FIRDC Final Report (Grant number 90/4)

1) Project objectives and the extent to which they were achieved.

The fishery for eastern king prawns is based on a major penaeid prawn resource shared between New South Wales and Queensland. Because the species is migratory and the resource shared between two states, the fishery offers some unique research and management challenges. The objectives of this twelve-month pilot project were to develop common methodologies for population parameter estimation for eastern king prawn populations in eastern Australia and to develop a common strategy to evaluate and recommend management measures for the fishery in Queensland and New South Wales.

Specific objectives of the research programme were to:

a) trial the introduction of a trawl fishery logbook programme in New South Wales coastal waters and undertake a temporal-spatial analysis of catch and effort for the eastern king prawn fishery in Queensland waters from the compulsory logbook database (CFISH) recently introduced (1988) in that State.

b) determine the population structure, particularly the size class composition and sex ratios of commercial catches from different locations.

c) to determine the geographic origins of eastern king prawns trawled from deep, offshore grounds in the northern limits of the fishery.

d) to describe maturation and the reproductive dynamics of eastern king prawns. To determine whether there is latitudinal variation in spawning activity over the relatively large geographic distribution of the species.

2) Research results and benefits.

a) Logbook programmes.

Staff from New South Wales Fisheries successfully trialled two logbook types for a month using commercial vessels based at major ports along the New South Wales coast. The data sheets were similar in format to those used in the Queensland CFISH logbook programme.

One sheet was shot by shot, whilst the other required a single entry of catch and effort per night. A prototype logbook, which incorporates the comments of industry, is currently being drafted. The first version of the logbook will be tentatively introduced to the New South Wales fleet by the end of 1992. This will result in a database which quantifies catch and effort for eastern king prawns over the entire distribution of fishery.

Analysis of Queensland's recently introduced compulsory logbook database shows that eastern king prawns are trawled commercially from the New South Wales - Queensland border to a latitude approximating Mackay (21° 30'S). About 1100 tonnes and 1500 tonnes of eastern king prawns were trawled from Queensland state waters in 1988 and 1989, respectively.

Table 1. The most productive logbook grids (30'x30') as determined from the Queensland compulsory logbook (CFISH) database, general description of grid locations and the annual landings of eastern king prawns, *Penaeus plebejus* associated with each area. (Data are taken from a CFISH summary file produced on July 13, 1990).

CFISH Logbook Grids	General Area Description	Metric Tonnes 1988	Metric Tonnes 1989
X39	Tweed Heads, Goldcoast	96	60
X38	South east of Stradbroke Is.	153	190
W37	Within Moreton Bay (Non-specific, mixed species fishery)	~ 200	~ 300
X36	Directly east of Moreton Is.	76	135
W36,X36	East of Caloundra to approx. 200m	239	302
X35	Depths > 100m east of Gympie	84	77
W34,W33	Tin Can Bay and east of central Fraser Is.	130	224
V30	Lady Elliot Is., Lady Musgrave Is.	33	27
W26,W27	East and South east Swain Reefs	80	102

In shallow areas (less than about 30m), particularly Moreton Bay, eastern kings are a component of mixed prawn species fisheries. In deeper parts of the species distribution the fishery is largely monospecific and effort is targeted at eastern king prawns. The most productive areas from the Queensland coast, as determined from the 30'x30' CFISH logbook grids, occur in the south east corner of the State (Table 1).

Seasonal variation in catch rates of eastern kings is quite marked in the shallower parts of the fishery. Regular lunar monthly research sampling of eastern king prawns in Moreton Bay indicates that abundance and recruitment to the fishery peak in October-November each year (Figure 1) with little interannual variation. High catch rates of eastern king prawns occur just outside "bottle-neck" areas, such as the Southport Bar, Amity Point and the Tin Can Bay Bar from November to January each year as sub-adults migrate out of the embayments. Some of these areas may be associated with growth overfishing of the resource. Analysis of the CFISH logbook data for 1988 and 1989 suggests that seasonal variation in catch rates in deepwater areas are not as marked as those associated with the shallow water parts of the fishery. There was no seasonal pattern in catch rates of prawns taken in the northern parts of the fishery associated with the Swain Reefs. Where seasonal variation occurs in deep water grounds, the peaks lag shallow water catch rate peaks by two to five months.

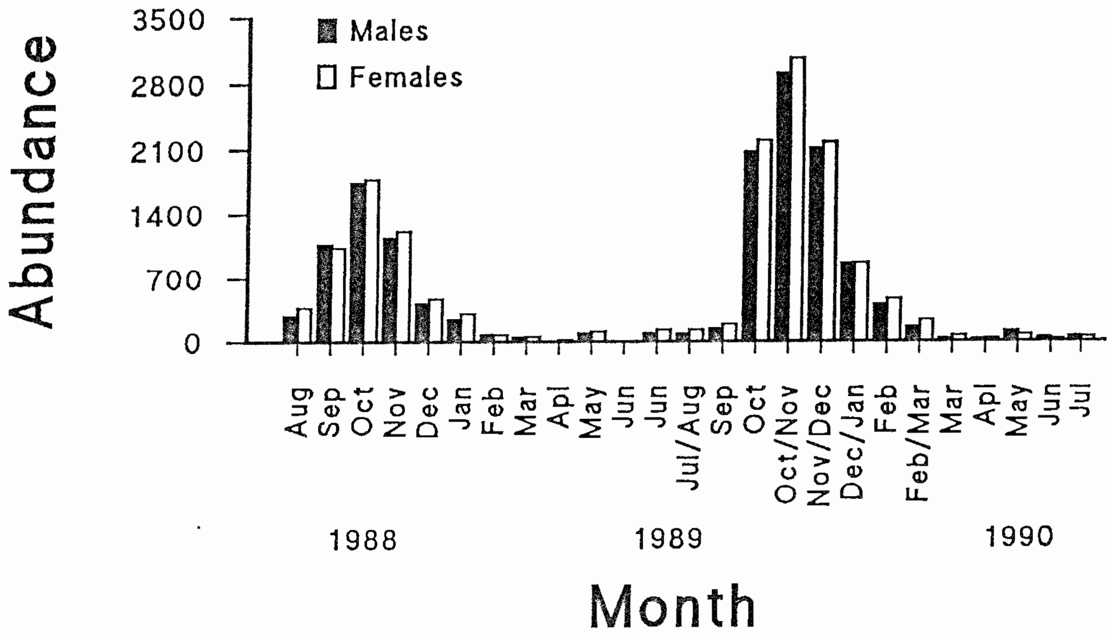


Figure 1. Seasonal variation in abundance of eastern king prawns in Moreton Bay. Abundance for each lunar month was based on the total number of king prawns trawled from nine sampling sites at the same speed and with the same trawl gear each month.

b) Population structure

Sampling programs carried out by research staff from both Queensland and New South Wales have generated current information on the population structure of commercial catches of eastern king prawns from a very broad distribution covering all of the major trawling regions. New South Wales Fisheries' staff, acting as observers on vessels, randomly collected 150 prawns from the catch for four nights per month, at four locations; Port Stephens, Coffs Harbour, Clarence River and Ballina. These samples were transported in ice to the Fisheries Research Institute (Cronulla) where the information on size and sex composition was collated. Similarly, staff from the Queensland Department of Primary Industries have been obtaining random commercial catch samples from areas east of Moreton Island, Mooloolaba, Wide Bay, Lady Elliot Is. and the Swain Reefs on regular lunar monthly periods for about 18 months.

c) Migration Patterns.

