exmouth Gulf and the Gulf of Carpentaria, an industrialist with extensive experience in prawn fisheries throughout Australian waters, as well as in Indonesia, Burma, India and Nigeria. The paper is divided into four parts; the first deals with objectives, the second with tasks, duties and decisions, the third with the basis upon which decisions are taken and the fourth part with a case history using the Exmouth Gulf closure as an example.

The purpose of the present paper is to cite an instance of institutional uncertainty and to propose the terms of a discussion on how disinterest and objectivity might be preserved in the administration of these fisheries.

Objectives

If we define objective as what we wish to get from an activity, then we must accept that the objectives of people engaged in and concerned with prawn fisheries of Australia vary from occupation to occupation. Behind a statement of objectives lies the question, what are the responsibilities for which we are answerable? Some people recognise responsibilities only with respect to themselves and their objectives are wholly selfish. Others recognise responsibilities to a group or to the community at large and set objectives accordingly. This distinction is important when considering the objectives of fisheries administration.

The deckhands of a trawler work for income, experience in preparation for another occupation or even for the enjoyment of working at sea. The objectives of a skipper are similar but, in addition he has longer-term commitments with respect to his vessel. The objectives of industry such as my own company are broader. We expect income but we have large commitments with respect to our capital investment, vessels, factories, administration, marketing, relations with government and above all, to our employees. Thus as an industry, we have individual and corporate objectives but these are not in conflict, and, I believe, what is good for my company is good for me and for all involved in the enterprise.

We cannot say the same, however, with regard to fisheries administration, by which we mean both fisheries administrators and also the higher levels of government. The objectives of administrators are related to, but are not the same as, those of the community. The community wants such things as food, employment, and foreign currency and authorises administration to do such things, as provided for by the constitution and the laws, as will encourage and guide industry to satisfy these objectives. It is my opinion that administration's own objective is the successful discharge of that task and the approval that goes with it. Seemingly these are three distinct and separate sets of objectives, and yet it may be unsafe to assume that they are kept separate, as is forcefully made clear by Hannesson (1984)—

'The basic fault with . . . conventional wisdom is that it assumes a well-informed and benevolent government which maximises some unselfish welfare function. Once we take a more realistic approach and view government and its branches as entities furthering their own selfish interests, these conclusions about uncertainty and fisheries management are no longer necessarily correct.'

Hannesson went on to examine two considerations—

1. Fisheries management may itself be a source of uncertainty. Therefore, by increasing the authority of fisheries management, institutional uncertainty may be substituted for the uncertainty of nature.
2. The elimination of risk or the mitigation of its consequences may in certain cases increase allocative inefficiency in the fisheries.

A third area of uncertainty also exists and I quote from Maxwell (1983-84)—

'A third option is that the "science" employed is inadequate in its level of understanding of the systems governing the responses of harvested populations to be a useful tool to use in the formulation of solutions to the questions asked of it. Although there is some realisation that this is a real possibility the implications of public admission of such a fact would be devastating professionally. It is also unlikely that the capacities of the individual research scientists themselves are in question and this in itself lends support to the possibility that so called "fisheries science" is the weak link in itself.'

Tasks, duties and decisions

Each of the aforementioned objectives implies a set of tasks to be performed and of duties to be discharged by each group of participants and which in turn imply decisions to be made by participants in performing these activities and discharge of duties. It is unnecessary for me to submit here a job description for each kind of position in each of the three sections of the industry. For the purposes of my argument however, I must list what I think the tasks of administration should be.

In the first place administration has a task of maintaining law and order in the industry and of ensuring observance of laws, such as those with respect to safety at sea, work conditions and hygiene. The principles that apply are the same as those that hold for any other industry and any other sphere of activity in the community. Secondly, in my opinion, there are matters such as employment, earnings and so forth with regard to which administration has a promotional task, to ensure that the community relations with the industry are such as to favour the industry's contribution to community objectives. Third, administration has the task of ensuring the conservation of the resource and the prevention of actions that directly or indirectly might destroy the resource. Note that in my opinion, conservation is not an objective in itself, it is part of the strategy by which the objectives of the community are sought indefinitely. It is in the performance of this last task that administration promulgates and seeks to enforce regulations which dictate when, where and how fishing shall take place, and how much shall be taken of the different available species and groups.

That these are three quite distinct sets of tasks will be apparent. The first applies to fisheries as it does to any other industry; if it has any particular application to fishing it is with respect to the special physical risks that accompany work at sea. The second is the matter of government policy and program of the time and in general should remain separate from the third. But I believe the conservation writ does not run in the field of economic decision; a conservational decision can be taken, but as long as the boundaries of that space are not transgressed, the conservation guardians should stand mute.

Decisions such as whether to take all or only part of an allowable catch, (the so called Maximum Economic Yield in place of the so called Maximum Sustainable Yield), and the level of profitability at which to operate, are quite separate from a decision as to the amount of allowable catch itself. Recognising this distinction, we can say that whereas the setting of an allowable catch unquestionably is an administrative task, intervention by government in managerial decisions of efficiency and profitability is not. Note that I am not saying that government should not intervene—only that intervention in these matters is not unquestionably a task of administration. But I add that such intervention should be in conformity with current forms of government policy applicable to all industry; this holds with

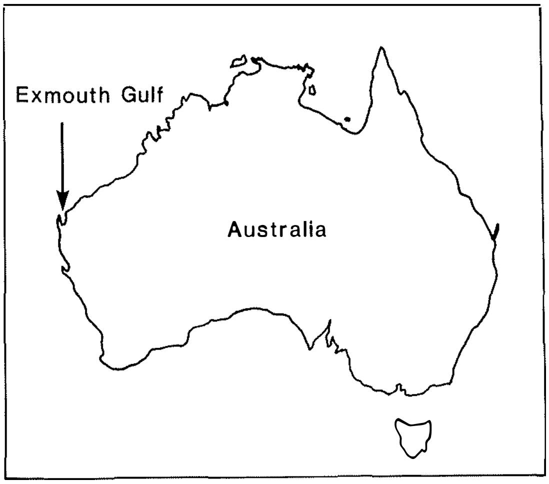

Figure 1. Australia showing position of Exmouth Gulf

regard to royalties or other means by which the community draws rent direct from the resource.

Decisions and the information base

To perform their tasks and properly discharge their duties the participants in each category must make decisions based on information that must be common property. We all know that individual skippers are extremely secretive about their special knowledge of particular grounds. However, the general biological knowledge of this resource including conclusions as to the state of a fishery, the grounds for setting an allowable catch and other such matters, cannot be the private property of any individual, institution or agency.

Most fishery resources have been discovered by industry and the bulk of the information on stock composition, distribution and abundance is drawn from the activities of fishermen. Individual fishermen, and fishing enterprises such as ours, are establishing their own systems for monitoring the composition and abundance of stock. In this situation it is neither realistic nor proper that a fishery department should believe that it has sole use of information relating to a fishery, or alone is possessed of the wisdom to analyse and interpret that information and reach decisions about the fishery. The time has come to make fishery management a collaborative task instead of an adversary game.

The Exmouth Gulf closure

The particular instance I wish to cite concerns the closure of fishing grounds in the south of

Table 1. Mean annual catch and effort data for tiger prawns from Exmouth Gulf from 1971 to 1980 (data from Penn and Caputi 1985). CPUE=Catch per unit effort.

	Catch (t)	Effort (h)	Annual mean CPUE
Mean	674.2	46750	14.25
SD	259.2	7180	5.19
Coefficient of variation	38.4%	15.4%	36.4%

Exmouth Gulf. This multi species prawn fishery was based originally on tiger prawns. The history of the Exmouth Gulf fishery is described by Penn and Caputi (1985).

A detailed knowledge of an area is necessary to appreciate unusual environmental happenings such as the lack of a common rainfall with wide variation over a small area—and man-made phenomena such as seismic surveys over several months. This information is not included in logbooks.

On the basis of annual averages, the industry could reasonably expect each year a catch of about 674t lying between 414t and 933t and taken at a rate of about 14.3 kg h^{-1}, lying between 9.0 and 19.4 kg h^{-1}. (Table 1).

It was obvious even before 1981 that recruitment was somewhat variable and therefore, variation outside the limits (see Table 1) could have been expected. Nevertheless, the low recruitment in 1981 and its persistence into 1982 and 1983 (Penn and Caputi 1985) were greeted with surprise. We, the industry, became aware of the change in 1981 and voluntarily took steps to reduce our effort—from 52700h in 1980 to 42200h in 1982 (Penn and Caputi 1985). This is shown in our company records, and hence our catch; but at no time in those two years, or before, were we told anything about an allowable catch which should not be exceeded. Therefore, in a limited entry fishery, it came as a surprise to us in 1983 when in discussions with the Western Australian Fisheries Department it was implied that it had been our responsibility to ascertain the allowable catch, and to avoid exceeding it, and that the fall in stock abundance was due to irresponsible overfishing.

Even more, it was with dismay that we learned that fishing was to be prohibited not only in

1983 but also in 1984 and 1985. Here was a clear case of administrative uncertainty over-riding natural uncertainty. Analysis of the evidence shows that the variation in recruitment, and therefore in fishable stocks, is essentially environmental in origin and depends on conditions in January and February, particularly rainfall (Penn and Caputi 1985). The prospects of one year cannot be forecast accurately from evidence of the preceding year; to make a three year forecast was especially rash.

We may then ask why such drastic action was taken. We do not care to attribute motive, but neither do we care to put the incident to one side with charitable reference to over-zealous caution.

Conclusion

From my experience in fishing and especially the Exmouth Gulf closures, I believe I can draw the following conclusions on how fishing companies, government departments and fishermen should act and interact in fisheries management. Fisheries management must co-ordinate biological and economic management of the fishery. It is wrong to formulate management plans in neglect of either one of these factors. The economic and social factors (sometimes neglected) that must be taken into account in Australian fisheries are—

1. We believe the Australian fisherman wants and has a right to a normal life style. Land-based installations provide permanent facilities for fishermen and their families, who are not itinerant workers—their stability and welfare must not be jeopardised by over-conservative biological management. By its very nature there will always be an element of risk in any fishery.

2. Long-range forecasts are to be avoided, since they rarely, if ever, can be made reliably. A pessimistic negative forecast has a destabilising effect on the credibility of fishermen with financial institutions, while an over-optimistic or positive forecast attracts over-capitalisation and risks over-exploitation.

3. To remain viable, industry must continually maximise its efficiency. This is distinct from the continually implied prime motive of fishermen and industry, ie greed, which I reject. Where biologists and managers of fisheries believe this to be the driving force behind all fishermen, it is not surprising that co-operation fails.

There is a potential conflict of interest where those managing a fishery also undertake research in the fishery, and thus there is a potential peril of confusing research goals with management goals. A conflict of interests is almost inevitable when an authority which controls licensing also stands in judgment on appeals. Such an authority, when it receives an appeal, is likely to give consideration only to the grounds on which it formed the measure appealed against and to disregard or negate other matters put forward by the applicant. There is a necessity in the public sphere for some administrative mechanism of appeal, independent of fisheries departments. A political mechanism would be expected to provide a more practical, comprehensive opinion, but since it is well nigh impossible for a politician to fully understand scientific methods and statistical jargon, the advice given by departmental officers tends to be in lay terms, only incorporating some technical conclusions.

The socio-economic reality of fishery management is people—therefore, we must think of all the implications before we make decisions, predictions and recommendations.

Acknowledgements

The views expressed are based on the experience shared by many people who contributed in various ways to their development. It would be difficult for me to identify particular contributions and, therefore, I acknowledge in general my indebtedness to members of the Kailis Group. In addition in this paper, I draw on advice given to me by various scientists who have collaborated in developing these ideas.

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The financial and economic health of the Northern Prawn Fishery and the effect of shipbuilding bounties

Abstract: This paper presents the findings of a financial and economic analysis of Australia's most important prawn fishery, the Declared Management Zone of the Northern Prawn Fishery. Data on the profitability of the fishery and the impacts of the shipbuilding bounty are presented. The data presented are based on a cost and earnings survey covering the years 1980-81 and 1981-82. In both years the fishery operated at a loss of $14.4 million and more than 50% of vessels showed negative rates of return. In 1980-81, 11%, and in 1981-82, 18% earned a rate of return of 20% or more. More than 70% of subsidised fishing boats in Australia have been built for the DMZ fishery. In June 1982 prices, the total amount of subsidy paid since 1973 has been more than $24 million. The effect of the bounty is discussed.

Introduction

Prawns have become Australia's most important fisheries product in terms of value. The Declared Management Zone of the Northern Prawn Fishery (hereafter the DMZ fishery), ranks first in order of economic importance. This paper focuses on the most recent financial and economic analysis of this fishery.

All of Australia's major prawn fisheries have been subject to financial and economic assessments. The Commonwealth Department of Primary Industry has assessed the northern prawn fishery (Anon. 1973, 1981), the South Australian prawn fishery (Anon. 1974), and the east coast prawn fishery (unpublished). Various state and territory governments have undertaken their own studies. In addition a number of individuals have published analyses of prawn fisheries, for example Copes (1977), Byrne (1982), MacLeod (1982), Waugh (1984), Hill and Pashen (in press) and Meany (in press). Some of these studies have been cost and earnings analyses which estimate the financial health of the fisheries at a point in time, while others have addressed management issues in a wider context. As a general rule these studies have found prawn fisheries to be over-capitalised, a fundamental economic problem in fisheries management. Over-capitalisation has occurred in spite of the various management regimes based on limited entry, which have been put in place in the majority of Australia's prawn fisheries.

The history of development of the prawn fishery in the DMZ has been outlined in Anon. (1973), Ruello (1975), Copes (1975, 1977), Australian Fisheries Council (AFC 1982) and MacLeod (1982). Two of the more interesting features of the fishery are firstly, a high degree of vertical integration with a number of the larger fishing companies being involved in the processing sector and some also involved in boat building and secondly, a significant number of vessels being built under the shipbuilding subsidy and bounty schemes.

Before 1975, vessels larger than 21 m or over 150 gross tons were the subject of a 25% government subsidy. After 1975, the Ship Construction Bounty Act 1975 and the Bounty (Ships) Act 1980 restricted the subsidy to vessels constructed in Australia for use in Australia. In this paper, the term bounty will be used to cover both schemes.

Methods

The survey was carried out by means of interviews with owners and/or their accountants. In cases where people could not be interviewed, a questionnaire was sent to them by mail. Economic data was obtained for 182 vessels of the 265 operating at the time. Vessels fell into two categories, company owned and independently owned. All 142 company owned vessels and 40 of the 123 independently owned vessels were surveyed. Independently owned vessels were chosen for sampling on the basis of size in order to obtain a representative coverage.

This paper is divided into two sections. The first is a presentation of some of the major results of a cost and earnings survey of the catching sector undertaken in December 1982 and January 1983. The inter-sectoral linkages with the processing and shipbuilding sectors are not analysed. The second section of the paper presents data on the shipbuilding bounty in relation to the DMZ. The data presented are organised under various headings. Where appropriate, total values and averages are given. In the tables the figures in brackets are relative standard errors, which are the standard errors expressed as a percentage of the mean.

The economic survey findings

The fleet

A fleet of 264 vessels is assumed for many of the calculations which follow. The number of vessels operating at the time of the survey was 265, but insufficient data were available on one boat to allow for its inclusion.

Table 1. Declared Management Zone: revenue of trawlers by average length strata for 1980-81 and 1981-82. Mean, and relative standard errors shown

Length stratum	Revenue 1980-81 ($K)	Revenue 1981-82 ($K)
<15.6m	82.9 (8)	103.3 (6)
15.6m and <17.6m	133.9 (16)	194.2 (18)
17.6m and <20.6m	175.5 (8)	189.4 (9)
20.6m and <23.6m	375.4 (2)	464.9 (2)
≥ 23.6m	438.6 (3)	426.6 (2)

The total market value of the operating fleet excluding the value of endorsements was estimated to be approximately $96000000 ($96M). It should be noted that market value was the operators' estimate and probably overstates the value. The average estimated market value of boats was $364000. The total estimated market value including endorsements was approximately $110M. The average was approximately $418000; therefore, operators estimated the value of an endorsement at approximately $54000. The total purchase price of the fleet was $90.4M. This figure is based on what present owners actually paid for their

Table 2. Declared Management Zone: itemised cost data for the total fleet in nominal terms. Mean, and relative standard errors shown

	1980-81		1981-82		Percentage change in nominal terms
Cost item	Cost ($K)	Percentage of total %	Cost ($K)	Percentage of total %	%
Payments to skipper and crew	19514	21 (2)	19398	20 (2)	-1
Repairs and maintenance: boat, engine and gear	17990	20 (3)	20868	21 (3)	+16
Fuel and oil	23649	26 (1)	24852	25 (2)	+5
Other trip costs (provisions for crew, other)	1598	2 (9)	1478	1 (8)	-8
Administrative costs	3868	4 (5)	4853	5 (4)	+25
Interest	6304	7 (5)	6415	6 (5)	+2
Insurance	2973	3 (4)	3425	3 (4)	+15
Depreciation	10534	11 (2)	11099	11 (1)	+5
Other miscellaneous costs (leasing or rental, selling and commission, licences, other)	5187	6 (6)	6897	7 (8)	+33
Total	91617	100	99285	99	+8

vessels. The average purchase price was approximately $342600. Estimated replacement cost of the fleet was $159M. The average replacement cost was approximately $600600.

Revenue

Total revenue includes income from the sale of prawns, other seafoods such as scallops, bugs and fish, and non-fishing income earned by the boats, though prawn revenue accounted for 97% of the total in 1980-81 and 98% in 1981-82. Total revenue earned by the sampled fleet in 1980-81 (282 boats) was approximately $82.4M. In 1981-82 with 264 boats in the fleet total revenue had increased to $89.5M. For purposes of direct comparison these figures have to be adjusted to constant terms. In mid 1981-82 values, the total revenue for 1980-81 was $91.7M. Where appropriate in the remainder of the paper 1980-81 values have been similarly converted, and where nominal values are presented this is stated. As expected larger vessels earned higher revenue on average. Broad length classes are used to present these data, in nominal terms (Table 1).

Costs

Total fleet costs in 1980-81 were approximately $101.9M and approximately $99.3M in 1981-82. The average cost of a vessel in the former year was $361 348 and the following year $376077. Fleet costs were divided into categories and compared in nominal terms (Table 2) because the movement in prices was not necessarily equal for all expenditure items.

With regard to the major cost items, the most noticeable nominal increase was for repairs, maintenance and gear purchases. Fuel costs increased only 5% in nominal terms (Table 2), which was a decrease in real terms. The increase in total costs for the fleet was approximately 8% in nominal terms, but since fewer vessels operated in 1981-82 the average increase per vessel was approximately 16%.

Table 3. Declared Management Zone fleet: revenue, costs (excluding interest) and return to capital, in nominal values. Mean, and relative standard errors shown

	1980-81 ($)	1981-82 ($)
Revenue	292082 (3)	338925 (2)
Costs	302530 (2)	351780 (1)
Return to capital	-10448 (26)	-12855 (34)
Rate of return %	-3 (43)	-3 (37)

Returns

Returns were calculated as the difference between revenue and costs, with the omission of interest payments. Profitability of the average boat operating in both years did not change (Table 3). The rate of return for the total fleet was -3% in both 1980-81 and 1981-82.

Returns on capital and rates of return were calculated for various length classes (Table 4). The most profitable length of vessel was in the 20.6 to 23.6 m class. The only other classes to achieve positive returns to capital were the 15.6 to 17.6m and the 23.6 to 25.6 m. Vessels between 17.6 and 20.5 m showed a high negative rate of return. In this category boats of 19.6 to 20.5 m showed the highest negative rates.

The results of a previous study (Anon. 1981) have been compared to this study. The earlier study presented data on return to capital, by length strata, for the years 1974-75 to 1977-78 inclusive. Taking into account the difference between the two studies, which are outlined

Table 4. Declared Management Zone fleet: revenue, costs and returns, averaged for length strata, in constant values. Relative standard errors are given in parentheses.

	Unit	Less than 15.6 m	15.6 m and <17.6 m	17.6 m and <18.6 m	18.6 m and <19.6 m	19.6 m and <20.6 m	20.6 m and <23.6 m	23.6 m and <25.6 m	$\geq$ 25.6 m
1980-81									
Revenue	$	92243 (8)	148938 (16)	124673 (16)	167313 (10)	284249 (13)	417530 (2)	532773 (4)	432405 (5)
Costs	$	102451 (6)	151480 (11)	147367 (10)	182927 (8)	365825 (7)	400075 (2)	511239 (4)	541720 (5)
Return on capital	$	-10208 (52)	-2542 (418)	-22694 (29)	-15614 (61)	-81576 (32)	17455 (31)	21534 (63)	-109315 (19)
Rate of return	%	-6 (52)	-1 (428)	-10	-5	-26	4 (30)	4	-19
1981-82									
Revenue	$	103328 (6)	194256 (18)	103720 (34)	189132 (11)	226164 (13)	464950 (2)	424942 (4)	430184 (0)
Costs	$	112554 (5)	188033 (12)	123226 (19)	212708 (11)	307163 (8)	426538 (1)	479582 (4)	574870 (0)
Return on capital	$	-9226 (84)	6223 (261)	-19506 (63)	-23576 (53)	-80999 (27)	38412 (15)	-54640 (26)	-144686 (0)
Rate of return	%	-6 (84)	2 (250)	-8	-7	-25	7 (14)	-10	-26

Table 5. Declared Management Zone fleet: average rate of return by length strata. Information for the period 1974-75 to 1977-78 from the Department of Primary Industry (Anon. 1981)

	Average rate of return on capital					
	1974-75 %	1975-76 %	1976-77 %	1977-78 %	1980-81 %	1981-82 %
Less than 15 m	loss	loss	10.0	4.8		
<15.6 m					loss	loss
15 m and <17 m	loss	loss	6.9	loss		
15.6 m and <17.6 m					loss	2.0
17 m and <19 m	loss	loss	4.0	8.3		
19 m and <21 m	loss	loss	14.2	loss		
17.6 m and <20.6 m					loss	loss
≥ 21 m	loss	loss	20.4	14.4		
20.6 m and <23.6 m					4.0	7.0
≥ 23.6 m					loss	loss

below, some comparisons can be made. Significant changes which have occurred in the fleet since the period covered by that study have prevented raising the sample data to represent the population. Another major difference is that the rates of return in the earlier study were based on the market value of boats without including the entitlement value. Mindful of these qualifications, it is interesting to compare the results from the two studies. The length class strata used in the previous study differed from the ones used in this study and the data are given accordingly.

The most important constraint in making any comparisons over time is the continually changing nature of the fleet. The data suggest that for all the broad length classes negative returns were more common than positive returns for the six years investigated (Table 5). However, investment in new and more costly vessels has continued in the fishery up to the time of the current survey. This may be explained by two factors: the spread of returns within the fishery indicates that some operators have shown very high returns on capital, and the ability of the vertically integrated sector (integration between the catching and processing sectors) to earn profits elsewhere in the chain between fishing and final sales to the consumer.

Information on the distribution of returns in the fishery in 1980-81 and 1981-82, showing the percentage of vessels in each length class earning different rates of return, illustrates the first point (Table 6). In both years approximately the same proportions of the fleet

Table 6. Declared Management Zone fleet: distribution of rate of return on capital, by length strata

Rate of return %	Less than 15.6 m %	15.6 m and <17.6 m %	17.6 m and <20.6 m %	20.6 m and <23.6 m subsidised %	20.6 m and <23.6 m non-subsidised %	≥ 23.6 m subsidised %	≥ 23.6 m non-subsidised %	Fleet %
1980-81								
Negative (loss)	66.7	59.0	63.7	30.9	69.9	55.3	88.9	55.9
Less than 5	16.7	4.8	15.9	10.7	—	2.1	11.1	8.2
5 to <10	—	18.1	10.6	16.8	—	10.8	—	10.7
10 to <20	8.3	18.1	5.3	23.3	11.5	17.1	—	14.3
20 and over	8.3	—	4.6	18.3	18.6	14.7	—	11.0
	100	100	100	100	100	100	100	100
1981-82								
Negative (loss)	66.7	42.0	65.0	25.7	76.8	61.3	100	54.5
Less than 5	—	32.1	7.0	15.1	3.6	6.0	—	9.7
5 to <10	8.3	13.0	14.0	4.3	—	6.0	—	8.9
10 to <20	8.3	—	—	25.0	3.6	18.7	—	9.0
20 and over	16.7	13.0	14.0	17.1	16.2	8.0	—	18.0
	100	100	100	100	100	100	100	100

Table 7. Declared Management Zone fleet: total costs and revenue in constant values

	1980-81 ($M)	1981-82 ($M)
Total cost including interest	101.9	99.3
Less interest	7.0	6.4
	94.9	92.9
Return to capital (10%)	11.2	11.0
Total cost	106.1	103.9
Total revenue	91.7	89.5
Return	-14.4	-14.4

did not break even (about 55%), and in both years approximately the same proportion achieved a 10% or greater return on capital (25% in 1980-81 to 27% in 1981-82). Because more vessels operated in the first year, the same number of vessels (71) achieved a 10% or better return in both years. The subsidised boats in the 20.6m and under 23.6m class had the lowest percentage showing a loss in both years and the highest percentage achieving a 10% or better return to capital.

Total costs for the fleet have been recalculated omitting interest but including a normal profit (return on capital) as a cost (Table 7). In both years, the fleet fell short by about $14.4M of a 10% return on capital (Table 7).

The Shipbuilding Bounty

By 1982, 129 DMZ endorsed vessels (representing 44% of the potential fleet of 292 endorsed vessels) had been constructed under one of the bounty schemes (Tables 8, 9). These schemes allow for the payment of a subsidy of approximately 25% of the cost of a boat if it is 21m or over or 150 gross tons. Although 57% of the fleet were 21m or over in length, some boats still operating then were built prior to the introduction of the scheme in 1972-73. A high percentage of the subsidised vessels were built for the fishing industry and most (>70%) were constructed for use in the DMZ. In historic cost Australian taxpayers outlaid close to $17M in subsidies to fishing boats up to June 1982. In June 1982 prices, the cost was more than $24M.

In his study Copes (1975, pp. 77-78) identified the likely effects of the bounty as follows—

> 'The sharp subsidy cut-off at the 67 foot mark (21m) . . . distorts the choice of vessel size selection and is likely to lead to non-optimal decisions from an overall economic viewpoint. The fishing vessel subsidy structure provides several incentives for over-capitalization. Insofar as the subsidy is in excess of what is necessary to stave off foreign competition, it tends to lower the domestic price of fishing vessels per se and thus encourages more vessels to be built than otherwise would be the case. In the second place, by discriminating in favour of larger vessels, the subsidy encourages the building of greater capacity than would be the case if smaller vessels were treated equally. Furthermore, as the subsidy is granted in relation to total construction cost, it encourages the installation of more expensive equipment (and thus enlarged fishing capacity) than would otherwise be undertaken on economic grounds. In view of the conclusions of this report that the Gulf of Carpentaria prawn fishery already has attracted an excessive number of vessels, the subsidy program, as presently structured, is adding to the burden of overcapacity.'

Table 8. Declared Management Zone fleet: vessels subject to bounty, under 6000 gross tons, completed under the various subsidy schemes. Data from the Department of Industry and Commerce, Industries Assistance Commission and Australian Shipbuilding Association (estimates made by the Department of Primary Industry differ marginally in some years and the variation for 1978-79 is caused by differing source data). The figure for other and unknown in the final line includes at least six and probably nine prawn trawlers.

		Fishing vessels by fishery						
	Non-fishing	DMZ	Tuna	Trawl	WA prawns	Other or unknown	Total fishing	Total all boats
1972-73	14	6	—	—	—	—	6	20
1973-74	14	15	1	—	—	—	16	30
1974-75	16	8	1	1	—	—	10	26
1975-76	17	3	1	1	—	1	6	23
1976-77	19	5	1	1	—	—	7	26
1977-78	9	10	—	2	—	—	12	21
1978-79	19-22	20	3	1	3	—	27	46-49
1979-80	2	30	2	2	—	1	35	37
1980-81	18	26	3	3	2	1	35	53
1981-82	31	6	10	—	—	11	27	58
Totals	159-162	129	22	11	5	14	181	340-343

Table 9. Declared Management Zone fleet: Vessels built under the bounty schemes by year and length. Data prepared by the Department of Industry and Commerce (unpublished)

Length (m)	1972-73	1973-74	1974-75	1975-76	1976-77	1977-78	1978-79	1979-80	1980-81	1981-82	Total
Under 21	—	—	—	—	—	—	2	2	—	2	6
21 and <22	—	—	—	—	—	1	4	7	17	—	29
22 and <23	—	—	—	—	—	—	3	4	7	1	15
23 and <24	—	—	3	—	—	3	9	16	2	2	35
24 and <25	2	4	—	—	4	6	2	—	—	1	19
25 and <26	3	5	3	—	—	—	—	1	—	—	12
26 and <27	1	4	1	1	1	—	—	—	—	—	8
27 and <28	—	—	—	1	—	—	—	—	—	—	1
28 and <29	—	1	1	1	—	—	—	—	—	—	3
29 and over	—	1	—	—	—	—	—	—	—	—	1
Total	6	15	8	3	5	10	20	30	26	6	129

The bounty schemes were devised so Australian boat buyers would be able to purchase locally at a price equivalent to that paid for vessels built overseas. That is, the concept was to protect and promote the local shipbuilding industry while not adding to the costs of other industries.

The following analysis is based on two major assumptions. Firstly, it is assumed that only boat owners vertically integrated with shipbuilding firms acquired boats at the subsidised price. Put alternatively, it is assumed that other boat owners with subsidised boats did not benefit by the bounty on the basis that it was retained by the shipbuilders. The second assumption is that those boat owners who have been assumed to benefit did so to the extent of the full bounty. Both of these assumptions may not reflect what actually occurred, but in the absence of data on the incidence of the bounty schemes these are useful assumptions to accept for the purpose of illustrating the effect.

Table 10. Declared Management Zone fleet: total costs and revenues in constant values taking the bounty into account. A 10% return to capital is based on a total capital value (market value of boats plus endorsements) of $117.5M in 1980-81 (282 vessels) and on $115.7M in 1981-82 (264 vessels).

	1980-81 ($M)	1981-82 ($M)
Total cost excluding interest	96.4	94.5
Return to capital (10%)	11.8	11.6
Total cost	108.2	106.1
Total revenue	91.7	89.5
Return	-16.5	-16.6

Vessel market prices and those costs which are a function of the value of the boat have been increased, in particular, insurance and depreciation. These changes increase the value of the fleet and its operating costs. For the purpose of calculating rates of return the key variable is boat market price plus the value of the endorsement. In the analysis presented above, this figure for the total fleet was $110M. Taking into account the bounty, the value of the fleet plus endorsements was $115.7M. The increased valuation of the bounty size length classes decreases the rates of return on capital for these boats.

A re-assessment of the fleet's overall performance, taking the bounty into account has been made (Table 10). The revised total revenue and total cost data have been brought together. A new rate of return is used, based on a 10% return on the higher level of capital invested in the fishery. The impact of the shipbuilding bounty, on the assumptions made above, is an increase in costs for the fishery of approximately $2.1M to $2.2M. The impacts of the bounty on the fishery can be summarised: In the early years of its operation the bounty would have provided an incentive to build vessels of bounty size, though that size might not then have been ideal for the fishery.

One possible interpretation of the analysis in this study is that the bounty size boats in the 20.6m to less than 23.6m length class were, on average, the best performers in financial terms. If this interpretation is correct, it could be argued that this size of vessel would have been built in increasing numbers had the bounty not existed. The major problem with this viewpoint is that there is no one most efficient size boat in this fishery as there are high and low net income earners in all length classes.

If the bounty has not distorted the length class structure of the fleet, its real impact on the fishery has been to increase total costs because of the greater amount of capital involved. In this manner the bounty is a burden on the fishery. On the basis of the assumptions made above, the annual extent of that burden was approximately $2.1M in additional costs. This means that profits and employment in the shipbuilding industry come at the expense of profits or rents in the fishery. Without detailed economic information on the shipbuilding industry it is not possible to evaluate the net benefits or costs of the bounty. Nevertheless, it is worth emphasising that in 1980-81 approximately $4.5M was paid out in bounties for prawn trawlers and the cost to the DMZ fishery was approximately $2.1M.

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International shrimp marketing situation

Abstract: Annual world supply of shrimp is now about 1.75 x 10^6 tonnes of which 85% is from tropical species. Aquaculture probably accounts for about 5% of the total supply. Capture fisheries appear to be at their limit but there is considerable potential for increase in aquaculture production which may reach 400 000 t by 1990. The major importers of shrimp are Japan (34% of total) and the US and Europe (28% each). The US is the strongest-growing import market for tropical shrimp: at present these come mainly from Ecuador and Mexico. US domestic catches have reached a maximum level and are now being adversely affected by increased operating costs and loss of access to Mexican grounds. Aquaculture has not been commercially successful in the US and consequently projected future increased demand will have to be met by imports. Demand in Japan is governed by the relationship between prices of shrimp and prices of competing products and projected increases in demand may be offset by price rises. Consumption of shrimp per capita in Europe is small by comparison with Japan and the US, and is believed to have the greatest long-term potential for expansion. Projected annual expansion is 1% for Japan and the US and 5% for Europe. This expansion will have to be met from aquaculture and will require an annual increase in production of about 168 000t.

Shrimp prices are related to size. In the past decade in the US, prices for small shrimp (over 36 count per pound) increased more rapidly than for large shrimp (under 20 count per pound). Because domestic fisheries no longer dominate the US market, seasonal fluctuations in price have largely disappeared. Seasonal closures in the Gulf of Mexico, aimed at increasing the total weight of the catch as well as the average size at capture, have not been successful and the percentage of small shrimp landed rose in 1982 and 1983. The shorter fishing season has resulted in a decline in quality due to difficulties in handling heavy catches in short periods of time.

Introduction

This paper deals with the world shrimp market and outlook, and is based on recent work, surveys and analyses undertaken by FAO as well as by other UN agencies and government institutions. The paper covers three aspects. Firstly world supply from both capture fisheries and aquaculture, secondly international shrimp trade, and thirdly a consideration of shrimp prices in the US market especially as they relate to size. The term shrimp is used to refer to both shrimps and prawns of all sizes.

World supply

The world supply of shrimp increased rapidly and steadily from just over one million tonnes (1 Mt) in the early 1970s to 1.62 Mt, live weight, in 1977 (FAO 1984). Catches then stabilised until 1982 when they rose to 1.69 Mt. According to FAO's most recent estimate (FISHDAB/FAO[1], pers. comm.) 1983 world shrimp catches reached a level of 1.80 Mt. India is still the largest producer, landing nearly 12% of the world total. The top four producing countries which contribute more than 45% of the total are all in the Asian region.

Of the three principal categories of shrimp in the world supply, tropical species presently constitute about 85% while the proportion of cold water shrimp varies between 12 and 18%. The quantity of freshwater species is minimal.

There are as yet no separate statistics for the aquaculture component of world catches. Current world production from cultured sources is estimated at between 55 000 and 85 000t (M. Pedini[2], pers. comm.). While these figures may be subject to a wide margin of error, it is unlikely that shrimp aquaculture production at present accounts for more than 5% of the total shrimp supply. The leading producers of cultured shrimp are countries in

[1] National Marine Fisheries Service, Fisheries Development Analysis Branch, St. Petersburg, Florida.
[2] M. Pedini, Fishery Resources and Environment Division, FAO, Rome.

South East Asia and Latin America, especially Indonesia, Ecuador, India, Mexico and Taiwan.

Shrimp landings from capture fisheries are thought to be approaching an upper limit since most major fisheries for shrimp have been discovered and are presently being harvested to full or nearly full capacity. Although there are wide fluctuations in the catches of individual countries from year to year, there seems to be no prospect of substantial increases.

On the other hand, the potential for increased production of cultured shrimp is considerable. Increasing investment and a rapid expansion of shrimp aquaculture projects is being undertaken especially in Latin America and the Indo-Pacific region. In these areas, extensive and semi-intensive shrimp culture is now a commercial reality. Rapid growth in farm production has already been experienced in Ecuador and Taiwan and is continuing. It has been estimated that world farm production will reach nearly 400000t, live weight, in 1990 (NMFS 1984).

This estimate needs however to be considered as very tentative, particularly with regard to the time frame. Many problems affect the future development of cultured shrimp and time is required to deal with them. Among these are the cost of wild postlarvae; limitation on the availability of areas suitable for aquaculture for political, legal and physical reasons; a shortage of trained and experienced hatchery and farm management personnel; availability of risk capital and of long-term loans at reasonable interest rates; and the supply of feed of acceptable quality and cost.

While cultured shrimp undoubtedly represents the primary new source of supply, consideration must also be given to imitation or substitute shrimp products manufactured from pollock or other low priced fish. These are beginning to enter the world's markets and supplies are capable of extremely rapid expansion. It remains to be seen whether they will compete directly with natural shrimp in traditional markets.

International trade in shrimp

Trade tends to flow from producing areas to the nearest of the three major markets. The Indo-Pacific region is the primary supplier to Japan; producers of North and South America are the major sources of supply to the US market, while Western Europe is supplied chiefly by countries in the North Atlantic and Africa. Geographical proximity facilitates communication as well as transportation of product. It also reduces exposure to market fluctuations while shipments are in transit.

World imports in 1982 amounted to about 450000t, product weight, with a value of about US$34.2t x 10^9 (ITC 1983). This represents an increase of about a quarter in volume and nearly two thirds in value over the past five years. During this period, the shares of the world shrimp trade have also changed. Since 1980, the US has replaced Japan as one of the strongest-growing import markets for tropical shrimp. Japan's share has declined from 39% to 34% while the share of the European market has increased from 24% to 28% (ITC 1983).

Japanese shrimp imports tripled from 1970 to 1981 but declined steadily in subsequent years. This has been attributed to a combination of speculative buying by trading companies, consumer resistance to high prices and a more cautious policy by importing companies.

During the same decade, shrimp imports to the US fluctuated between 87000 and 104500t (ITC 1983). In 1982 imports rose to 124000t, chiefly as a result of sharply increased supplies from Ecuador and Mexico. The total quantity imported continued to rise in 1983 and early 1984 with substantial increases from Ecuador, Thailand and Taiwan. Factors that appear to be responsible for the dramatic rise in US imports are: (1) the fall in domestic catches; (2) the high value of the US dollar; and (3) the recovery in domestic demand in 1982 and 1983.

Aggregate imports into the European market, not including internal trade, showed considerable increases between 1978 and 1983. Largely this increase came from coldwater shrimp mostly from Greenland and the Faroe Islands.

Market prospects

Despite an increase of 54% in world catch from 1970 to 1980, supply constraints have caused increased competition between buyers in the major shrimp markets. During the past decade and into the present one, prices have fluctuated in an overall upward direction.

United States of America

Until 1981, domestic landings usually

accounted for about half the total supply to the US market and the remainder was imported. As a result of relatively poor domestic catches combined with increases in imports, the share of domestic landings declined to about one third of total supply in 1983.

Domestic catches of tropical shrimp are thought to have reached maximum production levels. The fishery has been affected by increases in effort, by rising operating costs and by loss of access to Mexican fishing grounds. Domestic landings of coldwater species have declined sharply since reaching a peak in 1977 and there is so far no indication that stocks are recovering. This fishery has been further affected by the recent entry into the market of increasing quantities of coldwater shrimp from Norway. Shrimp farming in the US has not yet been commercially successful. As a result the total supply from domestic sources cannot be expected to show any substantial increase and the balance must continue to come from imports.

Latin America has traditionally provided the major part of imports into the US. Peeled shrimp comes chiefly from the Indo-Pacific region and the east coast of Mexico. Although the Indo-Pacific region exports shrimp principally to Japan, it is an important supplier to the US market. Continued growth in shrimp aquaculture can be expected from Ecuador, Panama and Peru as well as other countries in the region. Aquaculture is seen as the principal source of growth of production to satisfy additional demand, especially of the headless form, in the US market. A limiting factor for cultured shrimp however, is the range of sizes.

Consumption of shrimp in the US over the past decade has fluctuated as a result of uneven supply. In 1982 and 1983 however, consumption reached record levels and in 1984 both domestic production and imports were running ahead of 1983. Consumption for the first seven months of 1984 was more than 15000t (15%) higher than in the previous year,(Rackowe1984).

Since more than 80% of all shrimp is consumed away from home in the US, a key determinant is the availability of disposable personal income. Thus demand for shrimp is dampened when a slowdown in the economy reduces disposable personal income, and the demand is stronger as economic conditions improve.

A time series analysis was chosen as the most appropriate method of forecasting prices for the five years from 1982 (Infofish/FAO-ADB 1983). An average annual price increase of 9-10% was predicted for 26 to 30 count per pound Gulf of Mexico brown shrimp. To forecast demand, an econometric analysis was undertaken using these price predictions as well as data on per capita consumption of shrimp and disposable personal income. The analysis indicated that a 10% increase or decrease in price results in a 1.9% decrease or increase in consumption, a 10% change in per capita disposable income results in 11.7% change in consumption; and a 1% decline in per capita disposable personal income would need to be offset by 6% reduction in prices to keep consumption at the same level.

The population of the US is expected to grow at about 1% per year up to 1990. If real disposable personal income increases by an average of 1% per year and assuming that prices increase by the predicted 9-10% per year, then demand in 1990 would be about 23000t more than in 1981 (Infofish/FAO-ADB 1983).

The time series and econometric analyses used were designed to forecast long-term trends, so it is still too early to judge their validity in relation to actual prices and demand. However, sharp increases in supply between 1982 and 1984 have shown that the US market is capable of generating the additional demand required, although at reduced price levels.

Japan

Domestic catches in Japan declined from 79000t in 1974 to 51000t in 1980, live weight, then rose to 55000t in 1981 and 60000t in 1982 (Rackowe 1984). However, no further significant increase is expected in domestic production.

In recent years domestic production has accounted for about one quarter of the total supply to the Japanese market. The inability of domestic sources to meet demand has caused Japanese buyers to seek increasingly large quantities of shrimp from overseas suppliers, with the result that Japan passed the US as the largest importer by volume of tropical species between 1975 and 1982. The US regained the lead in 1983, but per capita consumption in Japan is about twice that of the US.

The Indo-Pacific region is the major supplier of shrimp to the Japanese market. In 1983, six countries: India, Indonesia, Taiwan, Australia,

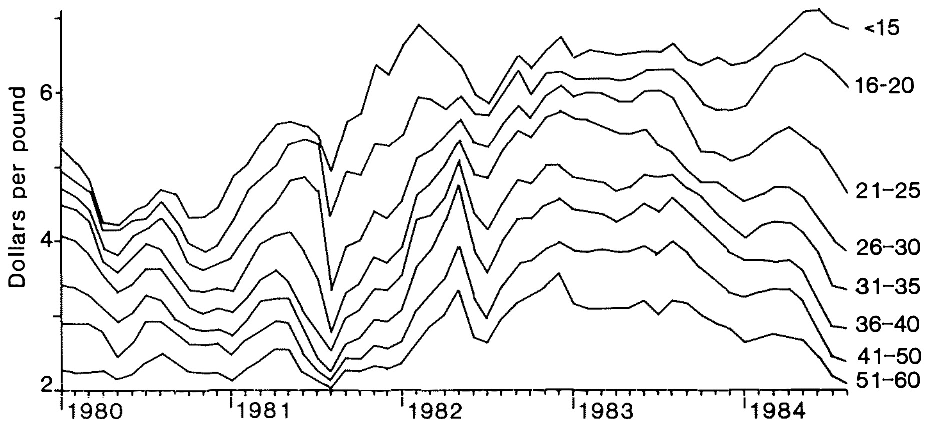

Figure 1. Ex-vessel prices (US dollars) for Gulf of Mexico shrimp by size grade (frozen tails only). Figures are for all species combined and are monthly averages.

Thailand and the People's Republic of China, provided 63% of total imports. Of particular significance is the rapid growth of imports especially of cultured shrimp, from Taiwan.

The expansion in demand for shrimp over the past two decades has resulted from a rapid rise in per capita income together with a movement of the population into urban areas. Demand for shrimp is influenced by the relationship between the price of shrimp and the prices of substitutes such as beef and chicken.

A forecast of prices and demand for shrimp in the Japanese market up to 1987 was undertaken by means of the same techniques as those used for the US market (Rackowe 1984). Prices were predicted to increase by an average of 5-6% per year. A 10% increase or decrease in prices results in 11.4% decrease or increase in consumption while a 10% change in per capita disposable income results in 0.6% change in consumption. According to the study, demand for shrimp is far more responsive to price changes than it is to changes in income.

Although the Japanese population is expected to grow about 1% per year, the predicted 5-6% increase in prices will cause a drop in per capita demand. Future trends in demand are likely to be affected by supply levels and these in turn will determine shrimp prices. Demand is controlled by the relationship between prices of shrimp and prices of competing product.

Europe

Domestic catches, of which a major part consists of coldwater species, account for an important part of the total supply to the European market. Shortages in supply have however encouraged imports of tropical shrimp, even in countries with a traditional preference for coldwater species. The major importers of tropical species are France, Spain, the Federal Republic of Germany and the United Kingdom. Although consumption of tropical shrimp has increased in recent years, total usage in Europe is still small by comparison with the US and Japan. In 1983 imports of tropical shrimp into Europe were about 66000t compared to 155000t imported by the USA and 149000t by Japan (ITC 1984). However, per capita consumption in most of these markets is still at a relatively low level and Europe appears to have the greatest potential for market expansion for tropical species. Although Japan and the US are much larger markets, growth of these markets is expected to be slower.

In the past two years, weakness of the European and Japanese currencies in relation to the US dollar has resulted in a shift in exports away from Europe and Japan to the US market. In recent years the markets have also been affected by high inflation and the general economic slowdown. High interest rates have had a serious impact on costs. Similarly, fluctuations in exchange rates have caused changes in the competitive position of buyers in relation to suppliers. All these factors are

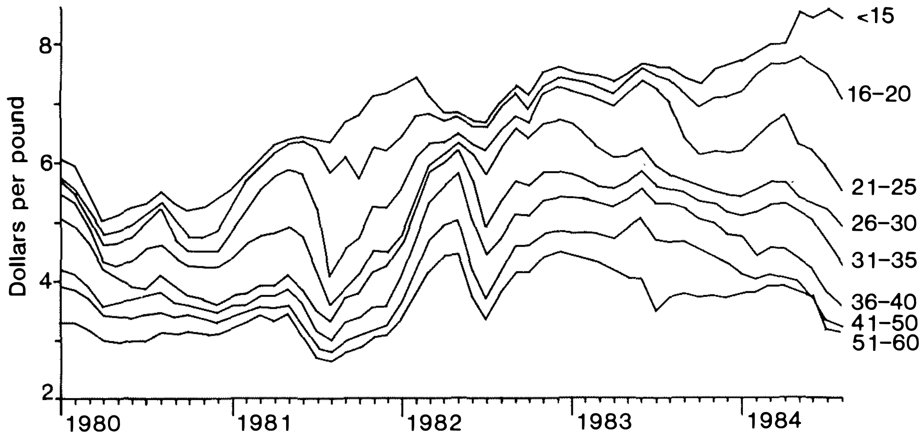

Figure 2. New York wholesale prices (US dollars) for Gulf of Mexico brown shrimp, *Penaeus aztecus*, by size grade (frozen tails only).

expected to continue to affect both exporters and markets in the future.

Almost all future expansion in the major markets is expected to come from imports. In order to predict the quantities of additional imports of tropical species for the three major markets, a projected annual growth rate in consumption is assumed of 1% each for Japan and the US and 5% for Europe (Infofish/FAO-ADB 1983). Using estimated consumption in 1981, the prediction is that total additional imports of 55200t, product weight, corresponding to about 84000t, live weight, will be required in 1990. Assuming that 50% of the world catch is consumed in the producing countries or exported to minor markets, than an increase of 168000t, live weight, will be needed to ensure that the three major markets receive an additional 55200t. Consumption in the producing countries and in the minor markets may well increase at a faster rate than in the major markets, because of a rapid growth in population and numbers of potential consumers. In this case, a proportionally greater increase in world production, possibly

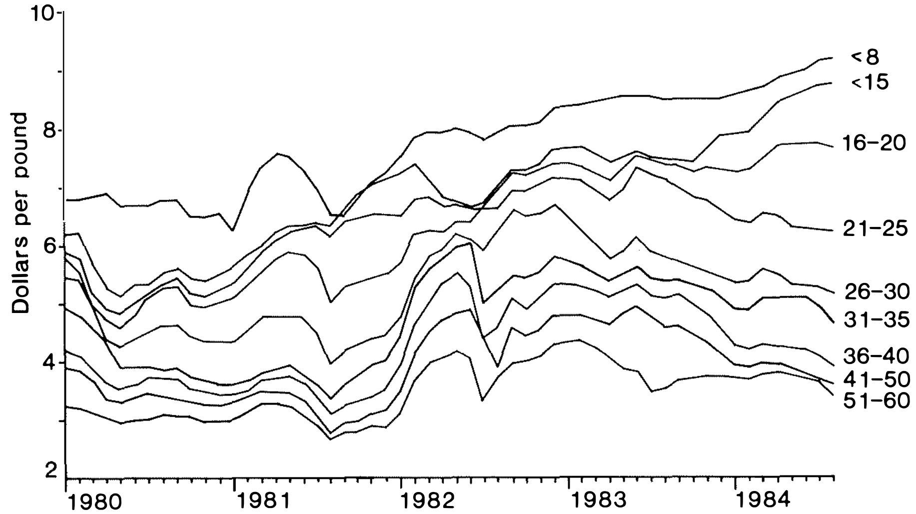

Figure 3. New York wholesale prices (US dollars) for Ecuador white shrimp, *Penaeus stylirostris* and *P. vannamei*, by size grade (frozen tails only).

Table 1. Average annual prices (US dollars per pound) and price differentials by size grade for New York wholesale, Gulf of Mexico brown shrimp, *Penaeus aztecus,* (frozen raw tails only).

Count size	1974 Average annual prices	1974 Difference between sizes	Differences 1974 to 1983	1983 Difference between sizes	1983 Average annual prices
<15	3.20				7.50
		.49	-.26	.23	
16-20	2.71				7.27
		.35	.09	.44	
21-25	2.36				6.83
		.25	.60	.85	
26-30	2.11				5.98
		.34	.09	.43	
31-35	1.77				5.55
		.24	.06	.31	
36-40	1.53				5.24
		.30	.26	.56	
41-50	1.23				4.68
		.12	.60	.72	
51-60	1.11				3.96
		.30		.50	
Average	2.00				5.88

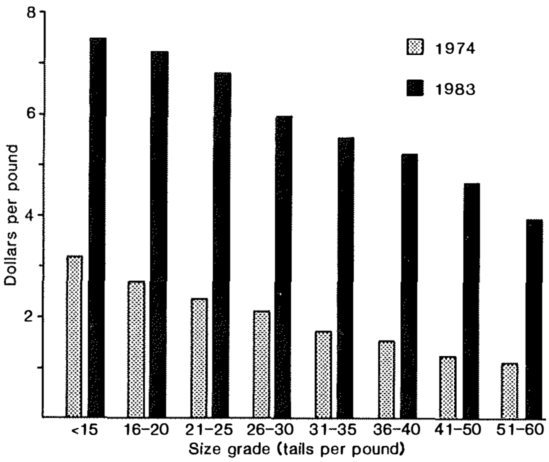

Figure 4. Average annual New York wholesale prices (US dollars) for Gulf of Mexico brown shrimp, *Penaeus aztecus,* by size grades (frozen tails only) for 1974 and 1983.

in excess of 200000t, live weight, will be needed to achieve the desired level of additional imports to the major markets.

Price-size relationship

The principal factors affecting the value of shrimp and shrimp products are size, quality, origin, and species or colour. Size has always played an important part in determining prices to the producer and consumer. Shrimp is graded in groups of sizes, expressed as count per pound or count per kg. Monthly average shrimp prices for the period 1980 to 1984 are shown for Gulf of Mexico ex-vessel production (Fig. 1); wholesale in New York for Gulf of Mexico brown shrimp (Fig. 2); and wholesale in New York for Ecuador white shrimp (Fig. 3). It can be seen that there is substantial fluctuation both in the price for each size and in price differences between sizes.