The geographic origins of eastern king prawns trawled from offshore, deepwater grounds are largely unknown, particularly for those stocks trawled from such areas as the Swain Reefs. These stocks may recruit from Tin Can Bay/Wide Bay, Moreton Bay or more southern waters off New South Wales. Tag-recapture experiments were deployed as a means of studying migration of eastern king prawns in the northern limits of their distribution (Table 2).

Table 2. Numbers of tagged eastern king prawns released at certain locations during part of the 12 month pilot study.

AREA	NUMBER OF TAGGED PRAWNS	DATE
Within Moreton Bay	1,081	9-10 November 1990
Off Moreton Island	1,575 1,650	13-15 November 1990 14-16 February 1991
Wide Bay	4,750	21-27 November 1990
Hervey Bay	50	23 November 1990

From 9th November, 1990 to 16th February, 1991 approximately 9,100 eastern king prawns were streamer-tagged and released in commercial trawl grounds in Moreton Bay, off Moreton Island, Wide Bay and Hervey Bay (Figure 2).

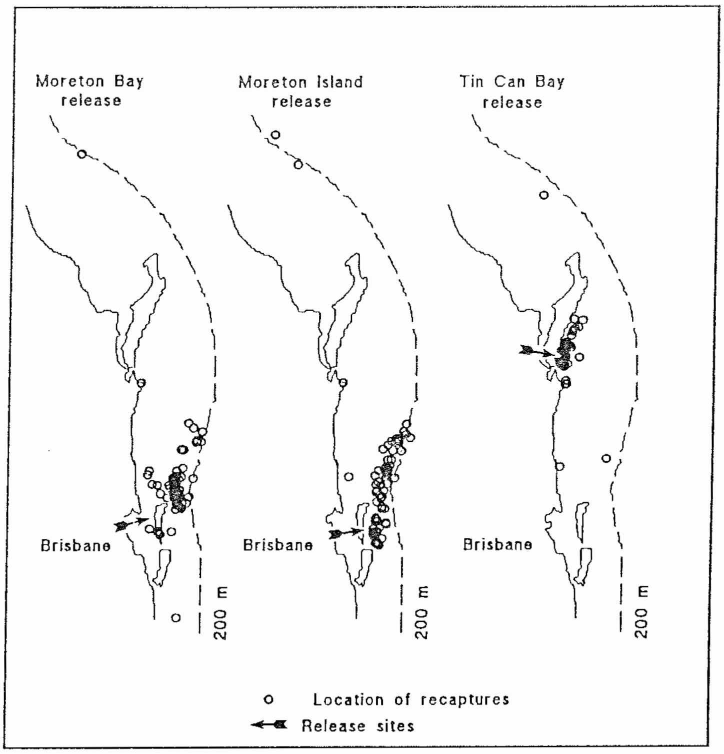


Figure 2. Release and recapture sites for tagged eastern king prawns, *Penaeus plebejus*.

To date, 1404 tagged prawns have been recaptured by commercial fishers, with recaptures from the Tin Can Bay/Wide Bay releases being about four times those from the Moreton releases. These results imply that fishing mortality on eastern king prawns is much greater in the Tin Can Bay/Wide Bay region than in the Moreton region. The distances travelled and migration speeds for eastern king prawns released in Tin Can Bay/Wide Bay appear to have been much lower than prawns tagged in the Moreton region. However, this may be due to an absence of fishing effort in waters directly north and/or east of Tin Can Bay/Wide Bay. More definitive statements on the migration patterns should not be made until the distribution of fishing effort has been determined through logbook analysis. To date, only one of the tagged prawn has been recorded from the Swain Reefs, an area approximating the northern limits of the fishery. This prawn was tagged off Moreton Island on 14th November, 1990 and migrated northward 275 nautical miles over 446 days and was recaptured by the fleet fishing at the Swain Reefs.

d) Reproductive biology.

Staff from both Queensland and New South Wales have been working in collaboration and attempting to standardise methods in order to make a quantitative statement about the reproductive dynamics of eastern king prawns throughout the very wide geographic range of the fishery. The reproductive biology of eastern king prawns is almost entirely unknown. It has been hypothesised that the migration along the east Australian coastline, (among the most significant for crustacea), is associated with spawning. The hypothesis that spawning occurs at different latitudes along the east Australian coastline is currently being tested.

The work has resulted in reproductive samples being obtained on a regular basis from a significant proportion of the known geographic distribution of the fishery. Ovary weights have been obtained from all of these samples and gonad indices have been calculated. Ovary tissue samples have been obtained from all female prawns. A collaborative effort was made to produce a standardised method for histologically staging maturation. This method has been used by staff from both Queensland and New South Wales in order to ensure that consistency in our approach to studying the reproductive biology of eastern king prawns.

The Queensland DPI R/V Deep Tempest has been deployed for approximately three nights per lunar month over the duration of the study obtaining samples of eastern king prawns from three depths (35m, 90m, and 200m) along a transect located east of Moreton Is. The function of this work was to study the influence of depth on adult prawn maturation; specifically any affects on ovary histology, weight or spermatophore insemination.

Officers from both New South Wales Fisheries and the Queensland Department of Primary Industries have also been obtaining regular random samples of eastern king prawns from fishermen trawling in certain areas for the duration of the project. These include areas near the Swain Reefs, Lady Elliot Is., Tin Can Bay, Mooloolaba, Port Stephens, Coffs Harbour, Clarence River, Ballina, Brunswick Heads, Crowdy Heads and Newcastle. These samples are approximately five kilograms in weight and data recorded includes location, month, sex ratio, ovary weight, ovary histology, moult stage and spermatophore presence. A database containing information on the reproductive status of eastern king prawns is currently being compiled for both states and eventually this data will be combined to provide a comprehensive coverage of the temporal and spatial spawning activity of eastern king prawns throughout most of their known distribution.

Preliminary results suggest that female eastern king prawns begin mating at approximately 30 mm CL (Figure 3). The proportion of females with spermatophores increases over the size range 30 mm CL to 44 mm CL and approximately 75% of females larger than 45 mm CL are inseminated. New South Wales staff have also undertaken a cost benefit analysis on a subset of data to ascertain the optimal sample size needed to study the spatial and temporal distribution of spawning female eastern king prawns. Image analysis techniques are also being trialled as an objective method for determining spawning periods, by way of measuring change in the modal sizes of oocyte diameters.