Differences between sizes fluctuate according to supply of and demand for each size. To illustrate this, the price differences between sizes for Gulf of Mexico brown shrimp on the wholesale market in New York are shown for 1974 and 1983 (Table 1 and Fig. 4). In 1974 the average difference in price between sizes was

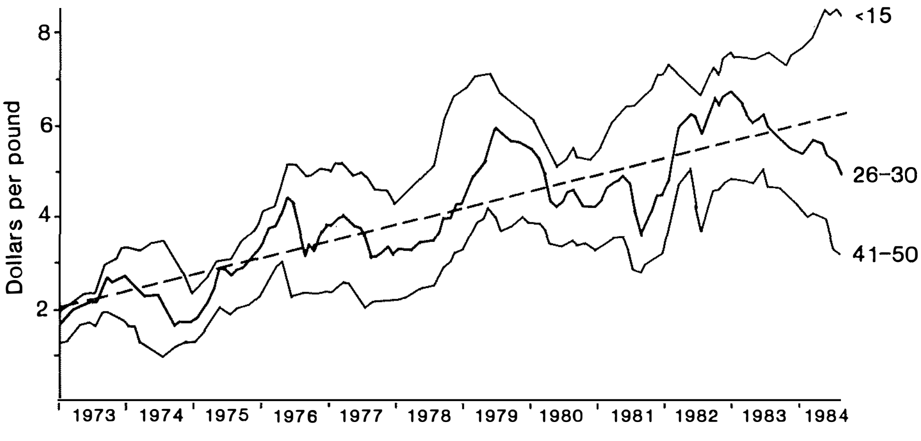

Figure 5. Monthly average New York wholesale prices (US dollars) for three size grades of Gulf of Mexico brown shrimp, *Penaeus aztecus,* from 1973 to 1984 inclusive. A regression line has been fitted to the 26-30 count grade ($y = 2.04 + 0.03x$, $r = 0.8715$, $n = 140$).

Table 2. Annual variations in prices, ex-vessel and New York wholesale, (US dollars per pound) by size grade for Gulf of Mexico brown shrimp, *Penaeus aztecus*, (frozen raw tails only).

Count	Gulf ex-vessel			New York wholesale		
Size	High	Low	Δ	High	Low	Δ
<15	6.67	6.37	.30	7.68	7.30	.38
16-20	6.32	5.78	.54	7.60	6.92	.68
21-25	6.04	5.09	.95	7.39	6.12	1.27
26-30	5.65	4.66	.99	6.64	5.45	1.19
31-35	4.90	4.21	.69	5.80	5.14	.66
36-40	4.59	3.85	.74	5.40	4.78	.62
41-50	4.00	3.31	.69	5.06	4.28	.78
51-60	3.20	2.82	.38	4.44	3.50	.94

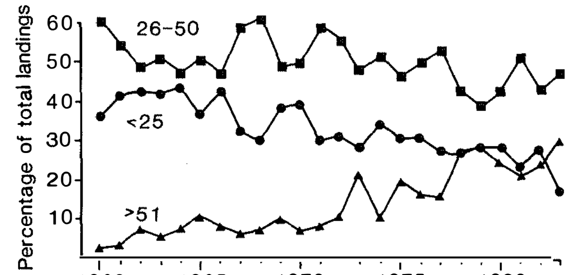

Figure 6. Percentage of landings by three size grades of Texas brown shrimp, *Penaeus aztecus*, from 1960 to 1983 inclusive.

US$0.30 per pound with the greatest spread between under 15 and 16-20 sizes and the least spread between 41-50 and 51-60. By comparison, in 1983 the average difference had increased to US$0.50 per pound and the least spread was between under 15 and 16-20 and the highest between 21-25 and 26-30.

Although it can be seen that long-term movement of prices for all sizes is generally in the same direction, in the short term price trends for individual sizes vary (Table 2). Indeed, there have been times when some sizes have moved up in price while others were declining, as can be seen from recent Ecuador white shrimp prices (Fig.3).

Seasonality and the effect of imports

Shrimp prices in the US used to follow a distinct seasonal pattern over the year. Prices were low during the summer months when the domestic production was at its peak and high during the winter and spring months when both domestic landings and imports were low. Import and domestic prices tended to follow the same patterns. Domestic production is no longer the principal factor affecting prices in the US. Recent rapid growth in imports, combined with relatively poor domestic catches has reduced the influence of domestic production on prices. Overall supply of each size now appears to be the major factor in determining prices for each size. This can be clearly seen in 1983 and 1984, where under 15 count shrimp have been in short supply while there have been good supplies of 26-30 and 41-50 count shrimp (Fig.5).

Long-term trends

Over the long term, wholesale prices for large shrimp have increased less than those for medium and small shrimp. Between 1974 and 1983, the average annual New York wholesale price of under 15 count Gulf of Mexico brown shrimp increased from US$3.20 to US$7.50 per pound, an increase of 134%. The 26-30 count shrimp increased by 183% during the period, while the 41-50 count size increased 280%. This situation began to change in mid-1983 as prices of the large sizes continued to climb while those of medium and small sizes weakened and drifted downward into 1984 (Fig.5). This is a result of limited supplies of large shrimp and more than adequate supplies of medium and small sizes. Shrimp prices in the US have tended to rise and fall with the general upturns and downturns of the economy. Nevertheless, the overall trend in shrimp prices since 1973 has been upward.

Effects of management

The US government felt that the Gulf of Mexico shrimp fleet would benefit from a delayed opening of the fishing season to permit the shrimp to grow to larger sizes (Rackowe 1984). This would have the effect both of increasing the total weight caught and of raising the value of the catch as a result of larger sizes. In 1981 the Texas closure was reported to have resulted in substantial additional income to the fleet. In 1982 and 1983 however it was apparently not successful and indeed, the percentage of small shrimp landed rose (Fig.6) (Rackowe 1984). One of the effects of the shorter Texas season appears to have been a decline in quality, as vessels and plants have had difficulty in handling very large catches in short periods of time.

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Aquaculture

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A review of the status of penaeid aquaculture in South East Asia

Abstract: The aquaculture of penaeids in South East Asia has particular relevance to the development of marine prawn farming in Australia. The major species suitable for culture are *Penaeus monodon, P. merguiensis, P. indicus, P. japonicus,* and *P. semisulcatus* which are all indigenous both to northern Australia and to the whole SE Asian zone. There are some similarities in the types of site available for aquaculture. Perhaps the most relevant factor is that the traditional premium awarded to Australian prawns by the principal regional market, Japan, is being eroded now that products of better quality, partly from farmed sources, are becoming available from such countries as Indonesia, Philippines, Taiwan and Thailand. It is estimated that extra world supplies of at least 200000 tonnes per year of marine prawns will be required by 1990. Since fishery productivity is not expected to yield much more, most of the increased demand will have to be met by aquaculture. Some 70% of the current world output of prawns is estimated to originate in SE Asia and the western Pacific. Tropical and semi-tropical Australia would seem well placed to help fill this gap, being geographically more suitable as a source, for Japanese needs at least, than Central or South America. However, Australia will have to compete with SE Asian countries in a highly sophisticated marketplace if farmed Australian prawns are to be profitably exported. This review presents a summary of the scale and nature of penaeid aquaculture in SE Asia, together with less detailed information on other Asian countries. This dynamic area is itself making strenuous efforts to increase both farm productivity and total output, based on its long experience in aquaculture. The development of penaeid aquaculture in SE Asia is being encouraged and supported by international aid agencies, international and national corporations, national and local government authorities and private entrepreneurs.

Introduction

This review is arranged primarily under country headings and concentrates on the status of penaeid aquaculture in SE Asia, especially in the five original ASEAN nations (Indonesia, Malaysia, Philippines, Thailand and Singapore) and in Taiwan, which were recently visited by the senior author. Less detailed information is also provided on shrimp aquaculture in other countries in South Asia (Indian sub-continent) and East Asia.

The final discussion section deals with comparative national production estimates for 1984 and attempts predictions for output in the year 1990, to examine how far Asian marine shrimp aquaculture may be able to contribute towards the increased world demand forecast for that date. Some of the problem areas in marine shrimp culture in the region are listed to help researchers decide which topics are most appropriate to this rapidly developing industry.

South Asia

Bangladesh

There are currently more than 3000 fish and shrimp farm units in Bangladesh, with a total area of 51812 ha and an output of 8228 t year^{-1} in 1983-84 (FAO 1984). Average productivity of fish and shrimp is low (159 kg ha^{-1} year^{-1}). Of

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this only 79 to 94 kg ha^{-1} is shrimp. Karim (1982) stated that there were 240 000 ha of available estuarine area for traditional shrimp culture. *Penaeus monodon* is the dominant species. There is currently no penaeid hatchery in Bangladesh but one is being provided, together with 700 ha of shrimp farming ponds, as part of an Asian Development Bank (ADB) Aquaculture Development Project. The project, which also includes 120 family sized (4.5 ha) ponds for fish and shrimp, is expected to generate US $6.1 million in shrimp exports per year, partly from freshwater prawns. Bangladesh has a huge potential for both freshwater prawn and penaeid aquaculture which has not yet been exploited.

India

Up to 1977, India practised only traditional forms of shrimp culture, mostly in Kerala and West Bengal. However, in 1977-78, experiments on the monoculture of *P. monodon* were carried out near Madras (Sundararajan et al 1979). From the production of 515 kg ha^{-1} in 80 days (average 32 g animals) from stocking at 2 m^{-2} (10.9 to 22.4‰), with fertiliser but no food, Sundararajan et al (1979) extrapolated that 1.0 to 1.5 t ha^{-1} $year^{-1}$ was commercially achievable. The authors stated that India had two million hectares of suitable brackishwater for fish and shrimp farming, of which only about 30 500 ha was used for coastal aquaculture in 1981 (Karim 1982). At this time shrimp culture was mostly seasonal, alternating with rice. *Penaeus indicus, Metapenaeus ensis,* and *M. monoceros* were the dominant species in West Bengal and *M. dobsonii* in Kerala. Total shrimp production from culture in 1981 was 8 000 t (Karim 1982). Aquaculture Development and Coordination Programme (ADCP 1984) reported that the total annual production of all farmed crustaceans had grown from 17 000 t in 1980 (Pillay 1982) to 20 750 t in 1983. Karim (1982) stated that over 1 t ha^{-1} $year^{-1}$ had been achieved in *P. monodon* monoculture in W. Bengal; about 30% of the average 750 kg ha^{-1} $year^{-1}$ of fish and shrimp production in that State was shrimp, and in Kerala 500 to 900 kg ha^{-1} $year^{-1}$ of low value small shrimp were being produced. At that time, there were only a few miniature hatcheries and virtually all farms were stocked.with natural seed. This is still believed to be the case although a large government hatchery is under development in Cochin and a Unilever subsidiary has a *P. monodon* hatchery near Madras.

Though India is the world's leading shrimp producer, supplying at least 170 000 t in 1982 (nearly 10% of world landings), inshore catches have reached a plateau (Rao 1984). India is also the largest shrimp exporting country (12% of world trade in 1982), being the principal supplier to Japan and the third largest to the USA and the EEC. *Penaeus monodon* and *P. indicus* are the important export species. Because of the importance of shrimp to the foreign exchange earnings of India it is certain that the government will make strenuous efforts to boost production from farming in the vast areas suitable for this purpose, thus maintaining or increasing India's prominence in the market. To date no loans have been given to India to promote brackishwater shrimp farming by the World Bank or the ADB.

Several local and foreign companies are exploring the possibility of establishing large shrimp farms in India. Among these is a group of companies in Dubai and a Brazilian firm, Macpesca, which are collaborating with the Gujarat Industrial Development Corporation (Drieberg 1983) to set up a 100% export oriented shrimp farming venture. Five or six 100 to 150 ha farms were planned, with commercial production set to commence in mid 1984.

Pakistan

There is no history of shrimp farming in Pakistan, though some 385 000 ha are said to be potentially utilisable in the Indus Delta region (Anon. 1983b). The Sind government has allotted 5 500 ha of land for long-term lease for shrimp farming. Currently 50 ha of research and demonstration ponds are being constructed as part of an ADB Aquaculture Development Project. Wild-caught postlarvae will be used at first for this project though a pilot-scale farm being developed by the Lipton's Tea Company nearby will initially be stocked with hatchery reared animals from the research laboratory of its parent company (Unilever) in Scotland. Another Unilever subsidiary operates a hatchery in Madras, India. Several local entrepreneurs are interested in establishing shrimp farms in Sind. Assuming that 30% of the land allotted for shrimp farming is developed and that a modest output of 600 kg ha^{-1} $year^{-1}$ is achieved, Pakistan should be producing at least 1 000 t $year^{-1}$ of farmed shrimp by 1990.

Sri Lanka

Like Pakistan, Sri Lanka has no history of marine shrimp farming but interest in its development is currently very active. Only one third of the 121460 ha of coastal brackishwater areas in Sri Lanka are shallow lagoons, mangrove swamps and tidal flats and marshes (Jayasekera 1982). Of this, probably less than 8000 ha is truly suitable for shrimp farming. Two external aid programs in this sector are planned to promote smallholder units. The World Bank is considering the establishment of a hatchery in Batticoloa on the west coast while the ADB has committed funds for a shrimp hatchery with a capacity rated at 20 million postlarvae per year (10 million per year within the life of the project) 25 ha of demonstration ponds and 25 ha of pens as a component of a mainly freshwater fish oriented Aquaculture Development Project. This project will also provide credit for the establishment of 200 ha of shrimp ponds in the private sector. When operational, this project is expected to generate about 200 t year^{-1} of shrimp for export. Shrimp exports from Sri Lanka averaged 2088 t year^{-1} from 1979 to 1981 and the 1981 export value of US$13.4 million represented 74% of all fish exports, the bulk (85%) of the shrimp going to Japan and the USA.

Of the several private shrimp farms being planned or under construction, those of Serendib Sea Foods (SSF) and Marine Resources Asia (MRA) are of significant scale. SSF and MRA each plan 405 ha of grow-out ponds. SSF is under construction and MRA expects to have its first ponds ready for stocking in early 1985. SSF will rear *P. monodon* while MRA will produce *P. monodon* and *P. indicus*. SSF have completed construction of a 5 to 10 million postlarvae per month hatchery (depending on the species produced) to supply its own farm and for sale to others. MRA will initially use this source for stocking its farm. Both farms are projecting an initial modest unit productivity of about 1.8 t ha^{-1} year^{-1}. Both farms are 51% locally owned. SSF has US partners and MRA is a joint venture with European partners. A third company, Lever Aquaproducts Ltd, a 100% owned subsidiary of Unilever, has been conducting pilot-scale work for some years, initially with the freshwater prawn *Macrobrachium rosenbergii* but now with *P. monodon,* and expects to achieve 7.4 t ha^{-1} year^{-1} (R.L. Ferdinando[2], pers. comm.) from a small commercial farm under intensive management.

[2] R.L. Ferdinando, Lever Aquaproducts Ltd, PO Box 283, Colombo, Sri Lanka.

Sri Lanka has the potential to produce at least 2000 t year^{-1} of farmed shrimp by 1990 if all these developments are realised. This figure, equal to Sri Lanka's annual shrimp exports in the early 1980s, will have a significant effect on its foreign exchange earnings.

East Asia

People's Republic of China

In 1982, the total catch of *P. chinensis (P. orientalis)* was 33000 t (FAO 1982), having declined significantly from 54000 t in 1979. This species is favoured in Japan and much interest has been shown in farming it since 1978. The White Fish Authority (WFA 1980) stated that 110 t of marine shrimp were produced in 1980 from 600 ha of ponds. A joint venture Hong Kong and People's Republic of China, company in Binhai, Tainjin, produced 60 t from 35 ha in a six month rearing cycle in 1981 but its current productivity is unknown. In 1982, penaeid shrimp were reported to be raised in 90 coastal counties and cities, compared with only 12 in 1978 (Anon. 1982a), and a national hatchery had been set up.

China has very great potential for expanded production of fish and shrimp in saltwater. It has 18000 km of coastline with tidal mudflats estimated to be about 10 million ha. Of these an area of about 2 million ha is reported to be suitable for some form of mariculture. Only about 200000 ha is at present being utilised, producing about 450000 t of cultured fishery products, mainly seaweeds and molluscs (oysters, clams, scallops, abalone, cockles, etc). A very limited area estimated to be about 20000 ha is being used for the production of shrimp and finfish. The finfish production, mainly mullets, is about 4000 to 6000 t year^{-1} (6000 t in 1983). Shrimp culture is also practised in this area with production rising rapidly from 1978 to as much as 10000 t in 1983 (Liu 1984).

Seed production through hatcheries has increased rapidly since 1978. Although these hatcheries do not have the sophistication in equipment, methodology and physical structures of hatcheries elsewhere (eg Japan) they appear to be productive. Liu (1984) claims that the production of these hatcheries has reached 4 x 10^9 year^{-1} for various species (*P. chinensis, P. penicillatus, P. merguiensis, P. monodon* and *Metapenaeus* spp.). He further explains that only 400 million of these are used for culture, and the rest are released naturally.

Technical assistance in this work is being sought through joint ventures with other countries having technology in this field and from bilateral and multilateral technical assistance agencies. For instance, the World Food Programme of FAO has an approved food-for-work project to start in mid 1985 to develop some 2860 ha of ponds in three counties of Shandong province and one county of Hebei province designed to produce upon its completion from 525 to 1125 kg of shrimp ha^{-1} $year^{-1}$ or about 3200 t $year^{-1}$ valued at US$9600000. In the next decade production of penaeid shrimp in China could treble or more. New economic policies calling for acceleration in foreign exchange earning, greater utilisation of available mudflats, and support for shrimp or finfish hatcheries especially for species used in mariculture, augurs well for rapid increases.

Japan

The techniques used in marine shrimp farming in Japan have been described by many authors including Ikenoue (1983), Rothlisberg (1984) and Spotts (1984). Though Japan was a pioneer in marine shrimp farming, its output of farmed shrimp (in enclosures, as opposed to ranching) has not grown as quickly as might at first have been expected. This is partly because of the shortage of suitable land and also because only southern Japan has a truly suitable climate. Japanese shrimp farming has also been plagued by a white turbid mid-gut disease of postlarvae which has caused a great loss of production (Liao 1984). Farming has concentrated on *P. japonicus* which is highly valued, especially live, in the local market. There is also some culture of *P. monodon* (I-Chiu Liao[3], pers. comm.).

Some Japanese ponds are earthen, but many farms now use the intensive Shigueno-style technique which is capable of producing more than 20 tha^{-1} $year^{-1}$ (Rothlisberg 1984). The record for this type of culture is stated to be 28 tha^{-1} $year^{-1}$ (Liao and Chao 1983). The grow-out cycle (7 to 11 months) to market size (Rothlisberg 1984) is very long compared with that in tropical countries for other species (3 to 6 months) though harvesting of 20 g animals can start in the fifth month (Ikenoue 1983). Production from farming was 300 t in 1969 and 1480 t in 1970 (Ikenoue 1983). Nambiar (1984) estimates 1983 production to be 2900 t from 120 farms. The market price of live shrimp sometimes exceeds US$50 kg^{-1} (Ikenoue 1983). Japanese shrimp farming production is less than 20% of that in Taiwan or Thailand and less than 10% of that in Indonesia. Much of the farmed shrimp in the latter two countries, however, is not exported.

Stocking rates in Shigueno tanks are very high (300 to 400 m^{-2}) and when the shrimp are about 5 g in size the density is reduced to about 140 to 150 m^{-2}. Initial water exchange rates are 50% per day but when the average size of the shrimp is 5 g the turnover is increased to 100% per day, rising to 200 to 300% per day by harvesting time (Spotts 1984). Spawners of *P. japonicus* are readily available from the fishery (Liao 1984). About 50 to 200 million of the 600 to 700 million postlarvae produced annually are used for farming; the rest are used for release into natural waters (sea ranching) (Liao and Chao 1983). Kuruma shrimp feed costs US$2700 to 3000 t^{-1}, a cost that could only be borne with the very high market prices of shrimp in Japan.

Republic of Korea

There are one or two farms in South Korea rearing *P. chinensis*, but the production volume is insignificant (V. Mancebo[4], pers. comm.). Total production of all farmed crustaceans was only 50 t in 1983 (ADCP 1984), down from 125 t in 1980 (Pillay 1982). *Penaeus chinensis* grows quite well in tropical conditions, although lower temperatures are required before spawning can be induced. Interest in its culture is being shown in several other countries in the region, including Taiwan and the Philippines.

South East Asia

Burma

The only species of marine shrimp being cultured in Burma is *P. monodon* (Taw 1982) although there are other penaeid and metapenaeid species in the natural fishery. Wild seed of *P. monodon* are abundant during pre-monsoon months (March to May). In 1982, two stations, one operated by the Fisheries Department and one by the People's Pearl and Fishery Corporation (PPFC) were stocking experimental ponds with wild-caught postlarvae (Taw 1982). The latter was a 28 ha pilot farm being operated by the PPFC with the aid of an ADB loan. An estimated 10000 acres (4049 ha) of modified rice fields were being used for *P. monodon* culture using trapped tidally borne

[3] Dr I-Chiu Liao, Tungkang Marine Laboratory, Tungkang, Pingtung, Taiwan.

[4] Dr V. Mancebo, San Miguel Corporation, 6766 Ayala Avenue, Makati, Metro Manila, Philippines.

postlarvae and annual production was estimated to be 322 to 650t year^{-1} (80 to 160 kg ha^{-1} year^{-1}) by Taw (1982). The farming area is close to the Burmese border with Bangladesh. A modification is now being sought by the Burmese government to an existing ADB assisted project, concerned originally with the catching and processing of the freshwater prawn *Macrobrachium rosenbergii,* to expand its aquaculture component to include both freshwater prawns and marine shrimp. This project was expected to start in 1985. Burma has many sites suitable for brackishwater shrimp farming and should significantly increase its output of farmed shrimp.

Indonesia

The cultivation of fish and shrimp in brackishwater ponds (tambaks) in Indonesia is several centuries old and there is a sound basis on which modern shrimp farming can be developed. The primary species cultured in Indonesian ponds now are milkfish and shrimp, but other low-value fish and crustaceans are also incidentally cropped.

Tambaks are designed primarily for milkfish culture, and because they are shallow, are not ideal for shrimp farming. Normally there is only one inlet or outlet gate per pond and the water supply canals are tortuous and used by many different farmers with adjacent ponds. Water quality is often poor and exchange less than adequate, especially in some parts of Java, where tidal fluctuation is small. Some farmers allow shrimp fry to enter on the tide, as in extensive culture in other SE Asian countries, while others stock with fry captured from the shore or with hatchery reared shrimp. Some farmers feed trash fish and rice bran, but very few use pelleted feed. Most use fertilisers but water management is generally poor. Productivity per unit area ranges from less than 100 kg ha^{-1} year^{-1} to more than 1 000 kg ha^{-1} year^{-1} (ADB 1983) with an average in 1981 of 171 kg ha^{-1} year^{-1} (Anon. 1982).

Though unit productivity is low, the national production of farmed shrimp is the highest in Asia because of the very large number of tambaks in operation which have a shrimp component. In 1982 there were 174 000 ha of tambaks (Anon. 1983d) with a shrimp production of more than 30 000t year^{-1}. Based on 1981 statistics, about 67% of this total is accounted for by *P. monodon* and *P. merguiensis (P. indicus* in Aceh Province, at the northern tip of Sumatra), the rest being *Metapenaeus* spp. In 1980, 78% of Indonesian shrimp exports went to Japan (ADB 1983).

Theoretically the potential for increased Indonesian production of farmed shrimp is vast, since increasing the productivity of existing tambaks alone to the still modest average of 350 kg ha^{-1} year^{-1} (on 1982 tambak area) would increase national production to more than 60000t year^{-1}. This level of productivity has already been exceeded in Thailand. In addition to existing tambaks there are six million hectares of untouched mangrove, of which perhaps two million can be made available for brackishwater aquaculture (S. Adisukresno[5], pers. comm.) more than 10 times the present area. (The government is insisting on the retention of a 200 m mangrove belt in future developments as mangroves in some existing tambak areas are virtually non-existent). The government plans to increase *P. monodon* production to nearly 44 000 tyear^{-1} by the end of the current five-year plan (1988), to be achieved by developing new tambaks and increasing the shrimp productivity of existing ponds to an average of 250 kg ha^{-1} year^{-1}. ADB (1983) estimated that about 20000 ha of new tambaks could be developed by 1988. Currently ADB is assisting the government in a project designed to increase productivity (and revenue) in 20 000 ha of existing tambaks through the improvement of 280 km of primary and secondary canals in Java, providing credit for intensification, providing extension and training services, and by establishing five hatcheries for brackishwater shrimp, each with a capacity of 40 million postlarvae per year (ADB 1982). The project is expected to increase shrimp production by a total of 4600t year^{-1}, mainly for export (together with 1500t year^{-1} of milkfish).

Though the potential for increased Indonesian shrimp production from ponds is vast (one aquaculturalist claims that Indonesia is the future Ecuador of Asia) the major problem in achieving their goals is seed supply. ADB (1983) estimates that the increases in production which are planned will require 1.75 x 10^9 postlarvae annually, but only 500 million can be supplied from the wild. Of the 1.25 x 10^9 required from hatcheries, the ADB project will generate a maximum of 200 million per year. More than 1 x 10^9 hatchery shrimp fry per year are therefore needed from the private

[5] S. Adisukresno, Central Java Provincial Fisheries Service, Jl. Imam Bonjol 134, Semarang, Indonesia.

sector; the current 34 hatcheries (Soemarno[6], pers. comm.) have a capacity of only about 110 million per year (ADB 1983). Transport and organisational problems also make the distribution of the wild fry difficult. If the need for hatcheries is to be met, at least 20 hatcheries, each with an annual capacity of 50 million fry, are required. ADB (1983) puts the investment level for such hatcheries at about US $950000 each. Though the value of fry (P_{30}) can be as high as US$30 per 1000, it has fallen to as low as US$7 per 1000 because of the inability of many farmers to stock at times of high salinity. This fluctuation is discouraging for would-be hatchery operators and the problem will be solved only when tambak water supplies are improved.

Wild spawners are preferred because artificially matured animals in Indonesian hatcheries result in low fecundity and poor larval survival. Despite this, unilaterally ablated pond reared animals have to be used through much of the year. Most farmers can stock their ponds only twice per year (September and March), in the rainy season. Wild spawners are not abundant in Central Java until April, which is past the stocking peak and may be available in other parts of Indonesia but command a higher price if sold abroad (eg to Taiwan). The shortage of spawners is accentuated by the current ban on trawling in all areas except Irian Jaya. The training and research activities of the Brackishwater Aquaculture Development Center at Jepara are planned to be extended to several regional sub-stations.

Tambak culture is mainly practised in South Sulawesi, Java and Sumatra; there are very few brackishwater ponds in Kalimantan or Irian Jaya to date, although several large projects are in the planning stages for Kalimantan. Existing farms average about 1.5 to 3.7 ha. Some large and well established Indonesian companies are showing interest in building large shrimp hatcheries and/or farms.

Developments in the embryo phases in 1984 were for a 300 and a 500 ha farm in North and South Sulawesi and an allocation of 5000 ha near Jakarta for 500 and 1000 ha farms to supply technology, fry and feed. Hatcheries for 10 to 20 million postlarvae per month at Cilacap, Central Java, and one, using NORAD funds, for 30 million in East Java as well as two of 3 million in West Java and one of 5 million on an island near Jakarta have been suggested. A feasibility study has been made for an integrated development comprising a 20 million fry per month hatchery, a feed mill, grow-out ponds and a processing unit in Central Sulawesi. Two 300 ha farms in West Java and an allotment of 1000 ha in Kalimantan for farming were also considered. The fate of an earlier plan for a 2500 ha farm on the island of Flores (Anon. 1983a) which has plenty of fry but little fresh water, is unknown.

There is thus much activity, both in the government and in the private sector which will result in Indonesia significantly increasing its production of farmed shrimp by 1990. This is particularly important since the fisheries catch has declined since 1979 (S. Adisukresno[5], pers. comm.) due to the ban on trawling. Indonesia looks set to remain one of the largest producers of farmed shrimp in Asia, though its production of exportable shrimp, primarily *P. monodon,* will probably still be surpassed by Taiwan.

Malaysia

Penaeid aquaculture in Malaysia has not developed as quickly as in its ASEAN neighbours, Indonesia, the Philippines and Thailand. This has also been the case with freshwater prawn farming, despite pioneer work in this field in Penang. Currently there are 30 to 35 penaeid shrimp farms in Malaysia with a total of approximately 650 ha under water, but few ponds are stocked at present. Total production of brackishwater shrimp from farms is estimated to be less than 500 t $year^{-1}$. Shrimp farming by trapping, holding and harvesting, without feeding, is traditional especially in the southern part of West Malaysia. About 18 farms now stock with juveniles produced by a number of small hatcheries. With one exception, the maximum stocking density is 10 m^{-2}.

There are said to be more than 6500 km^2 of mangroves in Malaysia (Rabanal 1984) of which perhaps 10% might safely be used for aquaculture without causing undue ecological harm. There are technical problems, however, of which the most serious is the difficulty of using acid-sulphate soils for pond construction, but these are not specific to Malaysia. The development of Malaysian brackishwater shrimp farming seems to have been hampered by poor site selection, unsuitable construction techniques and funding problems, both in the public and private sectors. However, there are encouraging signs of a resurgence of interest in

[6] Soemarno, Directorate General of Fisheries, Salemba Raya 16, Jakarta, Indonesia.

shrimp culture in Malaysia and it is to be hoped that the several large semi-intensive and small intensive ventures being constructed or in initial operation will be commercially successful, providing a much needed boost to shrimp farming development. Production of farmed shrimp could reach 3000t year^{-1} by 1990 if this occurs, but still leaving Malaysia significantly behind its ASEAN neighbours.

In the public sector, the Fisheries Research Institute operates a research shrimp hatchery in Penang and a grow-out farm in Johore, of which some 10ha is used for shrimp research. The Fisheries Department is building hatcheries in Kedah and Trengannu for extension work and seed supply to farmers. The Fisheries Development Authority of Malaysia has shrimp farms of 26ha in Kedah and 15ha in Johore. The Johore farm is now partnered by Guthrie Aquafarms, which owns 75% (Anon. 1984) but plans for Indonesian involvement in the Kedah farm seem to have failed. The latter farm is not used solely for shrimp culture. Konalayan (Fisheries and Fishermen's Development Corporation) also has a hatchery and a 30ha farm in Sabah (East Malaysia).

In the private sector only four farms are 45ha or more in water surface area. One of these is a traditional trapping farm. The others are Diaman Marine Products and Ternaken Marine (TM) in Johore Bahru and Syarikat Pelihara Udang (SPU) in Sabah. SPU has 800 to 1000ha of land available for ponds. A six million per month hatchery has been commissioned. The farm re-started operations in 1984; it has about 45 ha of renovated ponds and is planning a production of 150t in 1985, selling heads-on shrimp to Japan. A modified Taiwanese system will be used for some ponds. Both hatchery and grow-out salinity is about 30‰; adjacent river water cannot be used to dilute pond salinity to more favourable levels for *P. monodon* because of its high lead content. TM currently has the largest area under water for shrimp culture in Malaysia (~70ha) and is building another 70ha, with plans for a further 100% extension. It projects 300t year^{-1} by 1986-87. The company has a four million per month hatchery and a maturation program. Currently the water available for both grow-out ponds and hatchery is about 25 to 26‰. This farm, despite being close to a fisheries station with pH problems, has no problem with acid water, having constructed large ponds with minimal disturbance of the pond bottom and having used mud lobster casts (already neutralised) to provide a top layer to its bund walls. In Asia, TM is pioneering the construction and management techniques which have proved successful in Central and South America. Its use of six ha ponds, with lower flushing rates and lower projected output, contrasts with the high intensity techniques being used in Taiwan. Several new shrimp farms are being planned and constructed in Sabah (I-Chiu Liao[3] and N. Chwang[7], pers. comm.).

The current marketable shrimp size in Malaysia is 13 to 20g, as most of the farmed production is sold live or chilled either locally or in Singapore. The Singapore market is mainly for *P. merguiensis* or *P. indicus.* These species fetch US$10 to 11kg^{-1} at the farm gate. Few shrimp are exported from Malaysian farms now, except to Singapore, but in future Japan will again be the target market, with *P. monodon* the major cultured species. Marketable size will also change, to a 25 to 35g range. As elsewhere in SE Asia, maturation programs are not yet producing strong healthy larvae and hatcheries place almost total reliance on wild spawners, which are available in Malaysia, but expensive due to competition from home and abroad. Malaysian spawners, particularly from Sabah, have a high reputation in SE Asia.

Philippines

The output of farmed marine shrimp in the Philippines, despite the potential, is much lower than that of the other major producers in Asia. The International Finance Corporation (World Bank) states (IFC/WB 1984) that the production level was 3900t in 1982. By that date Thailand was producing more than 10000t year^{-1}. Indonesia had reached 7000t year^{-1} of penaeids (plus more than 10000t of non-penaeid shrimp) by 1980 (SEAFDEC 1982) and Taiwan had exceeded 9000t year^{-1} by 1982 (Table 1). About 250000ha of mangrove swamps are reserved for conservation in the Philippines (IFC/WB 1984) but there are already about 200000ha of existing coastal brackishwater ponds, of which about 10% are being used for shrimp monoculture, or polyculture with milkfish, at low stocking densities (0.1 to 3.0m^{-2}). Milkfish ponds are relatively unsuitable for shrimp culture, being very shallow (300mm) in the central areas to promote the growth of lab-lab (an association of many plants and animals but dominated by diatoms and blue-green algae).

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[7] N.L.M. Chwang, Argent Chemical Laboratories, Co. Ltd, Room 1227, New World Office Building, East Wing, 24 Salisbury Road, Kowloon, Hong Kong.

Farmers are, because of economic factors, converting milkfish ponds gradually to shrimp monoculture but, at present, IFC/WB (1984) estimates that only 10% of those ponds used for shrimp culture comply with adequate standards of water depth, separate inlet and outlet gates and canals, pumped water, and supplemental feed.

Shrimp ponds are stocked either through tidal inflow, or with wild-caught (beach seined) juveniles, or, more recently, with hatchery reared stock. Stocking densities are usually less than 3 m^{-2}, and survival is poor compared to the Taiwanese average of 50%, and yield low; the national average productivity in 1981 was 196 $kg ha^{-1} year^{-1}$ (IFC/WB 1984). However, these techniques provide low-risk extra revenue for milkfish farmers, especially in the provinces of Capiz, Aklan, and Central Luzon which have about 15000 ha of ponds used for extensive shrimp culture.

By 1983, about 48 private and eight government hatcheries were producing about 100 million postlarvae per year; another 20 million postlarvae were stocked in ponds from beach seining. A shortage of gravid females, untreated disease problems and inexperienced operators contribute to inconsistent and low production from existing hatcheries (IFC/WB 1984). Though wild spawners fetch from US$5.60 to US$50 each, captive maturation techniques are not generally being applied. If all the existing 20000 ha of shrimp ponds were stocked at 10 m^{-2} $year^{-1}$ (two crops stocked at 5 m^{-2}), 2 x 10^9 postlarvae would be required annually, more than 20 times current hatchery output. If the productivity of the existing ponds used for shrimp culture in the Philippines could be raised to that current in Thailand in 1983 (384 $kg ha^{-1} year^{-1}$, which is still low), annual production of penaeid shrimp in the Philippines would rise to nearly 7700 t and, if another 10% of milkfish ponds were converted to shrimp culture, to more than 15000 t.

An ADB Aquaculture Project focusing on the fish farmers of Aklan, Capiz and Iloilo in Panay Island includes the provision of 15 hatcheries producing 75 million shrimp fry per year, increasing shrimp exports by 1500 t $year^{-1}$ by 1990. This project and a number of large commercial developments may raise the Philippines output of farmed prawns to the level of 15000 t $year^{-1}$ by 1990. This level, more than three times current output, is equal to the present output in Thailand.

Penaeus monodon is much favoured in the local market and grows faster than any other species tried to date. *Penaeus semisulcatus* is often present in wild stocked ponds but grows slowly in estuarine conditions though it grows rapidly in the wild in highly saline conditions (G. Morgan[8], pers. comm.). *Penaeus merguiensis* and *P. indicus*, are also good candidates for culture, with global market acceptability. *Penaeus chinensis* is another candidate species for the Philippines. IFC/WB (1984) makes a strong plea for the Philippines to diversify the species currently cultured, an event which may be encouraged by a recent fall in the value of *P. monodon* in Japan (FAO/FIIU and INFOFISH 1984) due to an oversupply of farmed shrimp of this species.

Among several large companies and entrepreneurs entering brackishwater shrimp farming in the Philippines are the Ortigas Group (500 ha) and the Manila Bank Group, which is looking for sites in Luzon. The Ayala Corporation has completed a feasibility study for a 1000 ha farm. Pacific Aquaculture Development Corporation, using Taiwanese technology, produce 10 million penaeid fry per month (Anon. 1983c).

The San Miguel Corporation (SMC) began construction of a US$7 million development of an 800 m^2 covered hatchery and ponds on a 30 ha site in Negros Occidental in 1981 (Poblete 1984). Details of the rearing technique used are given in Poblete (1984) and by Liu and Mancebo (1983). Currently SMC have 38 intensive ponds of 0.25 ha and their hatchery is producing at the rate of three million fry per month (maximum output in any one month has been six million). Intensive ponds averaged 14 $t ha^{-1} year^{-1}$ in 1983 (V. Mancebo[4], pers. comm.) and were running at three crops per year of 8 $t ha^{-1}$ in 1984. A total of 18 $t ha^{-1} year^{-1}$ is projected for SMC's larger earthen ponds (three crops of 6 $t ha^{-1}$). There are also some semi-intensive ponds producing 3 $t ha^{-1} year^{-1}$. A food conversion ratio (FCR) of 1.6:1 can be achieved with good management (V. Mancebo[4], pers. comm.) but the feed costs US$1683 t^{-1}. SMC is expected to market 200 to 300 t of shrimp in 1984, rising to 500 t in 1985, partly from contracted growers using SMC feed and technology (Poblete 1984). SMC is experimenting with the culture of

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[8] Dr G. Morgan, Mariculture and Fisheries Department, Kuwait Institute for Scientific Research, PO Box 1638, Salmiya, Kuwait.

P. semisulcatus and *P. chinensis. Penaeus chinensis* has so far proved to grow as fast as *P. monodon* up to 20g but then to slow its growth rate under SMC conditions (V. Mancebo[4], pers. comm.). SMC has a maturation program but relies mostly on wild spawners.

Singapore

Although the Straits of Johore have been traditional areas for the extensive trapping style of shrimp culture for about 50 years (Tham 1968) this form of farming is, like other livestock farming in Singapore, on the decline due to the scarcity and high value of land and labour and to the development policies of the government. However, there are several small hatcheries in Singapore and some farmers stock from this source as well as from tidal movement. Most farms are held on a temporary occupation licence basis. There are estimated to be 10 to 20 farms in Singapore, mostly on Pulau Ubin and other islands in the Straits. Most consist of one large trapping pond, from 12 to 40ha in area; Tham (1968) states that trapping ponds of less than 12ha in area are uneconomical to run. More modern techniques are used by some farmers, one claiming to achieve 3 $t ha^{-1} year^{-1}$ by feeding and improved management. Farmers are concentrating on the market for live shrimp in Singapore (10 to 15g average size). The species demanded by the market are *P. indicus* and *P. merguiensis.* Singapore public were said to consume approximately 130t $year^{-1}$ in 1982 (Anon. 1982b). Whole live shrimp currently fetch US$14 to $16 kg^{-1} as opposed to US$4.60 to $9.30 kg^{-1} for chilled prawns. The price for chilled shrimp can rise to US$16 kg^{-1} in festive seasons, however. The total production from Singapore shrimp farms is variously estimated at 60 to 90t $year^{-1}$ from less than 300ha of ponds. The buoyant market for live shrimp is stimulating experiments on the cage farming of shrimp; this technique is used for fish culture in Singapore. One cage farm has a floating hatchery, using plastic bags instead of nets for the larvae. This hatchery is said to produce postlarvae (P_{20}) at US$2.31 per 1000 as opposed to US$11.60 per 1000 which is charged by local land based hatcheries (J. Walford[9], pers. comm.). The Singapore live shrimp market is very small, however, and could easily be swamped by supplies from the growing shrimp farming industry in Johore, Malaysia, just across the causeway from Singapore. It is anticipated that the area and production of farmed shrimp in Singapore will decrease unless the problems of cage culture (high mortality, high FCR, low density) are solved. A project which would have made a significant impact on the production of brackishwater shrimp in Singapore was announced in 1983 (Chew 1983). This was a S$50 million (US$23.2 million) farm based on the super-intensive technology developed in Hawaii by two US companies, W.R. Grace and F.H. Prince, and scientists from the University of Arizona. The National Iron and Steel Corporation of Singapore was to have been the local partner. Though the American partners were convinced that the scheme was commercially viable in Singapore, the deal has fallen through. The two American companies are now said to be scaling up their Hawaiian pilot plant to commercial scale. This development has its origins in work by the University of Arizona in Tucson and in Mexico more than 10 years ago; shrimp aquaculturalists internationally await news of its successful commercial application. Without this development, Singapore shrimp culture looks set to either stabilise at its present level or decline in the immediate future.

Taiwan

Juvenile *P. monodon* and *M. monoceros* have been captured and stocked in Taiwanese milkfish ponds to provide extra revenue for centuries (Chen 1976). *Penaeus monodon* is seldom seen in ponds at more than 120g, though it grows as large as 250g in the wild. It is marketed at about 35g. *Metapenaeus monoceros* is much favoured for its flavour in Taiwan and is marketed at 5 to 10g (I-Chiu Liao[3], pers. comm.). Without feeds and special care, shrimp survival in the traditional culture method was poor and the production rate only 100kg ha^{-1} $year^{-1}$ or less (Liao and Lei 1983). Following the artificial propagation of *P. monodon* in 1968 (Liao et al 1969) a revolution in Taiwanese shrimp farming began. By the end of that year the first commercial hatchery had been set up (Liao 1981). Though the growth of the industry was relatively slow for the first 10 years, Taiwanese marine shrimp farming has grown rapidly since 1977 (Table 1).

There are now about 1200 commercial marine shrimp hatcheries in Taiwan, mostly small family businesses, often crowded together. These hatcheries would be enough to supply Taiwanese needs for shrimp postlarvae until the 1990 target of 50000t $year^{-1}$ is attained. Like all aspects of shrimp farming there, the production

[9] J. Walford, Zoology Department, National University of Singapore, Singapore.

Table 1. Growth of shrimp farming in Taiwan, 1968 to 1983, with estimates for 1984, 1985 and 1990. Data from Liao 1981; Liao and Lei 1983; Liao and Chao 1983; Kuo 1984; I-C Liao[1], pers. comm.; Agricultural Bureau; China Fisheries News.

Year	1968	1977	1978	1979	1980	1981	1982	1983	1984	1985	1990
No. of hatcheries	1	150					400	1000	1200	1200	1200
Postlarvae (millions $year^{-1}$)		100		>300			500		1000		1800
Pond area (ha)					2000		3018		3500		5000
National production (t)	~400	1100	2600	4400	5000	6100	9600	~15000	17000		50000
Export of prawns (t $year^{-1}$)						69	>2000	8000	11000	15000	40000
Average productivity (t ha^{-1} $year^{-1}$)					2.5		3.2		4.9		10.0

[1]I-Chiu Liao, Tungkang Marine Laboratory, Tungkang, Pingtung, Taiwan.

of animals for stocking is highly compartmentalised. While some hatcheries rear from spawning to nursery stage, others buy nauplii from specialists and sell young postlarvae to nursery farmers. Hatchery water supplies usually come from beach filtration and chlorination is not normally practised. Mass mortalities are common and survival from nauplii to P_{12-15} averages about 40% (Liao 1981) under good management. *Artemia* and *Skeletonema* are the main cultured feeds; tanks are deep and shaded to reduce light intensity and conserve heat, especially during the protozoeal stages. Postlarvae are normally sold to farmers either from the hatcheries' own nursery tanks or from specialist nursery farmers at about P_{40} (0.02g).

Spawner supply is a major problem. Taiwan buys spawners from many other SE Asian countries, legally or illegally, because they are available in local waters only from March to November. Liao (1981) estimated that only 5 to 10% of spawners were the result of induced maturation. Although many hatcheries now have maturation programs, this technique is not yet fully established. Maturation tanks, as in other hatcheries in SE Asia, are often too small in area, although there are attempts to control other environmental parameters. The Tungkang Marine Laboratory is releasing 30 to 35g animals to the wild in an effort to increase the supply of naturally available spawners; tagging results indicate that this technique has potential (N-H Chao[10], pers. comm.).

Monoculture of shrimp was uncommon in Taiwan in 1976 (Chen 1976) but is now the major technique employed, though about 1000ha of the 3500ha under shrimp farming is still semi-intensive, producing 3t ha^{-1} $year^{-1}$ or less (C.T. Chueh[11], pers. comm.). The productivity level of these ponds depresses the national average to 4.9t ha^{-1} $year^{-1}$ which, though more than 10 times higher than any other SE Asian country, is significantly less than the productivity achieved by many intensive farmers in Taiwan. In southern Taiwan it takes three to four months to grow *P. monodon* from about P_{40} to market size (=35g) in the summer and five to six months in the winter. Pond production is 8.4 to 11.2t ha^{-1} $crop^{-1}$ (Liao and Chao 1983). In central and northern Taiwan only 1.5 crops per year are possible; the productivity of well managed intensive farms is therefore put at 12.6 to 22.4t ha^{-1} $year^{-1}$. Some farmers in cooler regions are growing *P. japonicus,* in the winter months.

Taiwanese shrimp farms are characteristically small in area (up to 8ha) but, for example, a 6ha farm producing 18t ha^{-1} $year^{-1}$ (as many do) would produce 108t of shrimp annually, with a 1984 farm-gate value of US$691200 to $831000. This quantity of shrimp would require a water surface area of 30 to 50ha if it were produced by semi-intensive techniques. The high cost of land in Taiwan is another of the major factors (Table 2) which make the intensive use of resources essential. Most farms are family-run businesses; the large farms existing or being constructed in other parts of SE Asia are absent here. The Taiwanese Sugar Company is the only group known to have contemplated utilising large land areas for shrimp culture, having had joint venture discussions with Cargills (USA) and Nippon Saibai (Japan).

[10] Dr Nai-Hsien Chao, Tungkang Marine Laboratory, Tungkang, Pingtung, Taiwan.

[11] C.T. Chueh, Taiwan Fisheries Consultants Inc. 14 Wenchow Street, Taipei, Taiwan.

Table 2. Comparative examples of some basic costs in penaeid aquaculture based on preliminary surveys in SE Asia (1984) and in Australia (Heasman 1984). Bold figures represent government facilities.

Item	Sri Lanka	Thailand	Philippines	Taiwan	Malaysia	Singapore	Indonesia	Australia
Labour (US\$ year^{-1})								
Pond supervisor	2185		670-1350	9600-12000	2500	3800-4400		25460
Skilled labour	990	1300	410		2000	3200		12730
Unskilled labour	520	580	300-400	4800-6000	1500	2800	900	
Secretary		1300	350	6000	3750	5600		
Land (US\$ ha^{-1})								
Purchase		8300-10900	2800-5600	50000-120000			3000-5000	424
Annual rental	**98**		170-1150[1]	3750[1]	**19** 60-230			
Fuel (US\$ l^{-1})								
Petrol	0.54	0.49	0.50	0.65	0.44	0.53	0.34	0.38
Diesel	0.32	0.29	0.36	0.35	0.25	0.26	0.22	
Construction								
Earthmoving (US\$m^{-3})	0.26	0.62	0.14-0.28	0.8-1.2	0.65			
Feed cost (US\$kg^{-1})								
Growers pellets	0.58-1.10	0.94	0.44-1.69	0.82-0.95	1.00-1.33	0.95	0.70-0.90	
Stocking costs								
P_{15}-P_{20} (US\$per 1000)								
P. merguiensis		**4.4**				11.6		
P. monodon	11.0	13.0-15.2 **8.7**	16.9-25.0	5.0-10.0	18.0-30.0	22.0-23.0	7.0-30.0	
Spawners (US\$each)								
P. merguiensis		0.9	8.5-16.9	2.0-3.0		14.0-19.0		
P. monodon		52.0	56.0	12.0-25.0	33.0-42.0	46.0	50.0	

[1] Pond rental.

A very detailed survey of the operational details of 50 Taiwanese shrimp farms growing *P. monodon* is currently being conducted by one of the local feed companies, Hanaqua Feed Corporation. Its results, which will be of great interest to aquaculturalists worldwide, will be published (Chiang and Liao in press). Meanwhile, Taiwanese marine shrimp grow-out technology can be summarised as follows. Pond bottoms are earthen; bund walls are either concrete or brick (to conserve land utilisation) or earthen. Seawater from beach wells is mixed with underground freshwater before distribution to the ponds. Salinity varies from farm to farm, 10 to 25‰ being optimal for *P. monodon* (I-Chiu Liao[3], pers. comm.); most farmers rear at 10 to 15‰, others as low as 5 to 10‰. Such low salinities may not be feasible in future, due to the limitations of freshwater supply. Ownership of an artesian freshwater well makes savings on seawater pumping costs possible if salinities are kept low. However, there are fewer disease problems at higher salinities (I-Chiu Liao[3], pers. comm.). Ponds are always above high water mark to allow proper draining and drying. Water, supplied by gravity from header and mixing tanks, enters the ponds by multiple inlets on one side of the pond and exits similarly on the other side by means of turn-down drains. Ponds, 0.1 to 3.0 ha in area, are drained from the corner where there is also sometimes the exit of a central drain which enables detritus to be regularly removed. Two or more paddle wheel aerators are placed in each pond. Shrimp ponds occupy almost all the coastal strip in some areas and often appear, illegally, in the middle of river estuaries.

Ponds are stocked at 10 to 30 m^{-2}; some farmers have experimented with up to to 70 m^{-2}. Shrimp are fed every four to six hours with commercial pelleted feed, often supplemented with trash fish, shrimp and sea snails. There are now more than 20 feed companies in Taiwan producing specialised shrimp feeds and competition is beginning to force prices down. The apparent feed conversion efficiency (the animals also receive other natural and supplemental feeds) of pelleted feed averages 2:1, though farmers with good management achieve 1.6:1. Water is maintained slightly green with doses of chicken manure, balanced by water exchange. Evaporation losses only are replaced up to an animal size of about 6 g; regular water exchange then begins, rising to 50% per day by the time market size animals are present. Paddle wheel aerators are first operated only when the dissolved oxygen level is low; later they are operated continuously. A specialised team is hired to harvest the ponds by electro-fishing. About 85 to 90% of the shrimp can be harvested in this way, the rest being removed by seining and by hand after draining. Some intermediate harvesting, which reduces the biomass, is also practised. The harvest is sold to a broker who sells to a processing unit. The harvesting team charges about US$42 t^{-1}, while the 1984 farm-gate value of the shrimp has been US$6400 to $7700 t^{-1} (C.T. Chueh[11], pers. comm.). The harvesting technique is very efficient, resulting in clean non-muddy shrimp which are normally at the processors within two hours of harvesting, being maintained in crushed ice meanwhile. Between cycles, ponds are treated with teaseed cake, drained, dried and tilled. Some farmers remove the top 30 to 80 mm of the pond bottom and exchange it for fresh earth (this is also practised in the Philippines by the San Miguel Corporation). Lime is used at about 100 kg ha^{-1}. The downtime between cycles can be up to one month, depending on weather.