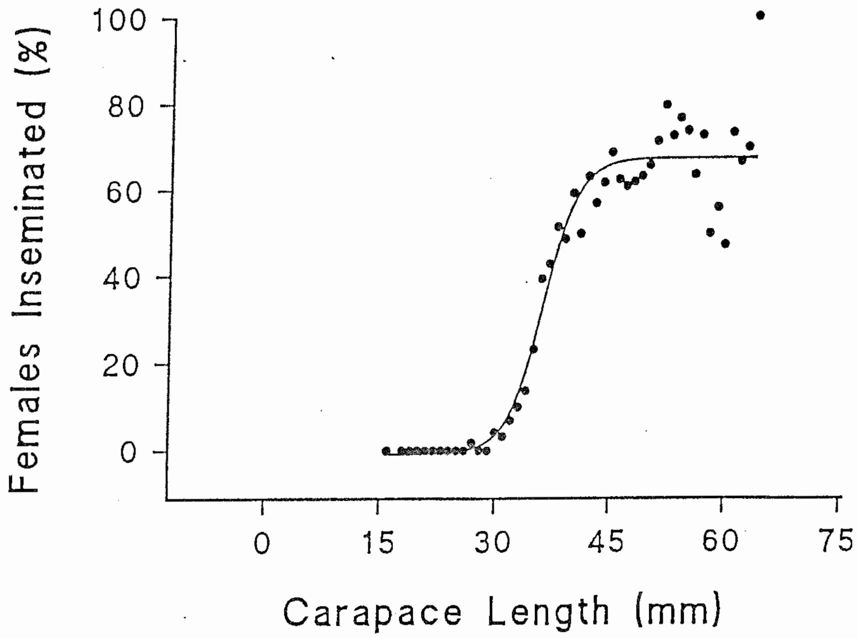


Figure 3. The proportion of inseminated female eastern king prawns, *Penaeus plebejus* in different size classes.

Histological results suggest that the majority of spawners are in the 39 mm CL to 57 mm CL size class range (Figure 4), (or 10/20 count per kilogram). A significant proportion of the sampled females are larger than this but have not been found in the ripe condition. Consequently, larger females may not contribute to the spawning stock.

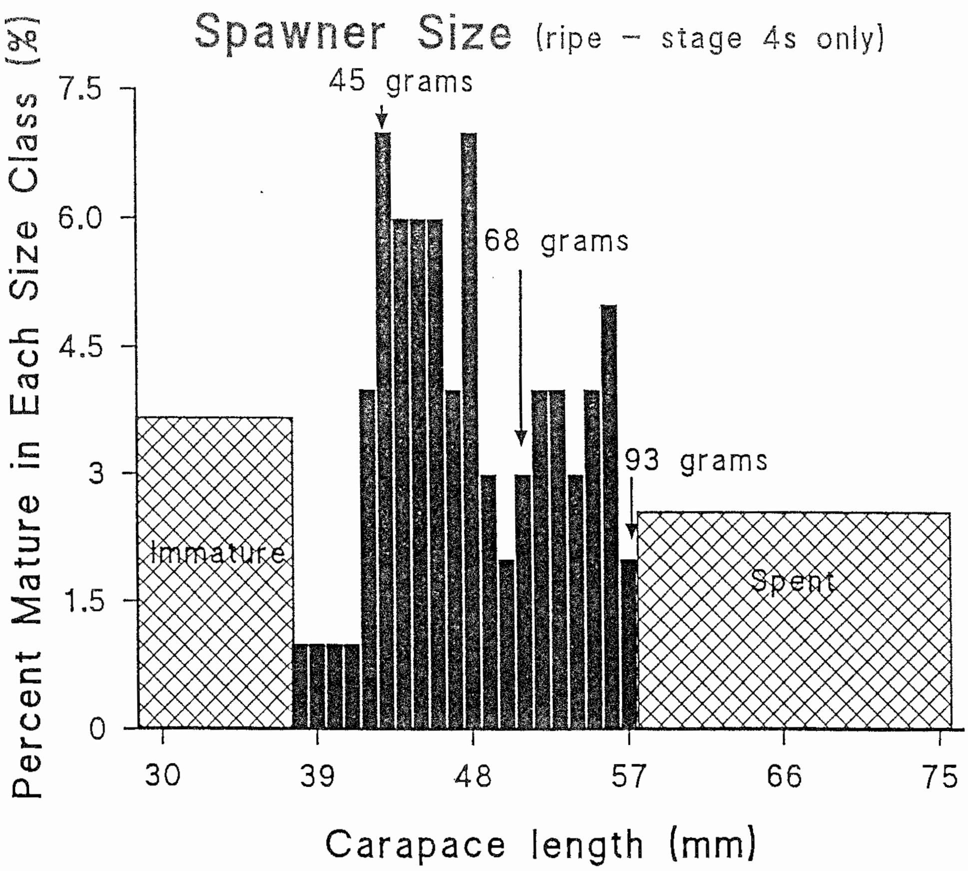


Figure 4. Size class range of eastern king prawn, *Penaeus plebejus* spawning stock (based on histological examination of ovaries.)

3) Difficulties encountered.

Most of the difficulties encountered were due to the nature of the species. Eastern king prawns are very mobile and the fishery is undoubtably the largest (geographically) for penaeid prawns in Australia. It is difficult to obtain representative samples of the population for size class analysis, determining recruitment patterns or for reproductive studies by deploying one or two research vessels at any one point in time. Samples from commercial vessels are required for these purposes and this requires a certain level of dependence on commercial fishermen. Failure of fishermen, who have commercial obligations, to provide samples from given areas at given times is inevitable and "gaps" or "holes" occur in the data.

4) Recommendations for further research.

Although FIRDC funding for the work has ceased there are aspects of the research that are continuing.

a) Tagged prawns continue to be returned and consequently, the database on growth and migration of eastern kings in their northern distribution is being continually added to. These late tag returns are of particular importance because the prawns have been at liberty for extended periods and have the opportunity to display long-term behavioural traits. In recent weeks a single tagged eastern king prawn was returned from the Swain Reefs. The prawn was tagged off Moreton Island and hence the results suggest that at least part of the Swain Reefs stocks recruit from the Moreton region. The origins of these deep water stocks are still largely unknown. We will be seeking funding for more research on delineating the stock structure of the eastern king prawn fishery, particularly in identifying the geographic origins of deep water stocks. We propose to study the concentration of certain trace elements, compounds and isotopes retained within the flesh of eastern king prawns from different nursery areas and estuaries from Australia's east coast.

b) It was also felt that 12 months of data on the temporal and spatial reproductive dynamics of eastern king prawns was too short. This work, therefore, is being continued in both States and is being funded in Queensland by the State's Fish Management Authority. All fishermen concerned are prepared to continue providing samples, as they have been since September 1990, until August 1992.

c) The majority of commercial trawlermen fishing for eastern king prawns in deepwater do so on, or close to, the full moon lunar phase. There is evidence to support the hypothesis that lunar phase influences abundance or catchability, moulting and reproduction. We propose to test these hypotheses and will be seeking funding from FIRDC in the near future.

5) Application of the results to industry.

Results from the experiments and analyses of the work are directly relevant and applicable to understanding and managing the eastern king prawn trawl resource. The trialing of a logbook for the New South Wales fleet and the tentative introduction of a logbook in New South Wales will mean that catch and effort data will be obtained for the entire eastern king prawn fishery for the first time.

The recapture of prawns tagged in the Moreton region has confirmed the general northerly migration described from previous studies. Speed of migration and distance travelled by prawns tagged in Tin Can Bay/Wide Bay was relatively low compared with the Moreton region releases. This may indicate that migratory behaviour in the Tin Can Bay/Wide Bay populations is reduced compared with more southern populations, or alternatively, it may simply reflect the distribution of fishing effort in space and time. Without undertaking a comprehensive analysis of the distribution of fishing effort during the tagging study there can be no definitive statement made pertaining to this apparent absence of migratory behaviour in populations from Tin Can Bay/Wide Bay. This will be undertaken as soon as all of the fishing effort for this period is submitted to the Queensland Fish Management Authority and entered into the CFISH database.

The high rate of recaptures from the Tin Can Bay/Wide Bay releases (around 27%) suggests that populations of eastern king prawns in that area may be more vulnerable to overfishing than those from the Moreton region.