Liao and Lei (1983) believe that manipulation of the culture system may make a unit productivity of 40 t ha^{-1} $year^{-1}$ feasible in the future. Increased unit productivity will contribute more to the Taiwanese target of 50000 t $year^{-1}$ by 1990 than increased pond area. The Tungkang Marine Laboratory is experimenting with many other species to try to diversify the market which Taiwan can supply, including *P. semisulcatus, P. stylirostris, P. vannamei, P. japonicus,* and *P. chinensis,* and believes that *P. penicillatus* (which grows well to a 20 g size and is very marketable) and *P. brasiliensis* (which spawns easily in ponds) are particularly good candidate species for farming (N-H Chao[10], pers. comm.).

Attempts are being made to export Taiwanese shrimp technology (I-Chiu Liao[3], pers. comm.), both in the private sector and through government missions, research and training. The success of shrimp farming in Taiwan, which has been spectacular, is due to a unique combination of circumstances, which include ideal water supplies, suitable land, hard-working agriculturally minded family businesses, a national entrepreneurial spirit, successful research and extension services, and significant government encouragement. It remains to be demonstrated whether Taiwanese technology can be applied successfully in other SE Asian countries or whether the American, less intensive, system will be more appropriate. In this context, San Miguel's introduction of the Taiwanese system will be an interesting model for the Philippines. Doubtless both types of system will prove successful in differing localities.

Thailand

By 1983 there were nearly 37000 ha of marine shrimp ponds in Thailand (Table 3) and another 23160 ha of the 160000 ha of mangroves had been determined by survey to be suitable for shrimp farming (Brackishwater Fisheries Division, Department of Fisheries, Thailand, unpublished data). The majority of the more than 5000 shrimp farmers own only one large pond, which is managed extensively. National average productivity is higher than in all other SE Asian countries except Taiwan, at just under 400 kg ha^{-1} $year^{-1}$ (Tharnbuppa 1984a). The major species cultured are *P. monodon,* and *P. merguiensis.* In 1982 total fishery landings of shrimp were 75600 t (FAO 1982) of which 20825 t consisted of these two species. Total shrimp exports have generally exceeded 20000 t $year^{-1}$ since 1979. Of the 27620 t exported in 1982, 22647 t were deep frozen; the rest were dry or salted products. In 1982, 54% of the deep frozen exports went to Japan and about 15% each to the US and Hong Kong.

Most Thai shrimp farmers rely on wild fry of the various species, mainly *P. merguiensis,* and water exchange by tidal movement. Feeding is not often practised, though this is now changing. Thai farmers achieve greater unit productivity than others through the use of push-pumps (made from second-hand diesel bus engines) to increase water exchange and natural stocking rates. About 80% of the farms are in four provinces bordering the Gulf of

Table 3. Number of marine shrimp farms, area and productivity in Thailand, 1974-1983 Data from Tharnbuppa 1984a.

Year	No. of farms	Total area (ha)	Average size (ha)	Total production (t $year^{-1}$)	Productivity (kg ha^{-1} $year^{-1}$)
1974	1518	12091	8.0	1775	147
1975	1568	12868	8.2	2538	197
1976	1541	12296	8.0	2533	206
1977	1437	12411	8.6	1590	128
1978	3045	24169	7.9	6395	265
1979	3378	24676	7.3	7064	286
1980	3572	26036	7.3	8063	310
1981	3657	27439	7.5	10728	391
1982	3943	30792	7.8	10091	328
1983	5334	36933	6.9	14196	384

Thailand, Samut Songkram, S. Prakarn, S. Sakorn, and Petchaburi. These provinces averaged 532 kg ha^{-1} $year^{-1}$ (in 1982) from ponds in the 0.8 to 4.6ha size range and 507kg ha^{-1} $year^{-1}$ from ponds in the 4.8 to 9.4ha range (Superviwan 1984). The 1983 national average productivity of 384 kg ha^{-1} $year^{-1}$ had risen from 147 kg ha^{-1} $year^{-1}$ in 1974 (Table 3) due to new management practices including better predator control with teaseed cake or derris root, the removal of mud between growing cycles from peripheral pond ditches through pumping, and the increased use of push-pumps (Tharnbuppa 1984b).

Typically, ponds have a single water gate which serves as the entry point for water and wild juveniles and the site of nightly harvesting on the spring tides. Farms are family operated; the major costs are for pumping water and, between cycles, mud. A significant quantity of fish is also harvested during draining. Ponds are dried once a year, and the cycles are 3.5 to 4 months in duration.

Experiments (Tharnbuppa 1984a) have shown that productivity can be increased to nearly 1500kg ha^{-1} $year^{-1}$ by predator control, pumping, pond cleaning, monoculture, and the use of feed. *Penaeus merguiensis* can be grown in ponds for only about 3.5 months before growth is said to slow due to the amount of mud in the pond. *Penaeus monodon* is more hardy and can remain in the pond for up to six months without draining (N. Kamaplasip[12], pers. comm.). *Penaeus monodon* is consistently more valuable than *P. merguiensis* on the local market; in 1983 the wholesale value of *P. monodon* in the Bangkok Market was US$2.27 to $8.25kg^{-1} (head-on, shell-on), depending on size, and *P. merguiensis* fetched US$1.98 to $7.54kg^{-1} (Brackishwater Fisheries Division, Department of Fisheries, Thailand, unpublished data).

Some farmers are now using hatchery reared postlarvae for stocking purposes. Between 1 October 1982 and 30 September 1983, the five major government brackishwater hatcheries (Rayong, Songkla, Satul, Phuket and Prachoap) produced nearly 32 million *P. merguiensis,* more than 8 million *P. monodon* and more than 1 million *P. semisulcatus* postlarvae. It is believed that government hatcheries are running at less than 20% of potential capacity. None can currently satisfy the local demand for *P. monodon* postlarvae. Government predictions show postlarval production from their hatcheries rising to 152 million per year by 1987. Mature spawners are often scarce in Thailand but are still exported to Taiwan. Maturation programs exist but are not yet significantly contributing to the number of nauplii available for rearing. The ADB and government hatcheries sell P_{15} *P. monodon* at US$8.70 per 1000 and *P. merguiensis* at US$4.35 per 1000. The price of postlarvae from one large commercial hatchery is the same for *P. merguiensis* but US$15.20 per 1000 for *P. monodon.* Details of the techniques used in Thai hatcheries are given by Jayasekera (1982) and Kungvankij (1982). Several private hatcheries switch from the production of shrimp postlarvae to the rearing of sea bass fry *Lates calcarifer,* according to demand and profitability.

[12] N. Kamaplasip, Brackishwater Fisheries Division, Department of Fisheries, Ministry of Agriculture, Kasetsart University Campus, Bangkok, Thailand.

Besides the efforts of the Department of Fisheries (DOF) to increase marine shrimp farm productivity and the supply of postlarvae, the current first ADB/DOF Aquaculture Development Project includes several subprojects on marine shrimp. These comprise the establishment of two hatcheries designed to produce 45 million postlarvae per year (only 2.1 million have been produced to date because of water supply problems, 93% of them *P. merguiensis*) (ADB 1984); the upgrading of more than 8000 ha of ponds in seven provinces, raising productivity from 150 kg ha^{-1} $year^{-1}$ to 450 kg ha^{-1} $year^{-1}$; and the development of more than 1900 ha of new ponds in mangrove areas. The total projected increase in shrimp production from this project is 3670 t $year^{-1}$, with another 500 t $year^{-1}$ to come from the Second Aquaculture Development Project, which has not yet been commissioned.

There are reports that several investors, including a Taiwanese feed company, are interested in setting up large semi-intensive marine shrimp farms in Thailand but only one large farm is known to be in the construction phase. This is owned by the World Aquaculture Company and has been developed by two Thai businessmen. Investments totalling US$7.8 million from the IFC/WB, in which the Commonwealth Development Corporation is participating, have been secured by this company. As part of this project, which includes sea bass production as well as marine shrimp, an existing hatchery will be expanded at Rayong and two nursery farms and a shrimp grow-out facility constructed. Thirty ha of shrimp ponds will be completed in 1984 and another 151 ha in 1985-86. At full operating capacity, the farm is projected to produce 742 t $year^{-1}$ (two crops per year, each of about 2.1 t ha^{-1}) from 300 nursery ponds of 30 m^2 and 288 grow-out ponds of 0.62 ha. Projections are based upon achieving 33 g market size *P. monodon* after 135 days grow-out, following a 45-day nursery period from P_{15} postlarvae (a total of 195 days from egg to harvest). Stocking rate will be 10 m^{-2} and survival is assumed at 70%. About 75% of the harvested animals will be exported to Japan with a projected market value of US$8.67 kg^{-1} in 1984, rising to US$9.56 kg^{-1} (heads-on) in 1986. Domestic sales are forecast to produce US$6.40 kg^{-1}. Excess shrimp (and sea bass) fry will be sold to other farmers.

Developments in the government sector, which will increase the area used for shrimp farming and the productivity of small farms, combined with the entrepreneurial Thai nature, are expected to result in significant increases in farmed marine shrimp production within the next five years. An estimated 35000 t $year^{-1}$ by 1990 seems an attainable target for Thailand.

Other countries

There is a known potential for shrimp farming in Brunei, Hong Kong, Kampuchea, Papua New Guinea, and Vietnam. No data are available on the current status of penaeid aquaculture in Kampuchea or Vietnam but natural stocking (trapping, holding, and growing) is known to be practised in Vietnamese shrimp ponds, fish ponds, and coastal paddy fields. In 1973, 50000 ha of shrimp ponds and 20000 ha of fish ponds were used for this purpose in Vietnam (Ling 1973). Using the lower rates given by Ling (1973) for shrimp and fish ponds (100 kg ha^{-1} $year^{-1}$ and 20 kg ha^{-1} $year^{-1}$ respectively) the production of shrimp in 1973 would have been at least 5400 t $year^{-1}$. Brunei has mangrove areas suitable for shrimp farming, especially in Temburong. Some government hatchery work has commenced but there is no significant commercial activity to date. Shrimp farming in Hong Kong to supply the local market is limited in size for the same reasons as in Singapore. Supplies of farmed shrimp in Hong Kong are most likely to originate in the People's Republic of China, in the same way as Singapore supplies are likely to be dominated by neighbouring West Malaysia. There is no data for shrimp farming in Papua New Guinea, though at least one foreign investor is known to be contemplating commercial shrimp farming.

Discussion

Brackishwater shrimp farming in Asia is already an industry of significant size. It was estimated that more than 108000 t of farmed shrimp would be produced in Asia in 1984 (Table 4), 73% of this from the countries of SE Asia. Production is expected to more than double by 1990, providing about an extra 130000 t of farmed shrimp from Asia per year. Rackowe (1983), commenting that the world production of shrimp since 1977 had stagnated at about 1.7 million t $year^{-1}$, put the likely demand for shrimp 200000 t higher, at 1.9 million t $year^{-1}$, in 1990. Most, if not all, of this extra demand will have to be met by aquaculture production. This review shows that more than half of the extra demand can be met by Asian aquaculture, 70% of it from SE Asia alone. The Australian fishing industry is

Table 4. Summary of current and projected output ot tarmed penaeid shrimp (all species) in Asia. Other countries in SE Asia include Kampuchea, Hong Kong, Brunei, and Papua New Guinea.

Country	Annual Output (t $year^{-1}$) Amount	Information date and source	Estimated output (t $year^{-1}$) 1984	1990
SE Asia				
Burma	322-650	1982 (Taw 1982)	700	1500
Indonesia	28637	1981[1]	33000	50000
Malaysia	<972[2]	1983 (ADCP 1984)	<500	3000
Philippines	3900	1982 (IFC/WB 1984)	4500	15000
Singapore			<100	100
Taiwan	15000	1983 (I-C Liao[3])	17000	50000
Thailand	14200	1983 (Tharnbuppa 1984)	16000	35000
Vietnam	5400	1973 (Ling 1973)	7000	10000
Other			500	1000
	Total		79300	165600
South Asia				
Bangladesh	2700	1981 (Karim 1982)	4000	10000
India	8000	1981 (Karim 1982)	11000	25000
Pakistan	Nil	—	Nil	1000
Sri Lanka	Nil	—	Nil	2000
	Total		15000	38000
East Asia				
P.R. of China	10000	1983 (Liu 1984)	11000	30000
Japan	2900	1983 (Nambiar 1984)	3000	4000
S. Korea	<50[2]	1983 (ADCP 1984)	50	500
	Total		14050	34500
	Grand total		108350	238100

[1] Anon. 1982.
[2] Includes all farmed crustaceans.
[3] I-Chiu Liao, Tungkang Marine Laboratory, Tungkang, Pingtung, Taiwan.

said to be worried by the possibility of competition from aquaculture if shrimp farming is introduced into Australia (W. Dall[13], pers. comm.). Competition already exists in the region, however, and is rapidly growing, whether Australian farmers join in it or not. Providing economic and marketing factors make it feasible to farm shrimp in Australia it would seem foolish to discourage this industry there. Even if Australian shrimp farming were not feasible, there is room for Australian investment in this field in the neighbouring countries of SE Asia, with enormous scope for collaborative research.

Indonesia produces the largest quantity of farmed shrimp at present (~33000t $year^{-1}$) and will remain one of the leaders in 1990 producing at least 50000t $year^{-1}$. The government's 1988 target is 43700t for *P. mondon* alone. The Philippines which has an even greater area of brackishwater ponds (about 200000ha) than Indonesia, produces only about 14% as much farmed shrimp (Table 4) because a smaller proportion of farmers include shrimp among their cultured species. Taiwan was expected to produce about 17000t of farmed shrimp in 1984 through highly intensive techniques and to equal Indonesian production by 1990 from about 2.5% of the area under water. Thailand is currently the third largest producer of farmed shrimp in Asia and should remain so in 1990. Currently, Thailand produces about 16000t $year^{-1}$. Production in the Philippines is expected to treble to 15000t $year^{-1}$ as existing extensive brackishwater farmers convert to shrimp culture. Vietnam is

[13] Dr W. Dall, CSIRO Division of Fisheries Research, PO Box 120, Cleveland, Qld 4163, Australia.

Table 5. Area of marine shrimp farms, productivity per unit area and total production of marine shrimp in the five original ASEAN nations, plus Taiwan and Burma.

Country	Area (ha)	Productivity (kg ha^{-1} $year^{-1}$)	Estimated output in 1984 (t)
Burma	4050 (1982)	80-160 (1982)	700
Indonesia	174000 (1982)	171 (1981)	33000
Malaysia	<650 (1984)	?	<500
Philippines	20000 (1983)	196 (1981)	4500
Singapore	<300 (1983)	200-300 (1983)	<100
Taiwan	3500 (1984 est.)	4900 (1984 est.)	17000
Thailand	37000 (1983)	384 (1983)	16000

the other significant producer of farmed shrimp in SE Asia, although other Asian countries, notably China, India and Bangladesh, farm considerable quantities and are expected to increase output greatly by 1990 (Table 4). Good potential exists for shrimp culture in Burma and Malaysia but the potential will not be fully realised by 1990. Production from Singapore is insignificant and is likely to remain so. Pakistan and Sri Lanka will have joined the shrimp farming community by 1990.

In terms of productivity per unit area, the national average in Taiwan is more than ten times that in any other SE Asian country, at 4.9t ha^{-1} $year^{-1}$ (Table 5). Though some semi-intensive and intensive shrimp farms exist in other countries in the region, the predominant techniques are still extensive in nature. Thailand, because farmers supplement tidal exchange with pumping and are increasingly converting to semi-intensive management techniques, has the highest average productivity per unit area after Taiwan, at nearly 0.4t ha^{-1} $year^{-1}$. Some Japanese farms exceed the unit productivity achieved in Taiwan but land and climatic constraints make the rapid growth of shrimp farming there unlikely.

It is worth noting that if shrimp farming grows as rapidly in the Americas as it has in SE Asia, the excess demand for shrimp internationally may be met by aquaculture during the early part of the last decade of this century. Price levels may then be expected to fall, generating further demand. Aquaculture will then have to compete with the traditional fishing industry and emphasis will have to be placed on increasing productivity per unit of area, fuel, labour, and feed. Some existing farms can be expected to fail under these competitive circumstances; the writing is also on the wall for the less efficient fishing operators.

Though most shrimp farming in SE Asia still relies mainly on extensive methods of culture (tidal water exchange, wild fry, and little or no feed) the pattern is rapidly changing, with the increasing availability of hatchery-reared postlarvae, the development of a range of commercial shrimp feeds, and the dissemination of better management techniques. The highest productivity is achieved by a combination of factors—the ability to control salinity, high stocking rates, high water exchange through pumping, aeration, and advanced methods of feeding and harvesting. It is likely that shrimp farming in SE Asia will develop along three parallel lines: (1) the spread of Taiwanese intensive techniques, with the potential of high unit productivity in areas where high technology is appropriate; (2) the establishment of large farms using the semi-intensive American system currently successful in Central and South America; and (3) increases in the area and unit productivity of extensive ponds. Of these three types of development, the last is most likely to produce significant increases in regional output; even small increases in unit productivity have an enormous cumulative effect because of the very large areas of brackishwater ponds already in existence.

Clearly marine shrimp farming in SE Asia is a dynamically expanding industry. However, it has its constraints and problems, which will be briefly reviewed here. It is particularly relevant to examine the areas where research has a role to play in solving these problems.

Maturation

Fry production is still hampered by shortages in the supply of wild spawners, which are favoured by most hatcheries. Though successful methods of induced maturation for local species exist (Simon 1982), this technology is not yet in widespread use and few, if any, commercial hatcheries sustain successful maturation programs in the region (Simon and Scura 1983). Application of existing technology and the development of more natural methods of induced maturation (Chamberlain in press) are essential if the vast requirements for fry of this expanding industry are to be met. Non-reliance on wild spawners will also make domestication of commercially farmed species possible. Freshwater prawn farming became really successful only when berried females were taken from farm ponds, rather than the wild.

Species selection

Although *P. merguiensis* and *P. indicus* are favoured in the market and are commercially farmed in SE Asia, *P. monodon* has proved more hardy and fast growing under ideal conditions and has overcome initially adverse market acceptability in Japan. It is now being introduced into the US market. *Penaeus japonicus* and *P. chinensis* are also cultured in the region and favoured in the Japanese market; however, *P. japonicus* has expensive dietary requirements and *P. chinensis* will not spawn under tropical conditions. There is clearly room for the development of other species for culture to diversify the range available to meet differing technical and market criteria. The potential for culture and optimal environmental conditions for other high-value species, such as *P. semisulcatus,* remains to be adequately investigated. The identification of a species which will grow quickly in tropical high salinity conditions is particularly important if Australia is to successfully introduce large-scale shrimp farming, since freshwater sources to reduce salinity, or consistently brackishwater sites are scarce. Some countries, notably Taiwan, are actively examining the farming potential of non-indigenous species, especially from the Americas. It is not suggested that Australia follow this route until its own species have been thoroughly investigated.

Hatchery technology

Although hatchery technology is well advanced there is still some room for improvements in efficiency and for reductions in cost. Included in these are the development of cheaper larval feeds (artificial plankton feeds developed by Shigueno are now commercially available; the Mars Group is also promoting encapsulated larval feeds) and the reduction of facility costs. Many Asian hatcheries are small, owner-managed, family enterprises. The concept of floating hatcheries to reduce costs is being tested by the National University of Singapore (J. Walford[9], pers. comm.). Although there are improvements to be made, it must be emphasised that funding agencies should not yield to the natural desire of researchers to concentrate on larval rearing. These experiments are easy to replicate and can quickly be repeated. The basic technology exists and research funds should be channelled towards aspects of grow-out technology, which are less well defined.

Water quality

Improved, but cheap, methods of filtering and treating hatchery water supplies are required. Most hatcheries in the region inadequately treat their water intake. Even sophisticated hatcheries still suffer from disease and other water-related problems, which reduce survival and productivity. Studies on disease prophylaxis would be appropriate. A better understanding of the role of water quality in grow-out ponds is needed.

Grow-out

Basic information on shrimp pond ecology and management is still inadequate. Fundamental studies on the maximal use of natural food, the control of predators and competitors, the effect of substrate quality on production, etc, would aid efficient pond mangement.

Engineering

At least four major areas in engineering require study. These are (1) The development and application of cost-effective techniques for high volume pumping systems for pond culture in tidal conditions. Installation and maintenance problems are still common. (2) Objective information on the most efficient and trouble-free method for pond aeration. (3) Improved harvesting techniques. Can the Taiwanese method of electro-fishing be scaled up for use in large ponds with minimal labour?
(4) Methods of pond construction in acid-sulphate soil conditions. Can the methods discussed by Pedini (1981) and put into effect by Ternaken Marine in Malaysia be generally applied? Are there other commercially feasible techniques to be studied?

Nutrition

Information on the dietary requirements of different high value shrimp species grown in ponds under semi-intensive and intensive conditions is still insufficient. Feed costs are the single most important factor in farm running expenses; cheaper diets will be essential in the competitive days ahead. Partial or complete substitutes for fish meal need to be found. The relative efficiency of moist versus dry diets needs examination. Optimum feeding frequency and time of presentation for each marketable species still needs quantification.

Ecology

Topics under the heading of ecology centre on the effect of the development of shrimp farming on terrestrial, avian and marine ecology. In particular, informed guidance on the proportion of the mangrove forests which can be developed for this purpose without irreparable harm is needed. Uninformed opinion must not, however, be allowed to stifle the industry. What is the optimum width of mangrove forest which should be left around shrimp farms?

Our general conclusion is that there is a place for Australia in the rapidly expanding field of penaeid aquaculture providing the techniques used are semi-intensive or intensive. Australia cannot compete with SE Asia if it attempts extensive culture. The Australian fishing industry must brace itself for increased competition from aquaculture.

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Marine shrimp culture in the western hemisphere

Abstract: In the past decade shrimp culture has developed from the experimental and testing phase to commercial production. For example, in Ecuador, shrimp are now the most valuable crop with a value for 1983 and 1984 of approximately $200 million per year. Ecuador produces more shrimp commercially than any other country in the western hemisphere. Most countries from Brazil and Peru north to the United States have commercial shrimp farms and pilot farms are operating in the US. Because of the limited growing season, use of non-native species and legal restrictions, the technology needed for shrimp farming to be commercially successful in the US is much greater than in the more tropical areas and in developing nations. Though shrimp farming is commercial, technology is still poorly developed and ventures into shrimp culture still must be considered as high risks. This paper reviews recent developments in commercial farm management, and research in the western hemisphere.

Introduction

Commercial shrimp farming has become a reality in the past decade in the western hemisphere. Neal (1975) during the first Australian National Prawn Seminar in 1973 adequately described the premature attempts to culture shrimp commercially in the United States. None of these initial attempts was successful, however, a US company, Sea Farms Inc., did establish one of the first successful shrimp farms in Honduras in the early 1970s. This farm became profitable within ten years and is still being operated. Ralston Purina established a research facility in Florida and a pilot shrimp farm in Panama which became commercially viable in the late 1970s. This pioneer effort by Ralston Purina and the research supported by the US National Sea Grant Program primarily at Texas A&M University and the US National Marine Fisheries Service at the Galveston, Texas laboratory were responsible for much of the technology developed during the 1970s. The largest commercial shrimp farm industry in the western hemisphere began in Ecuador, also in the early 1970s. It went almost unnoticed for nearly ten years though it was described by Wisely (1975) at the First Australian National Prawn Seminar. Ecuador is also an excellent example of how shrimp farming can be of significance to a country not only in terms of jobs but also foreign exchange. In 1977 Ecuador exported about 4000t of shrimp to the US (Table 1). In 1977, at least 90% of these exported shrimp came from landings from natural sources. Even though the yield from natural sources remained approximately the same from 1977 through 1983, the amount of shrimp exported to the US increased to 26000t in 1983. Shrimp became the most valuable renewable resource for Ecuador having a value of approximately US$200 million in 1983. In contrast, Mexico, which has had very little commercial shrimp culture development, has not expanded its export of shrimp to the US.

Rackowe (1983) estimates that world shrimp landings of live whole shrimp have reached a maximum sustainable yield of about 1.75×10^6 t. Because the supply does not meet the demand, shrimp must be considered as a luxury food with a concomitant high unit price. The high price means that shrimp farming can become profitable at a much lower level of technology than for other aquatic species such as fish. In fact, even with the relative low level of present

Table 1. United States imports of marine shrimp from Ecuador and Mexico. Values in thousand tonnes to the nearest thousand. Source: National Marine Fisheries Service (1978-1984).

Country	1977	1978	1979	1980	1981	1982	1983
Mexico	38	36	36	38	35	40	43
Ecuador	4	5	7	10	12	18	26

technology, the potential high profits and the large market have created great interest, resulting in a rapid increase in shrimp farms worldwide.

Another positive aspect is that most shrimp farms will be built using land marginal for traditional agriculture. This means that shrimp farming provides additional economic return to the country without reducing production of agricultural crops. The marginal land which can be used for shrimp farming not only includes coastal land but any land having ground water of adequate salinities. Commercial shrimp crops have been produced in Texas using ground water approximately 100 km inland (Smith and Lawrence 1984) and a successful pilot demonstration for culturing marine shrimp was accomplished approximately 1 200 km inland (Lawrence, unpublished).

Possibly the most significant positive aspect of shrimp farming is the large economic impact. Shrimp are cultured in ponds with extensive, semi-intensive and intensive pond management producing crops of 50 to 500, 500 to 3000 and 3000 to 10000 kg ha^{-1} respectively. Assuming only crops of 2000 kg ha^{-1} of 20 g whole shrimp and a conservative price of \$5 kg^{-1}, this means a gross income from a crop of \$10000 ha^{-1}. With processing, transportation, marketing, etc., the gross income can be multiplied by 3 to estimate the total economic impact to the country. The economic impact of a crop at \$30000 ha^{-1} is much greater than that realised for the traditional agricultural crops and means jobs and foreign exchange. For areas where two to three crops a year are possible, the economic impact per hectare is extremely impressive.

These positive aspects of shrimp farming have created considerable interest from not only private enterprise but also from governments. This in turn has resulted in the rapid development of commercial shrimp farming not only in the western hemisphere but also in the world. However, of great concern is that the rapid development has resulted in many farms being marginal in terms of inadequate capital, management, expertise and/or site selection.

This paper describes the current procedures of shrimp farming and the industry's present status, predicts future production, and finally, lists some of the research being done in the western hemisphere.

Current procedures

The species of shrimp being cultured in the western hemisphere are given followed by a discussion of the two distinct phases for commercial production. These two phases are seedstock (postlarvae) production and the grow-out phase for the production of marketable shrimp but it is not the purpose of this paper to discuss these in detail. The reader is referred to the following publications for a more detailed discussion: Lawrence et al (1983a, 1983b, 1985); Fox(1983); Malca (1983); McVey and Fox (1983); Lawrence and Huner (in press).

Species

Because of their availability and lower cost, native species were initially used to evaluate the commercial feasibility of shrimp culture. Essentially all species evaluated to date have been in the genus *Penaeus* which includes all the major commercial species of the western hemisphere. Native species evaluated, in order of decreasing productivity in ponds are *Penaeus vannamei, P. stylirostris, P. setiferus, P. occidentalis and P. aztecus, P. californiensis* and *P. duorarum.* The first four species are members of the subgenus *Litopenaeus* and the last three are members of the subgenus *Farfantepenaeus* (Holthuis 1980). It is significant that the species of the subgenus *Litopenaeus* are the only species in the genus *Penaeus* with open thelyca. This is significant in terms of the procedures used for maturation and reproduction of these shrimp in captivity. Another species of the subgenus *Litopenaeus* which is being evaluated in the US, Cuba, Venezuela, Colombia, and Brazil is *P. schmitti.* Preliminary information indicates that in this species, pond production will be very similar to that of *P. setiferus.*

The only non-native species being commercially farmed in the western hemisphere is *P. japonicus.* However, the commercial production of this species is occurring only in Brazil where extensive culturing strategies are being used, and the amount of *P. japonicus* produced is small (less than 400 kg ha^{-1} per crop). Very little evaluation on *P. monodon* has been done in the western hemisphere though there is considerable interest in this species because of its size and the success of commercial production in Asia.

In summary, more than 90% of pond production in the western hemisphere is from *P. vannamei* with the remaining production consisting of *P. japonicus, P. stylirostris, P. setiferus, P. schmitti, P. aztecus* and *P. occidentalis*.

Seedstock production

The hatchery phase of production can be divided into maturation and reproduction, and larviculture. Postlarvae for stocking the ponds can come either from bays, estuaries and near shore nursery grounds or from the production of postlarvae by larviculture. All of the original farms and at least 95% of present commercial shrimp production in the western hemisphere depend upon the collection of postlarvae from natural sources. However, it is recognised that for shrimp culture to reach its full commercial potential, production of postlarvae in captivity must be increased. Because a large number of ponds presently in production, particularly in Ecuador, remain empty a significant amount of the time, construction of larviculture facilities has increased dramatically. There are currently about 24 commercial larviculture facilities in production in the western hemisphere with approximately 60 more planned.

Larviculture used by most commercial farms utilises the best aspects of the two basic systems, the extensive large-scale production system, or Japanese method, and the intensive small-scale production system, or Galveston method. These commercial systems usually use larviculture tanks of 5 to 20 t with initial stocking densities of 30 to 70 nauplii l^{-1}. Survival to five-day-old postlarvae (PL_5) is usually between 30 and 50%. Larval diets are predominantly unicellular algae for the protozoea and *Artemia* for the mysis larval stages. Other foods such as yeast, copepods, minced clam or fish, nematodes, rotifers and even dry formulated feeds have been used. High quality oceanic water with a temperature range of 27 to 29° C and salinity of 30 to 35‰ is used. Though larviculture technology is viable, improvement is possible. Currently PL_5 sell for $10 to $20 per thousand. With increased efficiency and greater production of postlarvae from commercial larviculture these prices will probably be reduced to $6 to $10 per thousand.

Maturation and reproduction of penaeid shrimp in captivity has been another limiting phase for the development of commercial shrimp farming in the western hemisphere. This phase was completely experimental until the late 1970s when commercial production of nauplii in captivity was first obtained for *P. vannamei* and *P. stylirostris*. The original optimism was premature because of high production costs, inconsistent production levels and variable quality of the nauplii. However, during the last few years advances have been made which have resulted in commercial production of high quality nauplii. There are specific requirements for maturation and reproduction in captivity: (1) the physical system (eg round tanks 3.5 to 5 m diameter and 1.2 to 2 m high); (2) biological (eg 1:1 female:male ratio; 40 and 74 adult shrimp respectively per 4 and 5 m diameter tank); (3) environmental control (light intensity and photoperiod, water quality, 28 to 35‰ salinity, 26 to 29° C temperature); (4) dietary (eg a variety of fresh frozen foods such as oysters, bloodworms, fish, shrimp, squid, and 0 to 20% dry formulated diets); and (5) hormonal (eg most companies use unilateral eyestalk ablation of females). Today there are approximately 15 commercial maturation and reproduction facilities in operation in the western hemisphere and approximately another 40 planned. At this time only *P. vannamei* and *P. stylirostris* of the subgenus *Litopenaeus,* which both have open thelyca, are being matured and reproduced in captivity on a commercial scale. There are at least five maturation and reproduction facilities which are producing all their larval requirements in captivity including genetic selection of their second generation. This is of extreme significance for it demonstrates that the technology for maturation and reproduction in captivity is at least adequate though it is recognised that the technology is still minimal. Nauplii are being sold for $2 to $5 per thousand. With additional technology this price should reduce to $1 to $2.

Two other approaches are being used to obtain nauplii. One is to obtain mature, impregnated females from natural sources and to have them spawn in captivity. This is being used to either supplement the production of nauplii from maturation and reproduction in captivity or to supply all their nauplii. The second approach is the maturation and mating of *P. japonicus* in ponds as in Brazil. Mature, mated females are taken from the ponds and allowed to spawn in larviculture facilities. This method for obtaining nauplii is feasible in species with closed thelyca since 95% of the adult females are always impregnated. It is not as feasible in species with open thelyca because fewer than 5% of the adult females in a population are impregnated.

Grow-out

Almost all of the commercial production of shrimp in ponds is either extensive, single phase semi-intensive using a single pond or two phase semi-intensive using a nursery and a grow-out pond. The extensive system utilises very low stocking densities (5000 to 10000 postlarve ha^{-1}) and usually water exchange but no feeding, fertilisation or aeration. Between 50 and 300 kg ha^{-1} of 20 to 30 g shrimp are harvested after a five to six month culture period. The semi-intensive system using a single pond utilises a stocking density between 50000 and 70000 postlarvae ha^{-1} usually with water exchange, feeding, and fertilisation but no aeration. Between 600 and 1000 kg ha^{-1} of 15 to 25 g shrimp are harvested after a five to six month culture period. The two phase semi-intensive system utilises a stocking density in the nursery ponds of 750000 to 1250000 postlarvae ha^{-1}. A 70 to 80% survival is obtained producing 0.5 to 1.5 g juvenile shrimp in approximately one month. The juvenile shrimp are stocked into the grow-out ponds at an initial density of 50000 to 70000 ha^{-1} usually with water exchange, feeding and fertilisation but no aeration. Usually 800 to 1200 kg ha^{-1} of 15 to 25 g shrimp are harvested in four to five months. The most progressive shrimp farmers are using this latter pond management system.

Some farmers utilising the semi-intensive systems fertilise with manures but most farmers use urea and phosphate to enhance natural productivity. The protein level of the dry feeds is usually about 25% with a cost of \$400 to \$700 t^{-1}. Most of the better farmers obtain food conversion ratios of between 1.5:1 and 2.5:1. The major problem is keeping the ponds stocked at the desired levels and with the preferred species ie *P. vannamei.*

An estimation of the major production costs and gross revenue for a shrimp farm utilising the two phase semi-intensive system for a 100 ha shrimp farm with a year-round growing season is presented (Table 2). Assumptions made in this table are: 100 ha of water; 57000 juvenile shrimp ha^{-1} initial stocking density in grow-out pond; 75% and 80% survival in nursery and grow-out ponds, respectively; 22 g shrimp, heads-on, at harvest; 1000 kg ha^{-1} at harvest for 2.5 crops a year; price of shrimp (heads-on) \$5 kg^{-1}; postlarvae cost is \$12 for 1000; food conversion ratio is 2:1; price of dry feed \$500 t^{-1}.

Table 2. Estimated annual budget for a successful 100ha (pond area) marine shrimp farm in the western hemisphere using semi-intensive pond culture methods, based on the most successful farms and farms affected by lack of seedstock.

Item	Most successful	30% less production
Production (kg, heads-on)	250000	175000
Gross revenue ($US)	1250000	875000
Variable costs		
Seedstock (postlarvae at \$12 per 1000)	91000	64000
Feed (\$500 t^{-1})	250000	175000
Labour	100000	80000
Other (fertiliser, energy etc.)	75000	75000
Processing and packaging	120000	84000
Total variable costs	636000	478000
Fixed costs		
Salaries (supervisors)	100000	100000
Interest (15% on land plus capital improvement of \$1300000)	195000	195000
Depreciation and amortisation of \$750000 capital improvement over 10 years	75000	75000
Other (office supplies, travel, telephone, etc)	25000	25000
Total fixed costs	395000	395000
Grand total	1031000	873000
Total revenue above total costs	219000	2000
Revenue ha^{-1}	2190	20
Break-even price kg^{-1}	4.12	4.99

The example uses the above assumptions which are representative of the costs and revenue for pond management strategies used by the most successful farmers in the western hemisphere. A farm of 100 ha is too small to benefit from most of the economies of scale and a 400 ha farm would probably be more profitable than the example. A respectable profit can be made if the ponds are stocked continuously with the desired initial densities and species (Table 2). What is most impressive is the large gross revenue of \$1.25 million for only 100 ha.

If the production is reduced by 30%, due to unavailability of seedstock, the production, gross revenue and variable costs are reduced accordingly with no change in fixed costs. This reduction in production results in a very low profit ($20 ha^{-1}). This lack of available quality seedstock is causing an economic crisis for many shrimp farms in the western hemisphere.

Though the construction of new shrimp farms in the western hemisphere is still progressing rapidly there are major areas for improvement. These are (1) a guaranteed quality seedstock supply and (2) greater expertise in pond management. A guaranteed seedstock supply would increase production significantly and provide a greater probability of profit. However, there is also potential for large increases in production by increasing the efficiency of pond management. For example, the average annual production of the better farmers in Ecuador is above 2000 kg ha^{-1} whereas the average production in Ecuador is less than 700 kg ha^{-1}. This means there are many farms producing less than 500 kg ha^{-1}, or less than 25% of the annual production level of the better farms. By doubling the average production, which would still be only about half the production level of the better farms, the economic situation in Ecuador would be greatly improved.

Again, as with seedstock production, pond production strategies are far from optimal though current practices are adequate for commercial success. Increased research on shrimp nutrition and feed formulation; management strategies to increase the quality and quantity of pond natural productivity; developing of pond management strategies for different species; polyculture; and development of raceway management will all lead to increased pond production of shrimp at decreased costs.

Present and predicted production

I have made estimates for production of marine shrimp from commercial shrimp farms in 1984 and predictions of the production for 1994 for most countries in the western hemisphere (Table 3). Accurate values are extremely difficult to obtain because of the reluctance of owners to divulge procedures and production levels, and the tendency to exaggerate production values. The ranges of production values vary from country to country, reflecting the differences in values obtained from government reports, US embassy sources and personal communication with private sources in each country. Also, the values in Table 3 do not reflect the total range in values obtained but reflect what I feel is reasonable. For example, a low value of 15000 and a high value of 100000 t were predicted for Brazil in 1994 from different sources. I thought these values unrealistic and therefore used 20000 and 40000 t for 1994. It is emphasised that the values in Table 3 are estimates.

Table 3. Estimated production (t, heads-on) from marine shrimp farms in the western hemisphere, 1984 and 1994.

Region and country	1984		1994	
	Low	High	Low	High
North America				
Mexico	200	300	10000	20000
United States	400	600	30000	40000
Total North America	600	900	40000	60000
Caribbean				
Bahamas	120	140	600	1200
Cuba	—	1	1000	2000
Dominican Republic	1	4	2000	3000
Haiti	—	—	200	400
Jamaica	—	—	320	440
Leeward Islands	—	—	100	500
Puerto Rico	—	1	1000	2000
St. Croix	—	1	80	100
Total Caribbean	121	147	5300	9640
Central America				
Belize	5	10	2000	4000
Costa Rica	—	—	2500	4500
El Salvador	—	—	1000	2000
Guatemala	200	300	15000	25000
Honduras	350	450	3000	5000
Nicaragua	—	—	500	1000
Panama	2000	3000	5000	10000
Total Central America	2555	3750	29000	51500
South America				
Argentina	—	—	20	80
Brazil	600	800	20000	40000
Colombia	50	70	10000	20000
Ecuador	30000	35000	55000	70000
French Guiana	—	—	20	80
Guyana	—	—	20	80
Peru	1500	2500	5000	15000
Surinam	—	—	20	80
Uruguay	—	—	20	80
Venezuela	100	200	5000	15000
Total South America	32250	38570	95100	160400
Grand total	35526	43377	169400	281540

Essentially every country in the western hemisphere which has suitable environment and land has either existing farms or plans for farm construction. It is not surprising that South American countries have the highest production because of climate, available land and suitable native shrimp (Table 3). Ecuador, where commercial shrimp production has become the most valuable renewable resource, produces the majority of farmed shrimp in the western hemisphere. Production levels in other countries are still in the developmental stage with the exception of Panama, Brazil and Peru. However, commercial shrimp farms are developing in the US, Mexico, Belize, Guatemala, Honduras, Costa Rica, Colombia and Venezuela and significant commercial growth should soon occur there. Though production of farmed shrimp in 1984 was relatively small, compared to landings from natural sources, it was large enough to affect shrimp prices and cause concern to US fishermen.

Though the rate of increase in pond production in Ecuador will slow, Ecuador should still be the leading nation in 1994 with annual production between 55000 and 70000t (Table 3). Brazil, which has the potential of producing more shrimp than any other nation because of available land and suitable climate, will probably be ranked second or third. Even though the climate in the US is not ideal and there are legislative problems, the US will probably rank second or third in production by 1994. This is because the US has large amounts of available land, research capacity and capital, a stable government with a strong economy, a vertically integrated shrimp industry and the largest market in the world. Development of commercial culture in Mexico, which has the potential to rank second in the western hemisphere, is hindered by government policies. However, Mexico should have a significant shrimp farming industry in 1994. Colombia, which also has considerable potential, Guatemala, where very strong development is occurring, and Mexico, will rank fourth, fifth and sixth in the western hemisphere. Panama, Peru and Venezuela will have viable shrimp farming industries in 1994 with each producing at least 5000t. All of the remaining countries in North America, Central America and South America have limited potential because of the small amount of available land. The development of shrimp farming in some countries such as Nicaragua may be hindered for political reasons. In the Caribbean region development will be restricted not only by limited land but also by high salinity and low nutrient levels of the seawater.

Table 4. Estimated world production of shrimp, western and eastern hemispheres. Values in thousand tonnes to the nearest thousand.

	1984		1994	
Origin	t	Percent of total	t	Percent of total
Landings	1750	92.9	1750	73.7
Farms				
West	39	2.1	225	9.5
East	95	5.0	400	16.5
Total farms	134	7.1	625	26.3
Grand total	1884		2375	

By 1994, annual production of shrimp from ponds in the western hemisphere should reach about 169400 to 281540t with most of the shrimp produced in South America followed by North and Central America (Table 3). At this time it is not possible to predict more accurately the production levels which will actually be attained. This will depend on research, world shrimp prices and demand, as well as government stability and policies on imports. There is potential for significant developments within the next decade because the outlook for additional research funds looks much better.

I have estimated that about 39000 and 95000t were produced in ponds in 1984 in the western and eastern hemispheres respectively (Table 4). This constitutes only 2.1 and 5.0% or a total of 7.1% of world consumption of shrimp. Also, my estimate of the production of farmed shrimp from the eastern hemisphere is more than double that of the western hemisphere. Shrimp farming is having an impact on world supply and the price of shrimp. With landings from natural sources either at or near maximum sustainable yield and demand for shrimp increasing, there is no doubt that farmed shrimp will be a more and more important source of shrimp. What will be impressive is, if annual world production of farmed shrimp increases to 225000 and 400000t for each hemisphere by 1994. Then farmed shrimp will constitute at least 25% of world consumption of shrimp. This also assumes that annual landings from natural sources remain constant at 1750000t and the world market for shrimp will increase to 2375000t by 1994. However, this predicted increase in the world shrimp market is very speculative since this increase is greater than the present growth rate (Rackowe 1983). However, it is feasible that shrimp prices would decrease due to the additional supply of shrimp from farms. This would stimulate a faster growth in the market than at present.

Current research

There have been tremendous benefits from research during the last decade with the potential of even greater benefits during the next decade. There has also been a gradual change in the nature of research on shrimp from predominantly demonstration to higher quality problem solving research. Only the high market price of shrimp has allowed commercial success at this time in spite of limited knowledge of shrimp culture compared with other aquatic species. With the possibility of a decrease in the value of shrimp, strong research programs providing new and more efficient culturing techniques are critical for the continued development of this emerging crop.

There have been tremendous strides in the area of maturation and reproduction of captive shrimp with open thelyca. For example, information on environmental requirements (Aquacop 1979; Brown et al 1980; Chamberlain and Lawrence 1981b) and diets (Chamberlain and Lawrence 1981a) development of artificial insemination (Bray et al 1982, in press; Bray and Lawrence in press; Sandifer et al 1984), production of the first hybrid (Lawrence et al 1984), and male shrimp viability (Leung-Trujillo and Lawrence in press) was obtained on species of the subgenus *Litopenaeus* during the last decade. For the next decade, advances in the following areas are probable.

1. Endocrinology: This should provide not only a better understanding of the shrimp endocrine system but also the synthesis of analogs of some of the hormones (eg gonad inhibiting hormone) involved in reproduction. A gonad inhibiting hormone analog would provide the potential of enhancing reproduction in captivity without grossly changing the hormonal balance in the shrimp as is the case with unilateral eyestalk ablation. This would have the potential of increasing production of better nauplii.

2. Nutrition: a dry diet is needed to reduce costs of production, to determine nutritional needs, and to increase water quality for maturation and reproduction of shrimp in captivity.

3. Genetic selection and domestication: This area alone has the potential of significantly increasing productivity and reducing costs of shrimp cultivation. Optimism is very high for success in this area because: (a) female shrimp are now artificially inseminated on a routine basis, (b) the first hybrid shrimp have been produced, and (c) their high fecundity and short life cycle make shrimp species an ideal group from which to select more productive strains. Development of technology for in vitro fertilisation would enhance genetic selection and domestication even further. Estimates of increased annual production through genetic selection of approximately 5% have been made.

4. Cryobiology: Some success in storing shrimp nauplii at temperatures below freezing have been reported (Lawrence and Baust 1979, 1980). With the recent development of artificial insemination and procedures for shrimp semen evaluation, possibilities of successfully storing gametes, embryos and/or larvae in temperatures below freezing is good. This would significantly reduce shipping and production costs.

There have not been the dramatic advances in larviculture during the last decade that have occurred in the area of maturation and reproduction (McVey and Fox 1983). Yet the advances made in production system design and alternative larval food sources have increased the quality of the postlarvae, and lowered costs (Wilkenfeld et al 1981; Kuban et al 1983, in press; Wilkenfeld and Lawrence in press; Fuze et al in press). The development of a standardised small-scale experimental system for the culture of larvae should greatly enhance the development of larviculture research particularly in the area of diets (Wilkenfeld et al in press). The development of a satisfactory dry diet for postlarvae is almost a certainty and dry diets for shrimp larvae a possibility. Disease is a potential problem in this area and an excellent review of the status of diseases in shrimp has been written (Lightner 1983). Development of a shrimp cell culture line is essential for future disease studies. A vaccine for postlarvae has been tested and development of a vaccine for shrimp larvae is possible (Lewis and Lawrence in press).

Grow-out research is progressing toward an intensive pond culture system. Determination of species desirability (Conte 1978; Ojeda et al 1980; Trimble 1980; Chamberlain et al 1981), development of a two-phase pond system

(Hirono 1983), increased understanding of natural pond productivity and its importance to shrimp production (Rubright et al 1981) and additional information concerning shrimp nutritional requirements with the formulation of adequate feeds (Fenucci et al 1980, 1981, 1982; Smith et al in press; Lee et al 1984, in press) have been the basis for increasing pond production of shrimp at lower costs. Further advances in these areas will result in even more intensive culture methods and greater production. Higher quality formulated dry diets with a cost of \$300 to \$400t^{-1} will be developed. The use of raceways for the nursery phase will occur during the next decade, particularly in those geographical regions without a year-round growing season. The first shrimp farm utilising raceways for the grow-out phase will shortly be producing in the western hemisphere.

Though the preceding represents only a partial list of technological developments that have occurred and might occur during the next decade, the list is impressive and will maintain current optimism for shrimp farming.

Conclusions

1. Shrimp farming has become commercial during the last decade and is making a significant impact on shrimp markets in the western hemisphere.

2. Shrimp farming must still be considered as an emerging enterprise and concomitantly, there are still very large risks involved.

3. There will be a significant growth in shrimp production from farms during the next decade resulting in the possibility of reduced prices.

4. Technology is still relatively low for shrimp culture compared with that for other aquatic species and very significant advances will occur which will result in increased production with reduced costs.

5. It is an absolute necessity that strong and viable research programs be maintained at this time particularly with the possibility of a decreasing price for marketable shrimp.

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Development of methods for growing juvenile school prawns, *Metapenaeus macleayi,* in estuarine ponds

Abstract: Research using small scale experimental systems has identified the optimum conditions for growing school prawns, *Metapenaeus macleayi,* in terms of a wide range of environmental, nutritional and pond management variables. These include temperature, salinity, substrate, dietary protein and mineral levels, supplementary feed type and feed rate, stocking density, effects of predators and competitors, water exchange rate, polyculture and product quality. A pilot scale (1 ha) farming program provided prawn production data (825-930 kg ha^{-1} harvested from each two to three month trial) which supported some of the assumptions made in a favourable economic analysis of school prawn farming (up to 27% annual return on capital). These pilot scale trials also provided information on water quality management in non-tidal ponds and on other aspects of pond management, eg predator control. The school prawn farming industry in northern New South Wales has grown to the point where approximately 130 ha of large (3 to 9ha) ponds have been completed or are under construction. Future research and developments in commercial prawn farming technology will probably be directed towards improving supplementary diets, improving pond water and sediment quality management, and enhancing natural food levels within ponds. In addition, estuarine juvenile stocks will tend to be replaced by hatchery reared juveniles for pond stocking purposes. Diversification into the farming of larger penaeid species, eg eastern king prawns, *Penaeus plebejus,* is also likely to occur.

Introduction

The school prawn, *Metapenaeus macleayi,* is endemic to temperate, east coast Australian waters with a geographical range extending from Tin Can Bay, Queensland, to Corner Inlet, Victoria (Fig. 1). This species has a typical penaeid life cycle with an estuarine nursery phase followed by migration to oceanic waters where mating, spawning and larval development take place (Ruello 1973a). According to Ruello (1977) there are large populations of school prawns associated with five New South Wales (NSW) estuaries (Fig. 1) as evidenced by average annual commercial catches in each estuary exceeding 40t. Electrophoretic studies indicated that NSW school prawn populations south of and including the Clarence River are genetically homogeneous (Mulley and Latter 1981). However, the Clarence River, which supports the state's largest school prawn fishery, produces school prawns which are usually smaller than those from other estuaries and as a result fetch only a relatively low market price (Glaister 1976).

The Fisheries Division, NSW Department of Agriculture (formerly NSW State Fisheries) considered that the Clarence River would be a convenient source of juvenile school prawns for aquaculture, at least for pilot studies. A research program was initiated to develop a technology for growing school prawns in estuarine ponds. The initial studies were carried out in small scale experimental systems at the Brackish Water Fish Culture Research Station at Port Stephens and were aimed at optimising environmental, nutritional and pond management variables. Subsequently these results were applied in a series of farming trials in a 1 ha pilot scale farming pond adjacent to the Clarence River.

The major aim of this paper is to present an overview of this research program and the future prospects for the NSW prawn farming industry. Rather than presenting the large

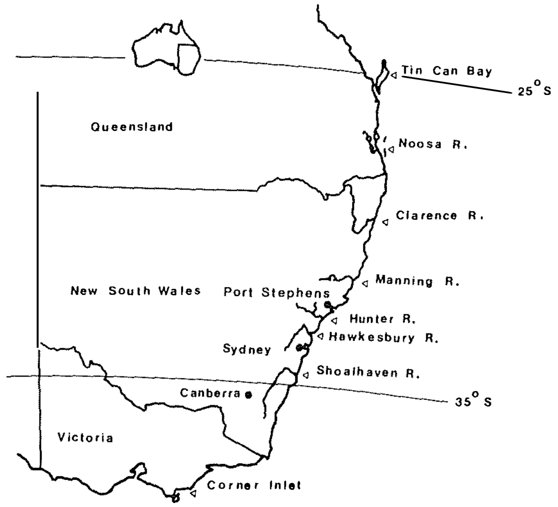

Figure 1. The geographic range of the school prawn, *Metapenaeus macleayi,* and the locations of Port Stephens and the river systems which support substantial school prawn fisheries.

amount of growth, water quality and specific methodological data arising from numerous small scale experiments, it was considered preferable to describe and evaluate these experimental systems and to provide a comprehensive summary of the major conclusions. Priority has been given to a detailed presentation and discussion of the pond management methods, growth, survival and production results, and the economic analysis pertaining to the pilot scale Clarence River farming trials.

Materials and methods

Port Stephens facilities

The experiments carried out in the aquaria, pen and pond (0.01 and 0.1 ha) systems were conducted at the Brackish Water Fish Culture Research Station at Port Stephens (32° 45′ S, 152° 04′ E). The prawns stocked into these various experimental systems were collected by otter trawling in the Port Stephens, Hunter River and Clarence River estuaries. While being transported from fishing grounds to the research station, prawns were held in a multilayered system of timber and 1.5 mm plastic flyscreen trays (0.9 m x 0.45 m x 0.05 m) immersed within 400 l, continuously aerated tanks. For lengthy road transport, the trays were placed in a 2000 l insulated tank with continuous aeration and water recirculation.