There is evidence to support the possibility of recruitment overfishing in eastern king prawns. This evidence is based on: a) results from a recent beam trawling study in Moreton Bay; and b) from comparing old logbook catch rates from the 1970's with new CFISH logbook catch rates. If recruitment overfishing is occurring it is likely to be the result of excessive fishing effort targeted at spawning stocks of eastern king prawns. Results from this study have provided basic information on the size at maturation, size at spawning, and information on the temporal and spatial components of the spawning stock for the first time for eastern king prawns. This information is critical in order to form a concept of the eastern king prawn spawning stock and if a reduction in fishing effort on spawning stock is ever to be considered for the fishery.

6) Scientific papers or publications resulting from the project.

a) Two posters were presented at the 1991 Australian Marine Science Association Annual Conference, held at the University of Queensland, July 8-11th. They were entitled

"**Observations on the reproductive dynamics of eastern king prawns *Penaeus plebejus* in south east Queensland waters**" by D.J. Green and A.R. Butcher.

and

"**Fauna on two *Zostera capricorni* beds in Moreton Bay, Queensland.** by J.M Masel, A.J. Courtney and D.G. Smallwood

b) A paper was also delivered at the 1991 Australian Marine Science Association Annual Conference entitled

"Preliminary results on long term changes in the Moreton Bay mixed prawn otter trawl fishery". by N. Trainor, N. and A.J. Courtney.

c) Further publications intended for science journals are in preparation.

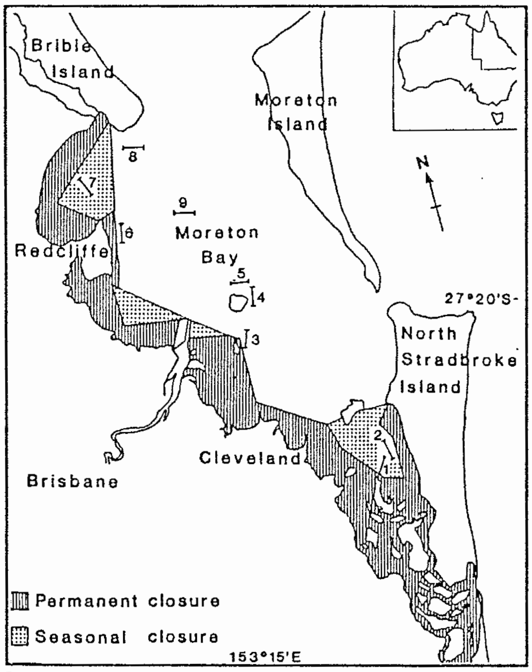
d) Much of the data obtained throughout the project has been presented to fishermen at Queensland Commercial Fishermen Organisation (QCFO) meetings in Mooloolaba and Bundaberg during 1991. A newsletter (Appendix 1), based around these research results has also been compiled and has been forwarded to all fishermen who returned tagged eastern king prawns, QCFO branch chairpersons, cooperatives and processors.

THE SOUTHEASTERN PRAWN HERALD

Volume 1. September 1991.
Published by the Southern Fisheries Centre, Deception Bay, Queensland Department of Primary Industries

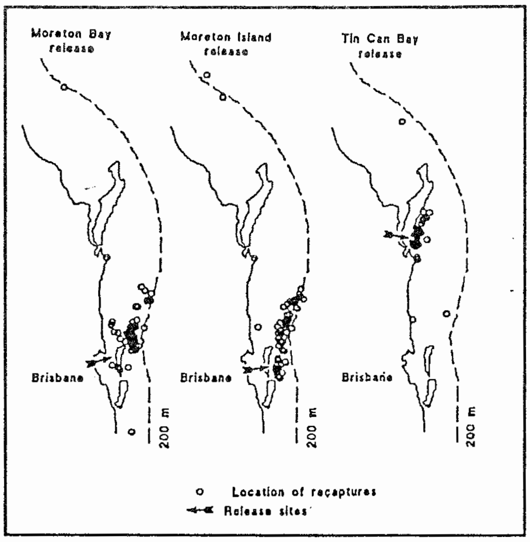
Prawn research ... what for?

We at the Southern Fisheries Centre have a long history of research on prawn biology and prawn fisheries. For the last 20 years scientists, from CSIRO and QDPI have put a considerable amount of effort in their prawn research out of the laboratories located at Deception Bay. Some of you may have been around when the pioneering research on eastern king prawns was carried out twenty years ago. Today our QDPI team of biologists and technicians is still searching for answers to some of the questions about prawn biology which still remain to be answered.



Moreton Bay prawn seasonal closures and sites sampled in QDPI study

You may have heard we were recently involved in a two year program aimed to evaluate the prawn seasonal closures inside Moreton Bay. Results from that research greatly increased our understanding of the effect of these seasonal closures on prawn production of the Moreton Bay fishery. Very soon the final report which summarises the results of that program will be released to the general public as a QDPI publication.



Locations of tagged prawn releases and recaptures

Today the major focus of our prawn research has shifted to the eastern king prawn fishery inside and outside Moreton Bay. Such research has focused this year on describing reproductive dynamics, offshore migration and catch and effort distributions from the NSW border to the Swains. The main aim of this newsletter will be to present to you results of this and any other research carried out at SFC on prawn fisheries. We hope this will become a vehicle of communication between us the scientists and you the industry.

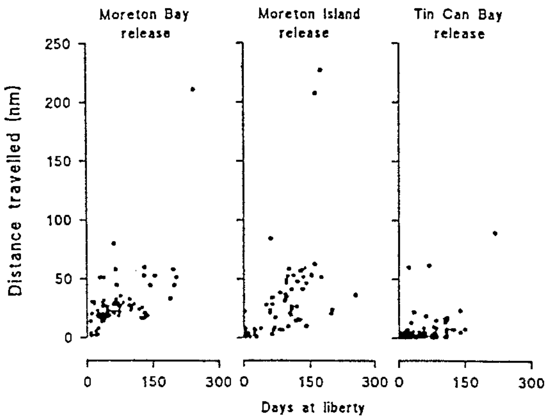
1990/91 eastern king prawn study

In July 1990 staff from SFC-QDPI and the NSW Department of Fisheries started a twelve month pilot study on the population and fishery dynamics of eastern king prawns.

The cooperative research was funded by FIRDC and QFMA to develop new methodologies for assessing the status of eastern king prawn stocks off the east coast of Australia. Research on eastern king prawns has focused on aspects of the reproduction, settlement and migration.

Samples for reproductive studies have been collected from fishers along the coast from the Clarence river in NSW to the Swains reef in Queensland. QDPI has also conducted regular samples on board their R.V. Deep Tempest offshore from Moreton Island.

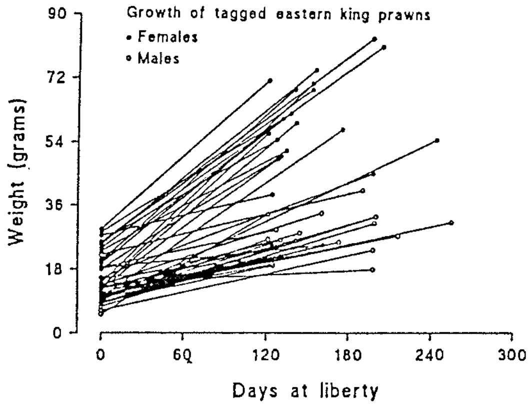
QDPI carried out a tagging experiment in late 1990 and released about 10,000 tagged prawns in three sites on the eastern and western sides off Moreton Island and the eastern side off Fraser Island. In NSW the Department of Fisheries has been conducting gear trials to determine the abundance of juvenile eastern king prawns in offshore grounds.