Aquarium experiments

Clear perspex 60 l aquaria were used for experiments on salinity, temperature, substrate and nutritional requirements. Each aerated aquarium usually contained a 25 mm deep layer of coarse beach sand and a plastic subsurface biofilter plate covering most of the aquarium floor area. The water temperature and salinity levels were usually in the ranges 24 to 26° C and 28 to 36‰. Fluorescent light tubes illuminated the aquaria (4.2 micro Einsteins m^{-2} s^{-1} at sand surface level) for the diurnal light: dark cycle of 12:12 h in a room without natural light. The water exchange rate was usually at least 60 l day^{-1} with sand or diatomaceous earth filtered seawater. Each aquarium was stocked with 10 juvenile prawns (1 to 5 g) individually tagged with saturn yellow fluorescent pigment in petroleum jelly injected into the musculature of one abdominal segment (Klima 1965). Freshly shucked beach pipi meat (*Plebidonax deltoides*) was fed daily to slight excess shortly before the onset of the dark period. Initial and final prawn weights were obtained by weighing all prawns individually.

Pen experiments

Steel framed pens with netting walls (2.5 mm or 6 mm mesh) were positioned in 0.1 ha ponds so that they enclosed 3.3 m^2 of pond bottom and gave the prawns (usually 15 to 20 juveniles m^{-2}) access to natural benthic food items. Prior to each experiment, ponds were usually fertilised with 50 kg ha^{-1} of urea (N : P_2O_5 : K ratio of 46 : 0 : 0) or nitram (ammonium nitrate 34 : 0 : 0) as a source of nitrogen and 20 kg ha^{-1} of superphosphate (single superphosphate 0 : 21 : 0) as a source of phosphorus. After fertilisation ponds received no water exchange until the pens were stocked. A restricted tidal water exchange regime ensured that the flyscreen lids of the pens were not regularly submerged. Pens were continuously aerated. A more detailed description of the pens and the colonising macrofauna is given by Maguire (1980) and Maguire and Bell (1981). Initial and final average prawn weights were determined by weighing in bulk all prawns for each pen (sexes separate).

Pond experiments

The 0.01 ha round ponds used in the earliest experiments have been described by Maguire (1980). Water exchange in these non-tidal, continuously aerated ponds was achieved by pumping. Three whole-pond experiments (Maguire 1980) were also conducted in fertilised 0.1 ha square ponds. The continuous aeration system, tidal water exchange patterns, biota and sediment temperature and salinity characteristics for these ponds have been described by Maguire and Bell (1982) and Maguire et al (1981, 1984). The diets used in the pen and pond trials were usually either pelleted poultry diets eg chicken broiler grower diets (20 to 25% protein) or pelleted trout diets (35 to 40% protein). The feed rate was usually 5% of the estimated daily biomass reduced to 2.5% by the end of each trial. Some experimental water-stable prawn diets varying in dietary protein or mineral levels (see Maguire and Hume 1982 for composition) or pipi meat were used in pen experiments. Prawns which died due to stress during capture or handling were replaced in the aquaria, pens and 0.01 ha pond experiments.

Clarence River facilities

Pool experiments and pilot scale prawn farming trials were conducted using a 1 ha pond adjoining the southern shoreline of Lake Wooloweyah, a shallow (usually <1 m deep) lagoon near the mouth of the Clarence River in northern NSW (29° 31′S, 153° 17′E).

Pool experiments

A total of 16 steel swimming pools with plastic liners (3.4 m diameter x 0.9 m) were positioned on two banks of the 1 ha pilot scale pond. The pools contained an 80 mm deep sand layer and water from Lake Wooloweyah was supplied to the pools via the main seawater supply line to the pond. The pools were continually aerated and two water exchange rate experiments (Table 1) were conducted. The rates were 0 to 80% of pool volume exchanged every second day by partial drainage and refilling (0 to 40% day^{-1}) and 0 to 60% every third day (0 to 20% day^{-1}). Stocking, feeding, initial fertilisation and water quality monitoring were similar to those used in pond trials, although uneaten food could be more readily observed in the pools, and feeding rates adjusted accordingly. The extent of initial mortality was estimated in each pool and extra prawns were stocked as required. Initial and final biomass values were obtained by weighing in bulk all prawns stocked into each pool (sexes separate).

Pilot scale pond

Four farming trials were conducted in a 1 ha pond (200 m x 50 m x 1 m deep) oriented north to south to maximise circulation and aeration by prevailing winds. The flood-proof walls were constructed of densely compacted silt containing calcareous bivalve shell deposits. A centrifugal pump drew water through a PVC pipeline from below the lake surface level but above lake bottom level to minimise the intake of silt and dilute seawater after heavy rain. Incoming water was sprayed over the pond water surface to improve aeration. The pond could be filled in 20h. Water exchange usually involved the pumping in of water and passive overflow from the pond through a 1 m wide concrete raceway at the opposite end of the pond. Where possible water was pumped in only when lake water turbidity levels were low. Despite these precautions an increasingly deep layer of silt developed over most of the pond bottom. This layer (0 to 100mm deep) may have resulted in part from a loosening of pond bottom soil due to immersion and netting activites.

Juvenile school prawns otter trawled by professional fishermen in Lake Wooloweyah were quickly sorted from live fish, jellyfish, bivalve shells and filamentous algae and then loaded into trays before being transported directly by punt to the pond. Each bound stack of wooden trays was drained and weighed with and without prawns to estimate the total weight of prawns stocked taking into account residual water within the stacks. Stocking activities were suspended if excessive muscle necrosis (Lakshmi et al 1978) was observed. This usually happened only if lake water temperatures or wave action were excessive. Initial mortality was difficult to estimate because of high pond turbidity levels. Estimates of the total weight of prawns stocked in each trial (Table 2) have been reduced by the relatively minor number of prawns which were actually moribund at time of stocking, but not by the subsequent initial mortality. The estimated optimum stocking density (20 juveniles m^{-2}) for school prawns in ponds (Maguire and Leedow 1983) was used as a guide. Stocking densities for pilot trials 1, 2 and 4 ranged from 17.4 to 21.3 juveniles m^{-2} but an unexpectedly large component of very small juveniles (an estimated 49.4% of prawns stocked weighed $\leq$1 g) made accurate stocking difficult for trial 3 and swelled the estimated initial density to 27 juveniles m^{-2} (Table 2). Stocking operations were usually completed within two to four days but in trial 4, prawns were stocked on two occasions two weeks apart.

In trials 1 and 2 and the second phase of the trial 4 stocking, initial prawn samples for average prawn weight and sex ratio determinations were taken directly from the stocking trays. Similarly samples from tubs of harvested prawns were taken prior to cooking to estimate these parameters for trials 1 and 2. All other initial, final and intervening samples for prawn size and sex ratio estimates were taken with a 1.8m beam net (10mm mesh) towed by punt through the pond the day after stocking was completed, the day prior to harvest and at intervening biweekly periods. A correction factor was determined to take account of weight losses caused by frozen storage of some of the prawn samples prior to weighing. Daily feed rates were initially set at 5% of biomass reducing by 0.5% decrements every two weeks to 2.5% of biomass. For the purpose of biomass and feeding rate estimations high overall survival rates (approximately 70%) were assumed. The feed was spread evenly over the pond at dusk. A pelleted trout diet (Allied Feeds) was used in pilot trials 2 and 3, and pelleted poultry diets were used in trials 1 (Steggles) and 4 (Supastok Products). This last diet had been modified by the inclusion of a water-stable binder. Feeding was suspended for up to three days prior to harvest to minimise the risk of discoloration of prawn heads caused by the use of these artificial diets.

The pond was harvested using a hand drawn seine net approximately 70m long (23mm mesh) with a 10m centre pocket (17mm mesh). Prawns were usually held alive in aerated seawater to remove silt particles which adhered to exoskeletons and gills, drained, weighed, cooked in a commercial gas prawn cooker, cooled, stored with ice and salt and transported by road to rail to the Sydney Fish Market for sale as 'cultured prawns'.

Prior to each stocking the 1 ha pond was fertilised to increase natural food levels by stimulating an algal bloom and hence increasing benthic detrital deposits. The fertiliser inputs were 100kg ha^{-1} each of superphosphate and nitram for trial 1, 1500kg ha^{-1} dry cow manure spread out over the dry pond bottom for trial 2, and 700kg ha^{-1} and 1100kg ha^{-1} of fresh, wet cow manure in trials 3 and 4 respectively. The wet manure was mixed into a slurry with water and pumped evenly over the pond water surface. Chemical fertilisers were largely dissolved before being dispersed in pond water during pond water exchanges.

Subsequent additions of fertilisers were used in each trial to maintain an algal bloom so that dissolved oxygen (DO) levels could be maintained and levels of dissolved nitrogenous wastes (ammonia and nitrite) minimised. Only one additional input of fertiliser was required in both trials 1 and 2 (25kg ha^{-1} of superphosphate and 100kg ha^{-1} of wet cow manure respectively). In trials 3 and 4 fertiliser input was needed at approximately biweekly intervals. The trial 3 inputs were 25kg ha^{-1} each of superphosphate and nitram or 60kg ha^{-1} wet cow manure and for trial 4 they were 10 to 25kg ha^{-1} each of superphosphate and nitram. Indicators of decreasing algal levels were the small diurnal variations in DO levels, low morning DO readings ($<$4.0mg l^{-1}) or a decline in afternoon pH values over several days despite sunny weather.

Pond water exchange was used to replace minor evaporative losses, provide circulation and aeration and to dilute excessively dense algal blooms (afternoon DO levels $>$ 15mg l^{-1} and pH levels $>$9.0). Water exchange during the first four weeks of trial 1 was minimal, but DO levels were adequate (range 4.0 to 11.4mg l^{-1}) and unionised ammonia levels were low ($\leq$ 0.17mg NH_3-N l^{-1}) relative to those considered by Wickins (1976) to be lethal to penaeid prawns (1.29mg NH_3-N l^{-1}). However when stressed or dead prawns were noticed at the pond edges or in the biweekly prawn samples a deleterious algal bloom was suspected and daily water exchange rate was increased to 6 to 60% ($\bar{x}$=23%) of pond volume. To avoid a recurrence of this situation in trials 2 to 4, a more liberal routine water exchange regime of 6 to 16% day^{-1} (usually $<$10%) was used. Pumping took place every second or third day so that an 8% day^{-1} regime could involve the pumping of 24% of pond volume every three days.

Two floating paddle wheel aerators powered by electric motors were moored in the pond. As a precaution against overnight dissolved oxygen crisis, these aerators were run on a timeclock for 4 to 10 hours during the night and early morning period when low DO levels were most likely to occur. The paddle wheels were also used if low DO levels ($<$4.5mg l^{-1}) occurred at other times, to alleviate DO stratification on still days during trial 4 and to help distribute dissolved fertilisers. This stratification was probably caused by high turbidity near the silt laden pond bottom.

Cormorants (*Phalacrocorax* spp.) were common during trial 1 but did not prey upon prawns in the pond. However during trials 2 and

3, five to ten cormorants were often chased from the pond each day. A gas scare gun which regularly produced two very loud consecutive discharges was largely ineffective in deterring these birds. They could be chased away by shotgun volleys aimed near them but this was labour intensive and aesthetically undesirable. A high frequency 'Electronic scarecrow' deterrent system (Hi-Tec Control Systems) was installed during trial 3 but technical problems prevented regular operation of the unit until trial 4 during which cormorants were uncommon.

Water quality sampling was carried out regularly using calibrated recording instruments for temperature, salinity, DO, pH and total ammonia. The standard calibration techniques used are described by Strickland and Parsons (1968), American Public Health Association (1971) and Dal Pont et al (1973). Nitrite and nitrate were measured using the spectrophotometric method (Major et al 1972). Temperature and DO were measured either continuously or early morning, noon and late afternoon, salinity after water exchange or rainfall, pH in the late afternoon, total ammonia and nitrite were sampled every one to three days and nitrate recorded at least weekly. The statistical analyses usually applied to experimental results from at least three replicates involved ANOVA techniques to assess overall treatment effects and the least significant difference (LSD) method to compare individual treatments (Steel and Torrie 1960).

Results

Port Stephens research

The results of the small scale experiments at Port Stephens are summarised in Table 1. The aquarium experiments showed that school prawn growth rates are favoured by water temperatures in the range 21 to 27° C and by high salinity levels ($\geq$ 25‰) but are not affected by the type of substrate.

A wide range of conclusions can be drawn from trials in pens and whole ponds. For stocking densities up to the estimated optimum of 20 juveniles m^{-2}, inexpensive poultry diets are adequate but more nutritionally adequate diets, eg pipi meat, are advantageous if higher stocking densities are used (38 juveniles m^{-2}). Furthermore, prawn growth rates in ponds can be affected by dietary protein and mineral levels and by supplementary feed rates. The optimum levels are 25 to 30% and $\leq$ 0.5% of the diet on a dry weight basis for dietary protein and calcium levels respectively and 5% of prawn biomass as dry feed for the supplementary feed rate.

A wide variety of animals inhabit prawn farming ponds and some can be harmful to the prawns as predators or as competitors for food, eg cormorants, eels, yellowfin bream and tarwhine. Benthic macrofauna can be abundant in ponds but do not appear to be as important as detritus as a natural food source for school prawns. Sydney rock oysters which do recruit naturally to the 0.1 ha ponds at Port Stephens were grown with school prawns in polyculture trials in these ponds. The oysters did not exhibit good shell growth or survival rates (Table 1).

Clarence River pilot scale pond trials

Production results

Prawn production results from the pilot scale pond trials are presented in Table 2. The total weight of prawns stocked in each trial (range 370 to 617, $\bar{x}$=489 kg ha^{-1}) varied depending on initial average prawn weight (1.5 to 3.2, $\bar{x}$=2.4g) and to a lesser extent on stocking density (17.4 to 27.0, $\bar{x}$=21.4 juveniles m^{-2}). The total weight of prawns harvested was relatively constant (825 to 950, $\bar{x}$=870 kg ha^{-1}) although the average prawn weight at harvest (5.4 to 7.6, $\bar{x}$=6.6g) and the survival rate (52.1 to 71.3, $\bar{x}$=63.2%) varied considerably among trails. The average prawn size at harvest tended to increase with initial prawn size but there were no clear relationships between survival rate and initial or final prawn size.

Growth rates recorded in each pilot scale pond trial were relatively uniform except for weeks 0 to 2 in trial 1 and weeks 2 to 6 in trial 4 when rapid growth rates were evident (Fig. 2). Overall weekly growth rates for the four trials were 0.40, 0.49 and 0.45 g for males, females and all prawns (sexes pooled), respectively. The biweekly prawn sampling results show that growth continued throughout each of the trials and there were no indications that a growth plateau had been reached (Fig.2). Size frequency analyses showed that both initial and final prawn sizes within each trial were quite variable. There was some general tendency for the initial distributions to change from an asymmetrical type with the smaller size classes constrained by zero to a bilaterally symmetrical distribution at harvest. Size variation among prawns harvested from each trial was most acceptable to buyers at the Sydney Fish Markets with the exception of those from trial 3.

Table 1. Summary of the effects of environmental, nutritional and pond management variables on the growth, survival and pond production rates for school prawns, *Metapenaeus macleayi.* Experiments were conducted in A aquaria, B 0.1 ha Port Stephens ponds, C Clarence River pond and pools, D pens, E pools, F Clarence River pond and G 0.01 ha Port Stephens ponds. All feed composition data are expressed on a dry weight basis.

Variable and results		Comment and reference
Temperature		
*Food consumption rate increased with temperature in range 15 to 27°C. Optimum temperature for growth was 21 to 27°C. Growth rates were depressed at 18 and 30°C and very slow at 15°C. Survival rate was unaffected by temperature in the range 15 to 30°C.	A	Prawns were obtained from pond at 18°C and acclimated gradually using 3°C changes every three to five days.[1]
Survival was unaffected by extreme pond temperature readings of 6 to 32°C.	B	
Salinity		
*Within an experimental range of 10-30‰, growth and survival rates increased as salinity increased from 10-25‰.	A	Prawns were obtained from pond at 28‰ and acclimated gradually using 5‰ changes every 2 days.[1]
*Growth rates at 30 to 33‰ were better than at 15 to 18‰.	G	Survival rates were highly variable but not inversely related to growth rates in this trial.[2]
High growth and survival rates were recorded during six weeks when pond salinity was approximately 36 to 38‰.	D	[2]
Slow growth rates but high survival rates obtained despite a pond salinity of approximately 5‰ for 12 weeks.	C	[1]
Substrate	A	Bare perspex, mud and fine and coarse sands were tested.[3]
*Substrate type had little consistent effect on growth and survival rates.	G	Fine to medium sand and concrete tested.[2]
Dissolved oxygen		
Survival was unaffected by extreme pond bottom dissolved oxygen readings of 3.2 to 18.9mg l^{-1}.	F	[3]
pH		
Survival was unaffected by extreme pool water pH reading of 9.4.	C	Rapid growth (0.8g $week^{-1}$ increase in mean prawn weight) over 4 weeks in pond with high pH levels (Average = 8.7, range = 8.1-9.1).[3]
Natural food levvels		
Gut contents predominantly composed of pelleted artificial diet. Detritus is the major natural food item with macrofauna being less important. *Covariance analyses indicate that sediment organic content may be a useful index of natural food levels.	B	[4 5 6]
Supplementary diets		
*Pelleted chicken broiler diets (20 to 25% protein) adequate at a density of 15 juveniles m^{-2}.	B,D	[2 7 8]
*Chicken broiler finisher pellets (20 to 22% protein) inferior to trout pellets (38% protein) and pipi flesh (*Plebidonax deltoides*) at densities of 20 and 15 to 38 juveniles m^{-2}.	D	[1 5]
*Pipi flesh can sustain very high growth (0.9g increase in average prawn weight per week) and survival rates (80%) at elevated stocking densities (38 juveniles m^{-2})	D	Pipi flesh is intended only for use as a control diet in nutritional experiments. Growth data is from a five week experiment.[5]
Dietary protein		
*The optimum dietary protein level for supplementary diets was 25 to 30%.	D	Slow growth rates recorded during experiment.[7]
Dietary mineral levels		
*Growth rates decreased as dietary calcium levels in supplementary diets increased from 0.5 to 2.0% but were unaffected by dietary phosphorus levels from 0.5 to 2.0%.	D	No evidence of interactive effects of dietary calcium and phosphorus levels on prawn growth rates.[7]

Table 1. continued.

Variable and results		Comment and reference
Dietary binders *Incorporation of alginates as dietary binders or alternatively as encapsulation for a water-stable diet did not improve growth rates.	D,A	Further testing of the effects of physical stability of diet on pond sediment deterioration (chemical reduction) is required.[1 7]
Effect of pipi *The growth promoting effects of pipi flesh in artificial diets are due to the lipid-free, water insoluble component.	A	This component is composed mostly of protein.[1]
Supplementary feed rate *The optimum daily feed rate using a pelleted trout diet was 5% of prawn biomass. The feed rate was reduced to 2.5% of biomass as biomass increased.	D	Overestimation of biomass levels can lead to overfeeding and sediment deterioration. The optimum feed rate is probably dependent on water temperature, natural food levels and on the type of supplementary diet.[1 8]
Optimum water exchange rate *Water exchange rates (0 to 40% day^{-1}) had no effect on prawn growth or survival rates at a stocking density of 20 juveniles m^{-2}. At 50 m^{-2} and an experimental range of 0 to 20% day^{-1}, growth was unaffected but mass mortality occurred in one 0% exchange rate pool.	E	Slow growth rates recorded in the pool experiments. Prawn stress symptoms have been observed in pools and ponds after extended periods without water exchange.[3]
Fertiliser input Managing pond algal blooms by addition of fertilisers as required (eg 25 kg nitram and 25 kg superphosphate ha^{-1} at about two week intervals) allows ready management of dissolved oxygen, ammonia and nitrite levels.	C	At least two weeks prior to stocking intensive fertilisation (100 kg ha^{-1}). Up to 1500 kg of cow manure (dry weight) ha^{-1} has been used. Fertiliser need can depend on site Aeration devices and avoidance of very dense algal blooms are desirable.[3 5]
Stocking density *Growth rates are usually inversely related to survival rates. Optimum stocking density in terms of economic return estimated to be 20 juveniles m^{-2} using chicken broiler diets.	D	Optimum stocking density depends on the type of supplementary diet used and probably also on natural food levels.[5 8]
Predators, competitors Cormorants are the most serious predators in ponds although eels (*Anguilla* spp.) can be troublesome. Sea mullet (*Mugil cephalus*), the most common fish in ponds, pose few problems. Yellowfin bream (*Acanthopagrus australis*) and tarwhine (*Rhabdosargus sarba*) are potential competitors for supplementary diets and the former is a potential predator.	B,C,D	Excessive numbers of sea mullet can interfere with harvesting operations.[1 4 9]
Polyculture *Sydney rock oysters improve meat condition rapidly in prawn farming ponds but are prone to mudworm (*Polydora* sp.) infections, high mortality, gill discoloration, overspatting and slow shell growth rates.	B	Sydney rock oysters (*Saccostrea commercialis*) were previously known as *Crassostrea commercialis*.[10]
Product quality *Taste panel studies and large scale marketing trials indicate that high product quality levels are attainable.	G,F	Mud adhesion to gills and exoskeleton can be a problem.[1 11]

*Conclusions based on statistical comparisons between replicated treatments.

[1] Maguire and Allan (unpublished data) [2] Maguire (1980) [3] Allan and Maguire (unpubl. data)
[4] Maguire and Bell (1981) [5] Maguire (unpublished data) [6] Maguire et al (1984)
[7] Maguire and Hume (1982) [8] Maguire and Leedow (1983) [9] Maguire and Bell (1982)
[10] Maguire et al (1981) [11] McBride and Maguire (1979)

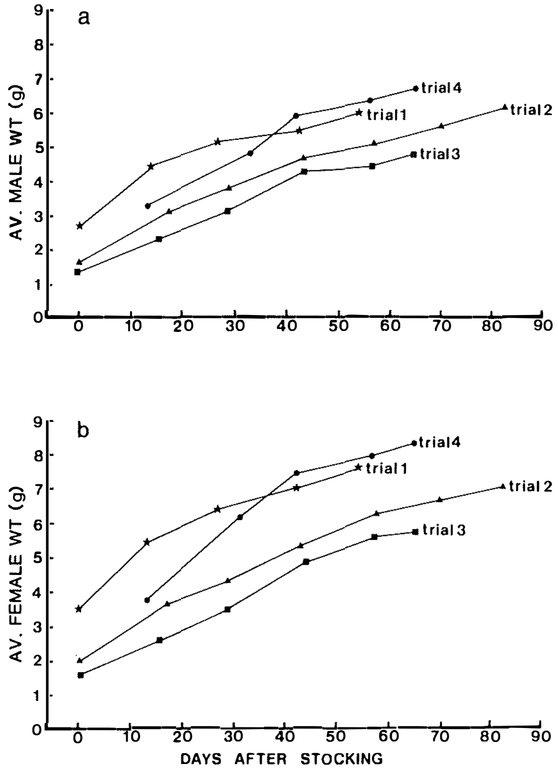

Figure 2. Growth of school prawns, *Metapenaeus macleayi*, **a.** male and **b.** female during four pilot scale (1 ha) Clarence River prawn farming trails. See Table 2 for SE values of initial and final weights.

The male and female size distributions for prawns harvested from this trial revealed that there were significant numbers of prawns of 3g or less and this adversely affected marketability.

Survival rates during the first two trials were relatively high (69 to 71%) despite the fact that prawn stress symptoms and mortality were observed in the latter part of trial 1 and that predation by cormorants was a problem in trial 2. The poorer survival rate in trial 3 (61%) may have been influenced by: (1) the difficulty of accurately assessing the true stocking density and hence survival rate because of the large number of small prawns stocked, (2) deterioration in pond sediment condition, ie chemical reduction, during the trial and (3) predation by cormorants and eels. There were approximately 100 eels ha^{-1} at harvest, mostly long-finned eels (*Anguilla reinhardtii*). The poorest survival rate (52%) occurred in trial 4 and the potential causes were: (1) further pond sediment deterioration, (2) abnormally high initial mortality (also observed in a concurrent pool trial) and (3) incidence of stress symptoms among prawns on several occasions during this trial. Biweekly sampling indicated continuing mortality during trial 4.

The average market price obtained for each crop varied widely (\$4.28 to 9.33, $\bar{x}$=\$6.67kg^{-1}) and was not dictated solely by the average prawn size at harvest (Table 2). On two occasions the prawns were marketed at times when maximum prices for school prawns are usually obtained, ie in the one week periods prior to Christmas (trial 3) and Easter (trial 4). The trial 3 harvesting operation was complicated by retention of large amounts of silt in the harvest net and by high water temperatures. Most of the prawns were moribund by the time they were placed in the aerated seawater tank prior to cooking and the slightly muddy appearance of these prawns in combination with their relatively small and uneven size depressed their market value. Product quality was high for all other crops with the slight exception of the prawns from trial 2, which had some digestive gland discoloration after cooking which may have resulted from the trout diet used. The problem diminished in trial 2 after feeding with the trout diet was stopped and was not evident in trial 3 when the trout diet was replaced by the Supastok poultry diet for the last week of feeding. The prawns produced in trial 1 were a high quality product but were sold at a time when the market was oversupplied. Although their average market price (\$4.28kg^{-1}) was low they did attract the highest prices for school prawns at the Sydney Fish Market on the day when most were sold.

Water quality

Water quality measurements taken during the four pilot scale pond trials are summarised in Table 3. The most variable water quality parameter among the four trials was salinity. This was usually >15‰ but declined rapidly during the last two weeks of trial 1 to 7.4‰ and remained low during all of trial 2 (4.4 to 7.1‰). Pond water temperature and DO results were characterised by progressive increases during daylight hours and the average diurnal variations were 2.8° C and 3.9mgl^{-1} respectively. Despite some quite high pond temperature readings in each trial (extreme maximum for each trial ranged from 30.8 to 31.6° C) there were no instances of widespread high temperature stress, as evidenced by muscle necrosis. Similarly, prawns in the pilot

Table 2. Summary of growth, survival, production and marketing results from four pilot scale (1 ha) Clarence River farming trials using school prawns, *Metapenaeus macleayi*. The duration of a trial is from the first day of pond stocking to the last day of harvesting.

Parameter	Farming trial number: 1 Nov to Jan	2 Feb to May	3 Oct to Dec	4 (Jan to April): First stocking	Second stocking	Combined result
Duration (weeks)	8	12	10	10	8	8 to 10
Average prawn weight (g ± SE)						
Male						
Initial	2.7 ± 0.07	1.6 ± 0.03	1.4 ± 0.06	2.6 ± 0.07	2.6 ± 0.08	—
Final	6.0 ± 0.06	6.1 ± 0.05	4.8 ± 0.07	—	—	6.7 ± 0.06
Female						
Initial	3.5 ± 0.08	2.0 ± 0.04	1.6 ± 0.06	3.2 ± 0.08	3.2 ± 0.13	—
Final	7.6 ± 0.08	7.1 ± 0.05	5.7 ± 0.08	—	—	8.4 ± 0.09
Sexes pooled						
Initial	3.2	1.8	1.5	3.0	2.9	—
Final	6.9	6.6	5.4	—	—	7.6
Number of prawns sampled						
Initial	1 371	1 494	838	822	755	—
Final	934	881	740	—	—	778
Sex ratio (male:female)						
Initial	1:1.47	1:1.27	1:1.10	1:1.39	1:0.95	—
Final	1:1.48	1:1.13	1:1.52	—	—	1:1.14
Thousands of prawns (ha^{-1})						
Initial	174	201	270	156	53	209
Final	120	144	164	—	—	109
Survival rate (%)	68.8	71.3	60.6	—	—	52.1
Total weight of prawns (kg ha^{-1})						
Initial	548	370	419	462	155	617
Final	829	950	877	—	—	825
Average market price (\$ kg^{-1})	4.28	6.77	6.31	—	—	9.33

scale pond were never observed to swim in large numbers near the pond surface during daylight hours in response to critically low DO levels as had occurred in commercial school prawn farming ponds (F. Roberts[1], pers. comm). Dissolved oxygen levels occasionally fell to 3.0 to 3.2 mg l^{-1} but never to levels approaching those considered lethal to penaeid prawns, ie <1 mg l^{-1} (Maguire 1980). High DO (>15 mg l^{-1}) and pH (>9.0) levels, indicative of dense algal blooms, were occasionally recorded but did not cause any apparent problems in terms of prawn growth or survival rates. Total ammonia readings were usually <0.1 mg total NH_3-N l^{-1} and the amounts of dissolved ammonia in its unionised toxic form were usually negligible in the pond samples. The upper acceptable level of dissolved unionised ammonia (0.1 mg free NH_3-N l^{-1}) for maximum penaeid growth (Wickins 1976) was exceeded only once and this was during a period of rapid prawn growth rates in trial 1. The amount of dissolved nitrite was always negligible (<0.02 mg NO_2-N l^{-1}) in the pilot scale pond samples.

Occasional inputs of fertilisers used to increase minimum DO levels usually stimulated an increase in algal activity as evidenced by increased daily maximum DO and pH readings. On only two occasions was a second input of fertiliser deemed to be necessary because DO levels failed to improve satisfactorily within five days of the first input.

[1] F. Roberts, School Road, Palmers Island, NSW, 2460

Table 3. Summary of pond water quality results from four pilot scale (1 ha) Clarence River farming trials using school prawns, ***Metapenaeus macleayi***.

Parameter	Farming trial number 1	2	3	4
Water temperature (°C)				
Range	20.0-31.4	16.0-30.9	17.8-31.6	21.3-30.8
Average minimum[1]	23.9	21.2	23.2	24.9
Average maximum[1]	26.8	23.6	26.4	27.9
Salinity (‰)				
Range	7.4-19.7	4.4-7.1	16.9-23.6	14.5-27.5
Average	13.8	5.2	20.0	20.1
Dissolved oxygen (mg l^{-1})				
Minimum[1]				
Range	3.2-6.8	3.7-9.4	3.2-8.8	3.0-6.7
Average	5.0	6.0	5.3	4.9
Maximum[1]				
Range	5.8-11.4	5.5-18.9	6.1-15.2	5.0-15.8
Average	8.1	9.3	9.5	9.9
pH				
Maximum[1]				
Range	7.0-8.8	7.4-9.1	7.3-9.1	7.5-9.1
Average	8.0	8.2	8.0	8.5
Ammonia (maximum[2] for each trial) (NH_3-N mg l^{-1})				
Total	1.2	1.2	0.9	1.6
Unionised	0.17	0.07	0.09	0.05
Nitrite (maximum for each trial) (NO_2-N mg l^{-1})	< 0.02	< 0.02	< 0.02	< 0.02

[1]Readings based on continuous recordings or individual readings taken at times of day when maximum or minimum readings usually occur for each parameter.
[2]The minimum total ammonia readings for each trial were all < 0.1 mg l^{-1} and 61% of all pond total ammonia readings were < 0.01 mg l^{-1}. At these levels unionised ammonia concentrations are negligible.

Discussion

Experimental systems

The conclusions presented in Table 1 arise from research carried out in a variety of experimental systems each of which has specific advantages and limitations. Aquarium systems allow precise control of experimental variables and accurate monitoring of growth, survival, moulting and food consumption rates. The small scale of each experimental unit allows for relatively harmless forms of individual tagging, easy replication and the inclusion of expensive or inconvenient ingredients. However, the results of aquarium experiments cannot always be directly applied to practical farming situations. One general problem is that these results do not reflect the influence of other organisms which may be abundant in prawn farming ponds. Hence dietary studies in aquaria assess total nutritional requirements and do not take into account the effects that natural food items in ponds have on the required levels of nutrients, eg dietary protein, in supplementary artifical prawn feeds (Maguire and Hume 1982). Aquarium experiments at Port Stephens usually involved high stocking densities, little natural food and often restricted water exchange. School prawn growth rates in aquaria usually did not exceed 0.5g week^{-1} increase in average prawn weight even when the prawns were fed pipi meat, the best diet tested so far. In contrast growth rates in pens and 0.1 ha ponds at Port Stephens approached 1.0g week^{-1} (Table 1 and Maguire 1980). It is usually preferable to assess the nutritional requirements of rapidly growing animals.

Salinity experiments in aquaria pose quite specific problems. High survival rates (90 to 100% in each aquarium) were recorded for juvenile school prawns grown for four weeks at 25 or 30‰ but survival at 10‰ was poor (0 to 40%). Blood samples taken from these prawns indicated well developed osmoregulatory abilities in salinities of 10 to 30‰, and careful monitoring of water quality did not provide an explanation for this high mortality. In contrast, a high overall survival rate (71%) was recorded in pilot scale trial 2 despite an average pond salinity of 5.2‰ (Tables 2 and 3). Furthermore, juvenile school prawns can be collected from estuarine areas with salinities below 1‰ (Ruello 1973a). Venkataramiah et al (1974) noted similar discrepancies between natural distributions of prawns and the results of salinity experiments in aquaria. It should be noted that the other major conclusion from the salinity experiment in aquaria, ie that school prawn growth rates were positively correlated with salinity levels, has been confirmed by the results from replicated 0.01 ha ponds (Table 1) although pilot scale pond trial 2 clearly indicates that substantial growth is still possible at very low salinities (Tables 2 and 3).

Research in pens utilised sections of an individual pond as the experimental units. This allowed easy replication and partially overcame the problem of the inherent variability between ponds. Pens have several advantages over aquaria systems. They allow the prawns access to natural benthic food items and hence supplementary diets can be more usefully compared. Furthermore both high growth and survival rates can usually be obtained in pens. Because these aerated enclosures have porous mesh walls, water quality factors do not complicate the interpretation of experimental results (Maguire and Bell 1981; Maguire and Hume 1982; Maguire and Leedow 1983). Pen walls, however, present certain problems. It is not possible to investigate the effects of different forms of pond management on water quality by using pens. The pen walls support dense fouling growths which could provide additional food sources not normally available in large quantities in ponds. Fortunately this does not seem to have occurred in school prawn experiments in pens (Maguire and Bell 1981).

Free standing pools are experimental units which allow the production of natural benthic food items through fertiliser input yet also allow the effects of experimental variables on water quality to be assessed. However, pools are unlikely to experience as much wind induced water circulation as ponds. Thus experimental pools are usually aerated and this negates the effects of experimental variables, eg low water exchange rates on pool DO levels. Pools can be replicated but large differences in water quality parameters, eg plant pigments, pH and dissolved ammonia levels, did occur between replicate pools in both water exchange rate experiments. Clearly, the validity of extrapolating results from pool systems to commercial farming ponds should be enhanced as the size of each pool increases. However this raises the costs of replication and also increases the scale of the pool stocking operation. Because prawn growth rates depend on density (number of prawns per unit area), the achievement of acceptable levels of variation in average growth rates between replicates relies on relatively uniform survival rates being recorded. Thus initial mortality, eg due to excessive stress during capture or weighing and sexing procedures, must be minimised and accurately estimated for each replicate. This becomes increasingly difficult in large pool systems.

Experimental systems which utilise whole ponds as replicates should provide the type of information which is most directly applicable to commercial farming operations. Firstly, the scale of each experimental unit allows for more realistic extrapolation of production results than for smaller systems. This is particularly important if alternative pond management methods are to be assessed in terms of cost effectiveness (Maguire and Leedow 1983). Secondly, all of the factors which influence commercial results, eg natural food levels, survival rates and pond water quality and sediment condition, can vary in response to the pond management variable being tested. However, the fact that so many parameters can vary at once makes it difficult to deduce how the management variable actually influenced production results. Also, it is not always possible to minimise variation between ponds, eg in sediment characteristics or fish recruitment, that is unrelated to the management variable being tested (Maguire et al 1984). Furthermore it is logistically difficult to conduct all replicate farming trials concurrently and those carried out consecutively can be affected by temporal changes in environmental parameters, eg pond salinity (see Table 3).

Each of these experimental systems has made specific contributions to the development of methods for farming school prawns. A major problem with all of the systems is that they usually allow only relatively few aspects of a topic to be investigated at one time. Frequently the refining of a particular facet of prawn farming involves numerous considerations. Thus the substrate experiment conducted in aquaria (Table 1) assessed the physical suitability of various types of sediment for school prawns. Ruello (1973b) demonstrated that juvenile school prawns prefer to bury in fine sand but the substrate experiment showed that these behavioural preferences did not affect school prawn growth or survival rates on different substrate types. However, the suitability of a pond sediment type for a commercial prawn farm can depend on several factors including its suitability for inexpensive construction and maintenance of ponds which are not prone to water loss through porous soils. Other considerations are the tendency for the sediment to become chemically reduced, its drying rate during pond rehabilitation periods between crops, the organic content (Table 1) and soil pH levels (Simpson et al 1983). Pond sediment with a high silt content can affect product quality (pilot scale trial 3) and lead to high pond turbidity levels which can adversely affect water quality management (pilot scale trial 4) and the availability of phosphate fertilisers (Boyd 1982). Given the complexity of this single variable, it is clear that pond siting and management strategies should not just be based on studies in small scale experimental systems. Valuable contributions could be made by a variety of other inputs, eg those of experienced pond operators, soil engineers, earthmoving contractors and water chemists.

Pilot scale pond trials

Although experimentation with school prawns in small scale experimental systems has been very useful (Table 1), it was considered necessary to conduct larger scale trials (1 ha) so that production results could be used with confidence in economic analyses. Furthermore it was important to obtain experience and assess problems in the type of pond system likely to be used commercially, ie large non-tidal earthen ponds. The problems which were anticipated were those of water quality management and predator control. The Clarence River site was chosen because it was hoped that its convenience for pond stocking operations would improve survival rates in ponds. A privately owned pond was made available. Unfortunately this was in a less than ideal location in terms of the shallowness, salinity variation and silt levels in the adjoining area of Lake Wooloweyah.

The results from the pilot scale trials were usually characterised by relatively high survival rates and product quality levels but growth rates were slower than those usually recorded in pens at Port Stephens. Specific comparisons can be made with the results of school prawn trials in 19 sets of three replicate pens which were stocked with school prawns at densities ranging from 12 to 30 juveniles m^{-2}. The pens received adequate inputs of poultry or trout diets for 5 to 9 week periods during October to April.

The overall mean growth and survival results for the pens were 0.54 ± 0.04 g $week^{-1}$ (range 0.22 to 0.83) and 87.8% $\pm$ 1.8 (range 78 to 98, N = 57) compared with 0.45 ± 0.03 (range 0.40 to 0.53) and 63.3% $\pm$ 4.3 (range 52.0 to 71.0) in pilot ponds indicating that more rapid growth rates are attainable at least in pen systems.

Similarly, rapid growth rates were recorded in the initial phases of trials 1 and 4 (Fig. 2) and in some but not all trials in 0.1 ha ponds at Port Stephens (Maguire 1980). As already discussed, whole pond trials are influenced by numerous factors and hence it is difficult to ascribe the disappointing growth results from the pilot scale pond trials to one pond variable. It is noteworthy that poor growth results in pens (<0.5 g increase in average prawn weight $week^{-1}$, sexes pooled) usually occurred when the pond sediment had deteriorated to a chemically reduced state or when natural food levels were low. The latter condition was indicated by very slow growth rates in control pens not supplied with supplementary feed.

Survival rates for the pen experiments were considerably higher than for the pilot scale pond trials but pen results were not affected by initial mortality, water quality factors or predation. Furthermore all prawns within a pen could be harvested and although harvesting procedures were thorough in the pilot scale pond they could not be exhaustive. Although trial 4 was disappointing, the survival rates for the pilot scale pond trials were adequate for commercial operations and were generally higher than in the 0.1 ha pond trials at Port Stephens where large scale collection of juvenile school prawns is less convenient and initial mortality is probably higher (Maguire 1980). One major concern was the finding of stressed or moribund prawns along pond edges on several occasions during pilot scale trials 1 and 4. Usually less than 10 prawns were found on any one day and there were no consistent abnormalities in the appearance of these prawns nor aberrant water quality parameter readings on these days. The stressed prawns were usually inactive and could often be collected by hand.

Harvest results from the pilot scale pond have been utilised for an economic analysis carried out by Commonwealth Development Bank staff (Table 4). The analysis was based on the results of the first three pilot scale trials and the better harvest results from one private farm as well as the estimated costs of facilities at this farm. The assumption was made that any poorer results from commercial farming ponds were the result of inexperience and were less likely to occur in the future. Provided the major assumptions noted in Table 4 can be realised, the analysis predicts an annual return to capital of up to 27% depending largely on the value of the harvested prawns. Although this initial analysis is an extremely useful contribution to the development of a prawn farming industry in NSW, it should be understood that it is in part hypothetical and is presently under revision. Some but not all of its major assumptions are consistent with the pilot scale results. The weight of prawns stocked in the pilot scale pond trials was usually greater than 400 kg ha^{-1},

Table 4. Summary of an economic analysis by Commonwealth Development Bank staff on a northern New South Wales school prawn, *Metapenaeus macleayi*, farming operation.

Variable	Input
Key assumptions	
Weight of prawns stocked	400 kg ha^{-1} crop^{-1}
Cost of prawns stocked	\$1 000 ha^{-1} crop^{-1}
Weight of prawns harvested	800 kg ha^{-1} crop^{-1}
Unit value of prawns harvested	\$6 kg^{-1}
Value of prawns harvested	\$14 400 ha^{-1} crop^{-1}
Number of crops per year	3
Total pond area	20 ha
Capital costs (\$)	
Land purchase and pond construction	130 200
Buildings and plant	87 360
	217 560
Annual income from sales	288 000
Annual costs	
Pond stocking	60 480
Feed, fertiliser and pond preparation	43 560
Marketing and processing	53 820
Other	14 580
	172 440
Annual overheads	
Maintenance of ponds and plant	6 570
Wages	19 890
Other	8 040
	34 500
Other annual costs	
Plant replacement and owner's labour	21 290
Surplus	59 770
Annual return on capital	27%
Sensitivity analysis—	
Value of prawns (\$ kg^{-1})	Return on capital (% pa)
4	-11
5	8
6	27

depending on average initial prawn size. However, the stocking of ponds with Clarence River school prawns at a density of 20 juveniles m^{-2} would often involve less than 400 kg ha^{-1} and these live prawns can at times be purchased for \$2 kg^{-1}. An important factor is the extent of initial mortality. The estimated harvest of 800 kg ha^{-1} was exceeded in all four trials although some weight losses during cooking and marketing should be expected.

The prawns from three of the four trials were sold for an average price well in excess of the estimated value of \$6 kg^{-1}. This estimate is higher than the average price paid for school prawns at the Sydney Fish Market (\$4.25 kg^{-1} for 1982 to 1984, according to Commonwealth Development Bank staff). However, the quality of farmed school prawns has been high both in terms of size and appearance and those prawns can be harvested at times which coincide with favourable market conditions. The other major assumption made in the analysis was the farming of three school prawn crops each year. If each crop is harvested approximately ten weeks after stocking, it should be possible to farm three crops each year provided that juvenile prawns can be collected for restocking purposes at appropriate times. The amount of time required for pond rehabilitation between crops would also have to be minimised or farming periods would extend into cooler months with resultant reductions in water temperatures (Wolf and Collins 1979) and hence growth rates (Table 1). Other important assumptions implicit in the analysis are low water exchange rates (supported by water exchange rate experiments in pools, Table 1) and relatively low land purchase and pond construction and maintenance costs. However, no provision has been made for equipment for aerating ponds or for controlling predation by cormorants. The experience gained during the pilot scale pond trials suggests that while careful monitoring of pH and DO levels and appropriate inputs of fertiliser can minimise the need for aeration equipment, it is occasionally necessary. Aeration devices are widely used in pond systems in other countries (Boyd 1982). Similarly, predation by cormorants appears to have been far more serious in commercial school prawn ponds than in the pilot scale trials (F. Roberts[1], pers. comm.) and hence deterrant equipment would probably be necessary for at least some farming sites.

Commercial prospects in NSW

Approximately 130 ha of commercial prawn farming ponds (3 to 9 ha pond^{-1}) have been at least partially constructed in northern NSW and several additional applications for prawn farming licences have been received. Should continued growth in this industry occur, several limitations are likely to become apparent. The collection of juvenile school prawns from the Clarence River has not proved to be an ideal method for stocking ponds for several reasons including fluctuations in availability and price of juvenile prawns, and occasional excessive mortality of prawns during and soon after stocking. The need for a hatchery reared supply of juveniles for pond stocking purposes is likely to become more acute as the number of farms increases. In addition, the marketing advantages that high quality farmed school prawns provide, especially in terms of being harvested to suit peak market conditions, would probably decline if very large amounts of farmed prawns were sold. For a major industry, export outlets may be necessary and a small prawn such as the school prawn would generally not be suitable. Thus it is likely that an expanded industry would need to be based on the farming of a larger penaeid species using juveniles reared in privately owned hatcheries. A large tropical penaeid species with proven aquaculture potential, eg *Penaeus monodon* (New and Rabanal 1985) could be farmed in ponds in NSW although it is likely that seasonal variation in pond water temperatures (Maguire and Bell 1981) would considerably restrict the growing season for this tropical species. Alternatively a large penaeid species endemic to more temperate Australian waters, eg the eastern king prawn, *Penaeus plebejus,* (Ruello 1975), could be farmed. Except for research on induced maturation and spawning (Kelemec and Smith 1980, 1984) little is known of the aquaculture potential of this species.

The Fisheries Division, NSW Department of Agriculture, takes a cautious view of the prospects for a prawn farming industry in this state. The results of the economic analysis discussed in this paper are heartening, but the major assumptions will have to be realised consistently on a commercial scale. Furthermore, the introduction of hatcheries and the farming of penaeid species other than school prawns would entail further economic analyses. Also there are few comparable examples of profitable, large scale, marine prawn farming industries in western temperate areas (Wickins 1982). At least in the short term, commercial prawn farming in NSW is likely to be best suited to investors who can afford to take a pioneering role or who cannot find alternative uses for existing land holdings.

Future research

There is a need for research into methods for increasing the amounts of natural food items within prawn farming ponds without leading to excessive deterioration of pond sediment conditions. This will require a more detailed understanding of nutrient dynamics in ponds.

Commercial producers in NSW are likely to diversify into the farming of larger temperate penaeids, and more aquaculture research on these species, eg eastern king prawns, seems warranted. If larger species are to be grown to export sizes, diets which are more nearer nutritionally complete will have to be developed as grow-out times and biomass levels in ponds increase.

The priority given to aquacultural research on school prawns is likely to depend on its suitability for pond culture at much higher densities than those used in the pilot trials (Table 1) and on interest from farmers particularly if ponds are constructed in lower salinity areas which would probably be unsuitable for eastern king prawns (Dall 1981).

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Appendices

Papers and posters

Papers

Bowen, B.K. and D.A. Hancock
Review of penaeid prawn fishery management regimes in Australia

Buckworth, R.C.
Preliminary results of the western Gulf of Carpentaria prawn fishery monitoring study

Burford, R., C. Esslemont and D. Murray
Northern prawn fishery—investment analysis and optimum deployment of fishing effort

Campbell, D.
Management of the northern prawn declared management zone and the enforcement of individual catch quotas

Carrick, N.
The biological basis for optimisation of harvesting strategies in Spencer Gulf prawn fishery, South Australia

Carter, D. and G. Kesteven
The conciliation of economic intention and conservational concern. The role of industry

Chopin, F.
The application of model tests on prawn trawls to fullscale trawls

Coles, R.G. and W. Lee Long
Preliminary studies of juvenile prawn biology and nursery ground characteristics in the south-east Gulf of Carpentaria

Crocos, P.J.
Appraisal of some factors relevant to the development of penaeid prawn population reproductive models

Dall, W.
A review of prawn biological research in Australia, 1974-1984

Dall, W. and D.M. Smith
Nitrogen metabolism in the tiger prawn, *Penaeus esculentus*

Dredge, M.C.L.
Hypotheses on the life cycle of the banana prawn *Penaeus merguiensis* de Man in the south-east limit of its distribution

Garcia, S.
The understanding of penaeid shrimp fisheries: A progress report

Gorman, T.B. and K.J. Graham
New South Wales deepwater prawn fishery research and development

Haysom, N.M.
Review of the penaeid prawn fisheries of Australia

Hill, B.J.
The effect of tides and temperature on duration and emergence of the tiger prawn *Penaeus esculentus*

Hundloe, T.J.
Reassessing the financial and economic health of DMZ fisheries

Hyland, S.
The Moreton Bay beam trawl fishery

Kailis, M.G.
Collaboration—An alternative to annihilation by regulation

Kelemec, J.A. and I. Smith
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Kirkwood, G.P.
Fitting stock production models to prawn catch and effort data

Lawrence, A.L.
Shrimp culture in the western hemisphere

Lawrence, A.L. and J. Wilkenfeld
Studies on nutritional requirements of penaeidean shrimp larvae using a new small scale experimental system

Leary, T.R.
Review of the U.S. Gulf of Mexico management plan for shrimp

Maguire, G.B. and G. Allan
Development of methods for fattening juvenile school prawns *Metapenaeus macleayi* in estuarine ponds

Montgomery, S.S.
Movements of the eastern king prawn *Penaeus plebejus* along the Australian east coast

Moriarty, D.J.W.
Detrital food chains in aquaculture

Nell, J.A.
Microparticulate diets for aquaculture

New, M. and H.R. Rabanal
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Num, D.
The northern prawn database on the Australian Fishing Zone information system

Owens, L. and J.S. Glazebrook
The biology of bopyrid isopods on commercial penaeid prawns

Paynter, J.L., D.V. Lightner and R.J.G. Lester
Viral diseases of juvenile prawns

Penn, J.W. and N. Caputi
Spawning stock-recruitment relationships and environmental influences on the tiger prawn (*Penaeus esculentus*) fishery in Exmouth Gulf, Western Australia

Poiner, I.R. and A.N.M. Harris
The effect of commercial prawn trawling on the demersal fish communities of the south-eastern Gulf of Carpentaria

Potter, M.A. and M.C.L. Dredge
Deepwater prawns off southern and central Queensland

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Pyne, R.R. and N. Carroll
Potential for aquaculture in Australia

Robertson, J.W.A.
The biology of commercial prawn species in the Mornington Island fishery in the south-east Gulf of Carpentaria

Rothlisberg, P.C., C.J. Jackson and R.C. Pendrey
Distribution, abundance and dispersal of penaeid larvae in the Gulf of Carpentaria

Rothlisberg, P.C., D.J. Staples and P.J. Crocos
The life history of *Penaeus merguiensis* in the Gulf of Carpentaria

Salini, J.P. and L.E. Moore
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Maximising value per recruit in the Gulf of Carpentaria banana prawn fishery

Sribhibhadh, A.
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Staples, D.J.
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Staples, D.J. and D.J. Vance
Habitat requirements of juvenile penaeid prawns and their relationship to offshore fisheries

Stratton, J. and M.R. France
Fleet operations and management

Wallner, B.
The influence of coastal geomorphology upon patterns of recruitment, catch and spawning behaviour in the western king prawn, *Penaeus latisulcatus,* fishery of the South Australian west coast

Warburton, K.
The distribution of prawns in differentially-disturbed habitats

Wassenberg, T.J.
A study of the fate of otter trawl by-catch in Moreton Bay

Posters

Carter, D.
Saudi Arabian prawn fishery

Craik, W. and S. Driml
Great Barrier Reef Marine Park Authority's role in research and management of prawns in the Great Barrier Reef region

Frusher, S.D.
Migration and effect of vinyl streamer tags on the banana prawn *Penaeus merguiensis* in the Gulf of Papua, Papua New Guinea

Glaister, J.P.
The Melville-Essington prawn fishery

Grey, D.L., W. Dall and A. Baker
A guide to the Australian penaeid prawns

Heales, D.S., H.G. Polzin and D.J. Staples
A provisional key to Australian postlarval *Penaeus* species

Jackson, C.J.
The effects of salinity, temperature and intra-moult growth on the morphology of larvae of *Penaeus semisulcatus*

King, M.G.
Fisheries potential and life-history patterns of tropical deepwater prawns

Smith, D.M.
A method for moult staging the tiger prawn *Penaeus esculentus* Haswell (using microscopic examination of the setae of the uropods)

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