Movement rates of recaptured prawns

1990-91 Tagging

Some of you have asked, why did we tag eastern king prawns again this last year given that CSIRO and QDPI did the same thing already twenty years ago?. It is a good question. The truth is that the fishery has expanded and possibly intensified since that time. More boats are fishing in deep water and a few are doing it as far as the Swains reef. We hope that this tagging will provide information into the present pattern and intensity of fishing operations as well as information on prawn migration in the northernmost areas occupied by the stock. Out of the 10,000 eastern king prawns released 5,000 were released in the Tin Can Bay area off Fraser Island. About 800 were also released in Moreton Bay and the other 4,200 off eastern Moreton Island, north of the Amity Bar.



Growth of tagged eastern king prawns

1,350 prawns have been recaptured and reported by fishers from the Queesland fleet. Out of these, 1,000 had been released at Tin Can Bay, 250 off Moreton Island and 100 within Moreton Bay.

Most prawns recaptured seem to have travelled northward and to deeper grounds, and very few moved southward. Prawns released in Tin Can Bay were caught closer to their release site than the other two groups of tagged prawns. This may be because the prawns did not move very much but more likely it is because there is not much fishing immediately north of Fraser Island.

Detailed analysis of prawn movement has not yet being completed. A few of the prawns have been already captured off Lady Elliot and Lady Musgrave islands. Measurement of tagged prawns at release and upon recapture has allowed us to get growth data. Eastern king prawn females which remained at liberty for more than three months trebled their weight, however males only doubled their weight in the same period.

Tagging Lottery

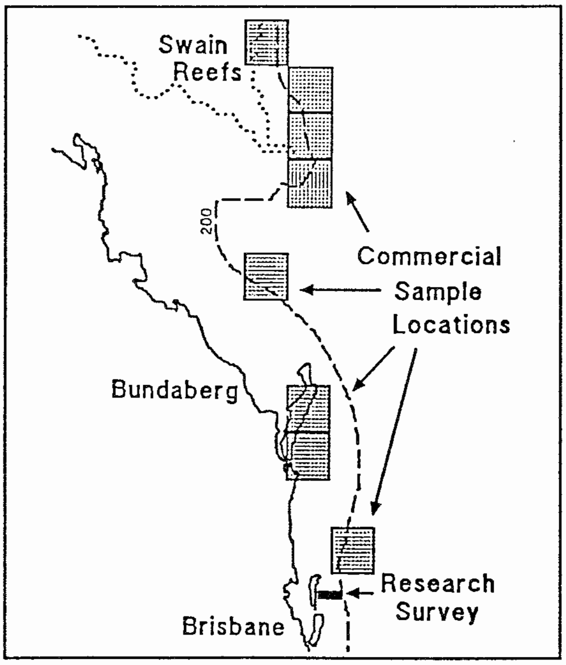
The 5th of July 1991 was a day where a couple of lucky fishers got their efforts rewarded with two great prizes. Mr. Peter Bannister of Mooloolaba won a Windsurfer (first prize) and Mr. Kevin Lee from Tin Can Bay won a colour T.V. Thanks to all of you who came to share the excitement at SFC and to all that contributed recaptured tags. You made it all possible!!

Late recaptures

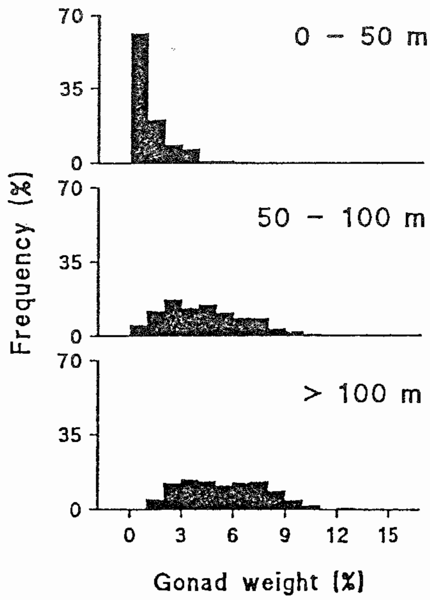
Although the lottery is over there are still prawns with tags out there. Some of you are still bringing them in, and we want to make sure that everybody contributes. These late recaptures are probably the most valuable of all, because prawns which have been at large for very long periods have usually moved far away from the release site.

Reproductive dynamics study

Since September 1990, each lunar month, we have sampled at three different depths (15, 45, 95 fathoms) on grounds offshore from Moreton Island. We have also collected samples from cooperating fishers along the Queensland coast (Mooloolaba ., Tin Can Bay, Lady Elliot, Swains reef). We hope to establish basic aspects of the reproduction of eastern kings such as when and where do they spawn, at what size and whether there are differences in reproductive activity along the coast. These questions are very important given the lack of information on eastern king reproduction.



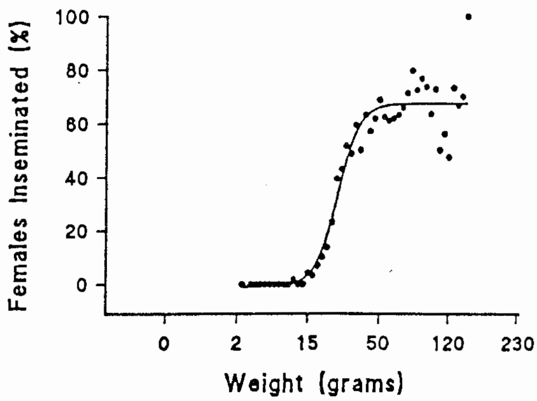
Sample locations for reproductive study



Female gonad indices at different depths

Preliminary analysis of the reproductive data collected up to date suggests that female eastern kings do not mature up or get inseminated by males until they reach a size of about 25 grams. Up until that point their ovary weight is less than two percent of their total body weight. Ripe females on the other hand may have an ovary weight of about 10 percent their total body weight.

We have also found that mature eastern king females are only abundant in waters deeper than around 50 meters. This is consistent with observations elsewhere which suggests that maturation only occurs once the animals move out of the estuaries towards the deep ocean waters.



Insemination of female kings

Who's who in our Prawn Group

Presently the prawn group at SFC is three persons strong. Many of you may know Debbie Green, she is the one that was in charge of all the liaison work in our project, she sent you the lottery stubs, picked the recaptured prawns up, collected prawn samples from some fishers etc... She also did most of the survey work, sample preparation and managed the tagging database. Unfortunately Debbie is leaving us at the end of the month for a better life away from prawn trawlers (is there one?). We will miss her. The second person you may know is Tony Courtney. Tony has been to several trawl meetings and has met some of you out there in the real world. Tony is our specialist in prawn reproduction and has also participated in last years tagging, and survey work. Tony has previously worked on prawn fisheries in Moreton Bay and Townsville. The last person in the Prawn Group is me, David Die. I am the number cruncher and population dynamics specialist. I have only been at SFC for one and a half years but had previously worked on other prawn fisheries of the Atlantic ocean.

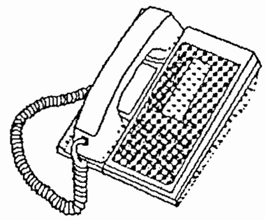
Future Research

This summer we are planning an experiment within Moreton Bay which will try to estimate survival of small (less than 200 count) king and greasy ("bays") prawns. We will be tagging a relatively small amount of them but you may catch some. Tags will be smaller than the ones you are used to (so we can tag juvenile prawns) but of the same shape and colour. Please if you find any give us a ring. At the same time we will conduct experimental fishing in the same area of Moreton Bay to determine the efficiency of commercial prawn nets (the proportion of prawns within the path of the trawl net which enter the cod-end). More details on the next issue of the newsletter.

Cooking: "Garlic prawns"

500 grams of large peeled prawns, 1/4 cup olive oil, 8 garlic cloves, 2 tbs parsley, 4 tsp lemon juice, salt and pepper.

Peel and clean the prawns, put oil on a deep pan and heat it. Add garlic and cook until light golden, add prawns, lemon, salt and pepper. Cook until prawns are done, then add parsley and serve hot.



Prawn hotline

If you want a copy of our newsletter, have any comments about our research results, or have recaptured tagged prawns please contact any of us at:

THE PRAWN GROUP
S.F.C., QDPI
P.O. Box 76, Deception Bay
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Marine Biology (1995) 122: 547–556

A. J. Courtney · S. S. Montgomery · D. J. Die
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Maturation in the female eastern king prawn *Penaeus plebejus* from coastal waters of eastern Australia, and considerations for quantifying egg production in penaeid prawns

Received: 19 December 1994 /Accepted: 23 December 1994

Abstract The trawl fishery for eastern king prawns, *Penaeus plebejus*, is of major commercial significance on the east coast of Australia. This paper describes the reproductive biology of female *P. plebejus* and presents new information relevant to quantifying egg production in penaeid prawn populations. The study concluded that the gonosomatic index (GSI) covaried with prawn size and was, therefore, likely to be a poor indicator of reproductive activity for penaeid prawn populations. GSI was also found to be not independent of ovary histological stage, moult stage, insemination status and parasitisation by bopyrid isopods. An histological description of ovarian development and the incidence of each stage of development is provided. This includes a description of the ovulation stage, which has not been previously recorded in naturally-occurring populations. Fifty percent of female *P. plebejus* were classed as mature at 42 mm CL. The relationships between GSI, percent mature, and percent inseminated with size suggest that there is a decline in the capacity of large (> 60 mm CL) females to produce and fertilise eggs. The declines in both GSI and percent mature is indicative of ovarian senescence in large(old) females, which has not been recorded previously in penaeid prawns. An index which considers the relationships between the percent mature, fecundity and the percent inseminated with size, as well as the influence of mortality on the population, is put forward to determine the relative contribution of different size classes of females to egg production. The index suggests that females > 50 mm CL contribute little to egg production, and that the bulk of eggs are produced by 35 to 48 mm CL females.

Communicated by G.F. Humphrey, Sydney

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Introduction

The eastern king prawn *Penaeus plebejus* is endemic to the east coast of Australia (Grey et al. 1983), and is of major commercial significance (Dall 1985). Between 1974 and 1981, the total reported annual oceanic catch ranged between 2068 and 3390 t (Glaister et al. 1987), worth ≃ $25 to 35 million annually.

Penaeus plebejus undertake extensive northerly migrations against the East Australian Current, and move from shallow estuarine nursery areas to deeper waters that generally do not exceed 250 m in depth (Potter 1975; Ruello 1975; Glaister et al. 1987; Montgomery 1990). These migrations are among the longest recorded movements of penaeid prawns. Ruello noted that as the prawns migrated there were more mature individuals in the northern parts of the fishery than in the southern part, and consequently referred to this as a breeding migration. However, the reproductive biology of *P. plebejus* is largely unknown and the scant understanding of the fishery's spawning stock is based largely upon incidental field observations. Dakin (1938) and Racek (1959) made inferences about the spawning stock based upon plankton samples, but the value of their comments was limited due to difficulties in identifying prawn larvae to species level.

In the past, it was generally considered that marine prawn spawning stocks could not be overfished (Neal 1975) and that there was no demonstrable relationship between spawning stock size and recruitment (Garcia 1983). Gulland (1984) noted that delineating the relationship was complicated by problems in estimating spawning-stock indices. However, more recent studies have described the spawning stock–recruitment relationship for some marine prawn species (Penn and Caputi 1986; Gracia 1991), and results of these studies indicate that spawning stocks can be overfished. Thus, there is increasing evidence to suggest that spawning stocks should be monitored.

This paper describes the reproductive biology of female *Penaeus plebejus*. A histological description of ovarian maturation is provided which considers recent advances from laboratory-based studies (Clark and Pillai 1991) on maturation that have yet to be applied to studying spawning in naturally-occurring populations. The usefulness of the gonosomatic index (GSI) in *P. plebejus* as a means of studying the temporal–spatial spawning patterns in penaeid prawn populations is evaluated. Several factors suspected of influencing GSI are examined, and the hypotheses that GSI is independent of prawn size is tested. Finally, the information obtained on the reproductive biology (maturation, insemination and fecundity) of female *P. plebejus* is combined with other population parameters (growth and mortality) to produce an index of egg production for different size classes of females. The index identifies the size range of females which contribute most to the population's total egg production.

Materials and methods

Sampling and laboratory procedure

Samples of *Penaeus plebejus* were obtained on a monthly basis for two years (August 1990 to July 1992) from four sites ranging in depth from 30 to 260 m off the coast of southeast Queensland (Australia; Fig. 1). Each sample weighed ~5 kg and consisted of about 100 prawns (both sexes) chosen randomly from the sorting tray. A research trawler and three other commercial trawlers collected the samples each month. Each sample was placed in a plastic bag, immediately frozen on board, and subsequently processed in the laboratory.

The carapace length (CL) of each female prawn was measured to the nearest 0.1 mm, moult condition was estimated (either soft or hard cuticle) and the presence of epicaridean bopyrid parasites was noted. The thelycum was opened and the presence or absence of a spermatophore was ascertained. Ovaries were dissected from every second female and weighed to the nearest 0.01 g. Tissue from the posterior ovarian lobes, in the region of the first abdominal segment, was removed for each female for histological examination. Tissue sections were cut at 6 μm and stained with haematoxylin and eosin. The histological stage of development was determined for each individual female and a description of maturation in *Penaeus plebejus* was documented, based upon previous laboratory studies on prawn maturation (Yano 1988; Clark and Pillai 1991). The development stage of each female prawn was estimated on the basis of dominant cell type. A particular cell type was considered dominant if it occupied >50% of the area of the histological section.

Analysis of variance was used to determine if GSI was independent of prawn size. The influence of histological stage, moult stage, presence/absence of spermatophore and presence/absence of bopyrid parasites on the gonosomatic index (GSI; ovary weight: total weight) was determined using one-way analyses of variance with carapace length as a covariate.

Fecundity

The measurement of fecundity was based upon the volumetric displacement of ripe ovaries and ripe oocytes. Once the displacement of

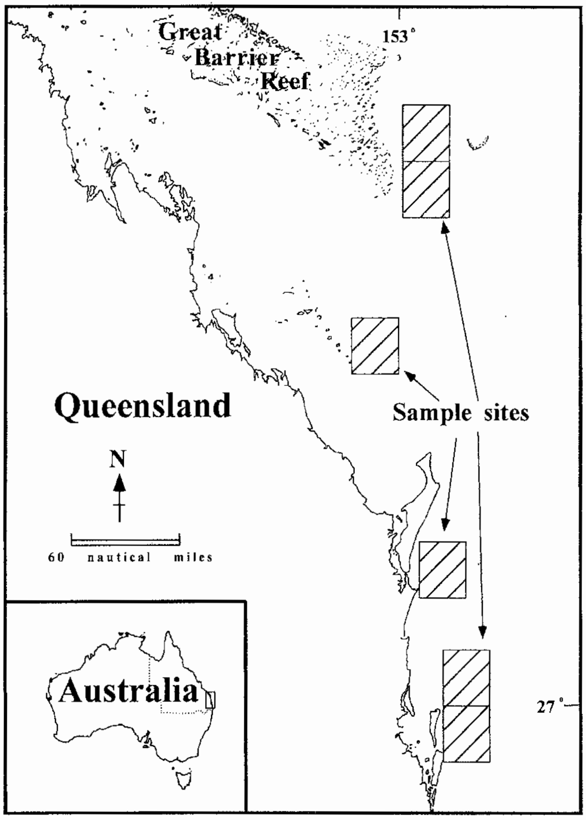


Fig. 1 Coastline of southeast Queensland showing four sites where samples of eastern king prawns, *Penaeus plebejus*, were obtained on monthly basis over 2 yr period

ripe ovaries and ripe oocytes was attained, fecundity was estimated by dividing the former by the latter. Five steps were required using this method: (i) The volume of ripe ovaries was measured by placing each ovary in a water-filled graduated cylinder and recording its displacement. (ii) In order to account for the displacement due to non-oocyte structures (connective tissue and ovary wall), the displacement of "empty" ovaries – those in spent or resorbed conditions – was also determined as in Step i; a regression for carapace length vs spent/resorbed ovary volume was then produced. (iii) The displacement of each ripe ovary was then adjusted by subtracting the displacement equivalent to that of a spent/resorbed ovary from a female of the same size (estimated using the foregoing regression). (iv) Ripe oocytes were defined as those with cortical crypts (peripheral bodies) present; the mean diameter of a ripe oocyte was calculated by randomly selecting and measuring the diameter in ≃10 ripe oocytes in each of 20 females using an image-analysis system; the volume of a single ripe oocyte of average size was then calculated using the formula $4/3\pi r^3$ (volume of a sphere). (v) Fecundity of each ripe female was then estimated, by dividing its adjusted ovarian displacement (Step iii above) by the volume of a single ripe oocyte of average diameter, calculated in Step iv.

Relative number of fertile eggs

An index incorporating maturation, fecundity, insemination and survival was derived to estimate the relative contribution of different size classes to the population's egg production. The percentage of recruits surviving at a given size class, i, was estimated by

$$\%\ \text{surviving}_i = 100\, e^{-z\Delta t_i},$$

where,

$$\Delta t_i = \frac{1}{k} \ln \left(\frac{L_\infty - L_r}{L_\infty - L_i} \right);$$

L_r represents the size at recruitment to the fishery, estimated to be 20 mm CL (Glaister et al. 1990). The growth parameters (k and L_∞) were obtained from the growth curve produced by Glaister et al. (1987). The indices were estimated for three different values of Z, 0.700, 1.024 and 1.300 mo^{-1}, which included Lucas' (1974) estimate of mortality for *Penaeus plebejus* ($Z = 0.256\ wk^{-1}$ or $1.024\ mo^{-1}$). The index, referred herein as the relative number of fertile eggs (RNFE) index, was calculated for sizes between 20 and 60 mm CL as follows:

$$RNFE_i = \%mature_i \times \%inseminated_i \times fecundity_i \times \%surviving_i$$

Results

Ovary weight–carapace length relationship and gonad index

Ovary weight was negligible (usually < 1.0 g) in female *Penaeus plebejus* < 35 mm CL. In larger females it was highly variable in all size classes, but generally increased with carapace length (Fig. 2a). A maximum ovary weight of 16.4 g was recorded for a female of 65.6 mm CL. The relationship was less variable for females with ripe ovaries (Fig. 2b):

$$\text{Ripe ovary weight (g)} = 0.0000286\ CL^{3.105}$$

$$(n = 355,\ r^2 = 0.73,\ p < 0.01).$$

For females > 35 mm CL, the GSI was highly variable. The maximum was 0.132 for a female of 56.1 mm CL. Females that were classed histologically as ripe (oocytes with peripheral bodies), and were therefore likely to spawn within a few days, had GSIs that ranged from ≃0.06 to 0.13 (Fig. 2c). Immature (pre-vitellogenic) females had GSIs that were almost always < 0.03, and the GSIs of vitellogenic (oocytes with yolk but without peripheral bodies) females ranged from ≃0.02 to 0.12.

Analysis of variance revealed that, in 40 to 60 mm CL females, GSI covaried with carapace length. The hypothesis that GSI was independent of prawn size, was therefore rejected. Mean GSI generally increased with carapace length (Fig. 2c) in females up to ≃60 mm CL. Approximately 4.5% of all females that had their ovaries dissected out were > 60 mm CL. In these large females there was evidence that mean GSI declined with increasing carapace length.

Analyses of variance for 40 to 60 mm CL females, using carapace length as the covariate, also revealed that GSI was not independent of histological stage, moult stage (hard/soft), presence/absence of a spermatophore and presence/absence of bopyrid parasites ($p < 0.01$).

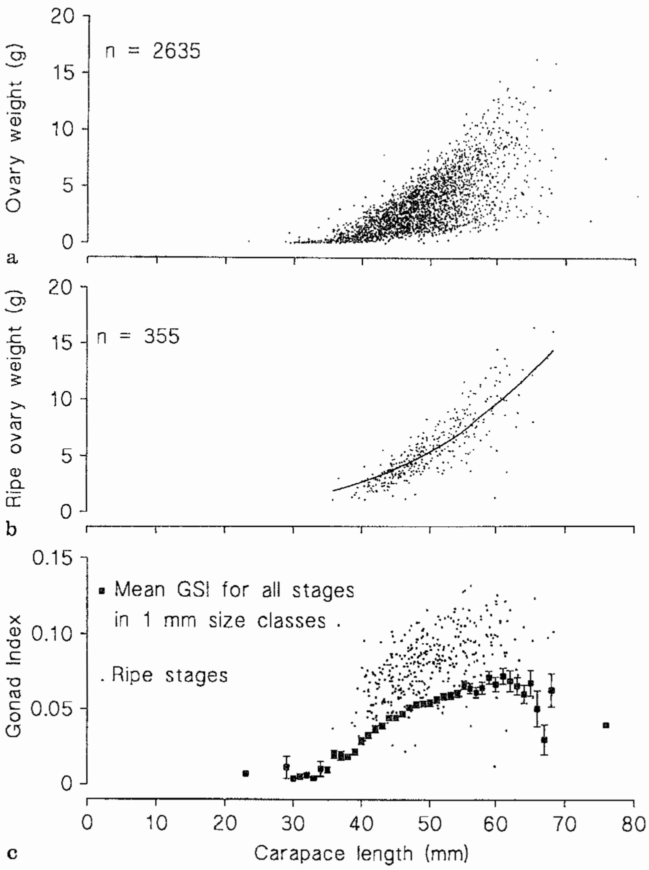
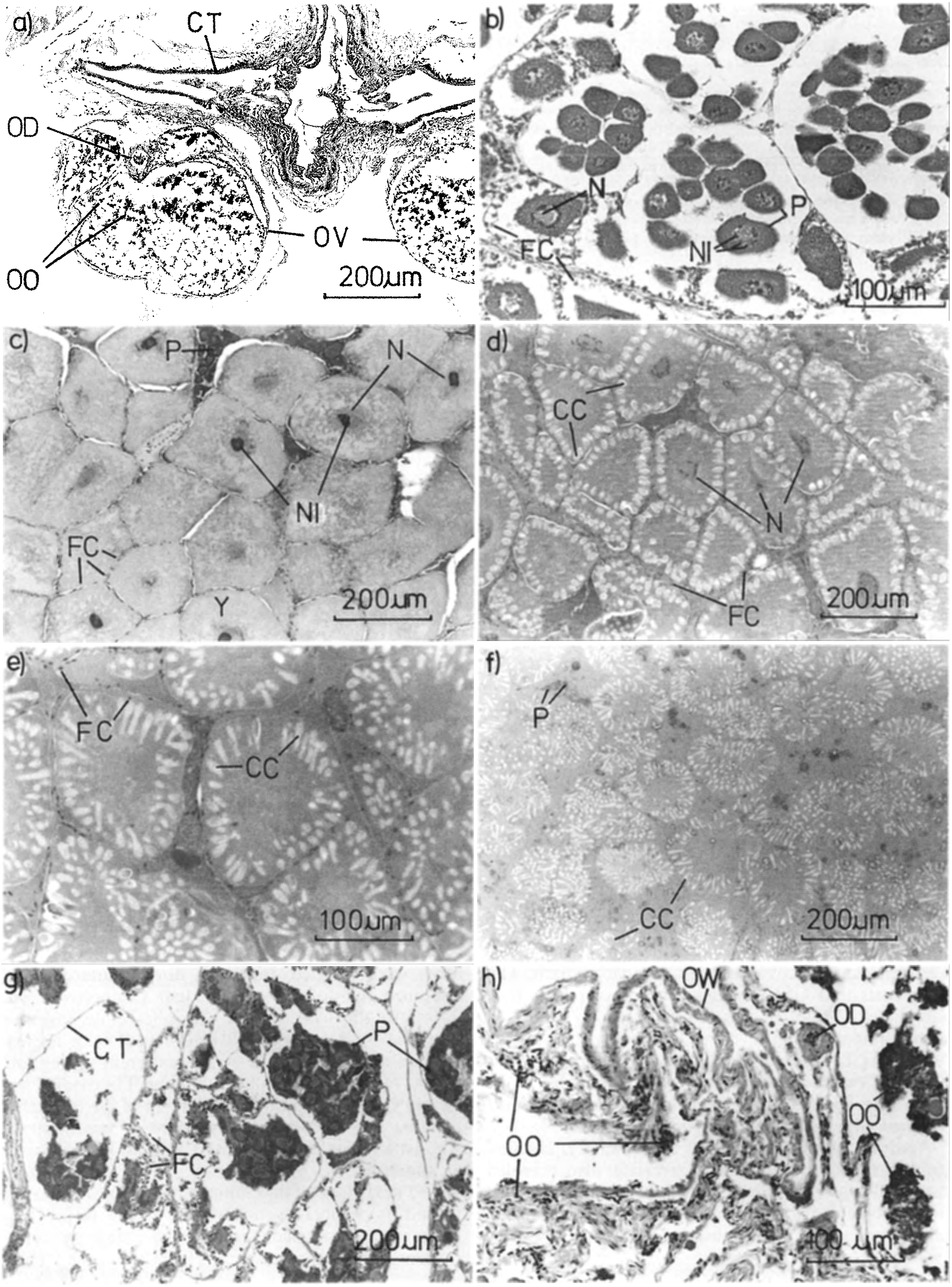


Fig. 2 *Penaeus plebejus*. Ovary weight and gonosomatic index (GSI) relationships with carapace length. **a** Scatter-plot of ovary weight against carapace length for all stages of development. **b** Relationship between ripe ovary weight and carapace length; ripe ovaries defined as those with cortical crypts present. **c** Scatter-plot of mean GSI for different size classes and GSIs of ripe females; vertical lines represent one standard error either side of mean GSI

Histological maturation

Ovaries were present in all females examined and could be discerned in individuals as small as 10 mm CL. In immature females (Fig. 3a), the two posterior ovarian lobes, left and right, had not developed beyond the oogonia stage and were < 500 μm in diameter. The two lobes were situated under the dorsal surface of the abdomen and dorsal to the hindgut. Connective tissue dorsal to the ovaries held the lobes close together. Oogonia were basophilic when stained with haematoxylin and eosin, and were scattered throughout a loose meshwork of connective tissue. The oviduct was clearly visible and a large proportion of the intercellular area within each lobe appeared as vacant space. Almost all females < 35 mm CL (Fig. 4a) were classed as immature.

The next stage of development (Fig. 3b) was characterised by an increase in cell size (30 to 60 μm), the appearance of nucleoli around the periphery of the nucleus, and the presence of follicle cells. These


a)
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perinucleolus stage oocytes were strongly basophilic. The nucleus stained slightly lighter than the cytoplasm and the nucleoli appeared darker than the cytoplasm. The oocytes were still in a pre-vitellogenic condition. Follicle cells appeared as small (<5 μm), oval-shaped basophilic bodies external to and distributed around the perimeter of the oocytes. Occurrence of this stage was rare (<2%) compared with the other stages (Fig. 4b).

Vitellogenesis (Fig. 3c) followed the perinucleolus stage and was characterised by a noticeable increase in mean oocyte diameter to 210 μm (± 31 SD, $n = 259$). The volume of cytoplasm increased several-fold and consisted of acidophilic oil globules and yolk granules. The nucleus in these cells lay centrally within the cytoplasm and remained basophilic, with one or two large dark-staining nucleoli. Follicle cells were distributed around the perimeter of the oocytes and were easily discernible as small (< 5 μm) dark-staining bodies. The oocytes were large and rounded and gave the ovary a relatively uniform appearance with good contrast between the dark-staining follicle cells and nuclear material and the lighter-staining, acidophilic yolk. The large vacant intercellular areas associated with the previous stages were no longer present. Small groups of perinucleolus stage oocytes were also present, but the vitellogenic oocytes predominated (by area). This stage of development was rare in females < 35 mm CL, but common (54%) in females >40 mm CL (Fig. 4c).

The next stage of maturation (Fig. 3d) was characterised by the appearance of cortical crypts (also referred to as cortical rods or peripheral bodies) and has been referred to by Clark and Pillai (1991) as the cortical specialisation phase. The crypts appeared jelly-like and in the early cortical specialisation phase they were circular; in later stages they became elongate, extending radially inward. The nucleus was lying centrally within the cytoplasm and follicle cells were present around the periphery of the oocyte. The nucleus stained basophilic, the cytoplasm and cortical crypts acidophilic. Mean oocyte diameter increased to 228 μm (± 47SD, $n = 217$) and differed significantly ($p < 0.01$) from the previous vitellogenic stage. Approximately 10% of females > 40 mm CL were in the cortical specialisation phase (Fig. 4d). This was relatively low, but not as rare as the perinucleolus stage.

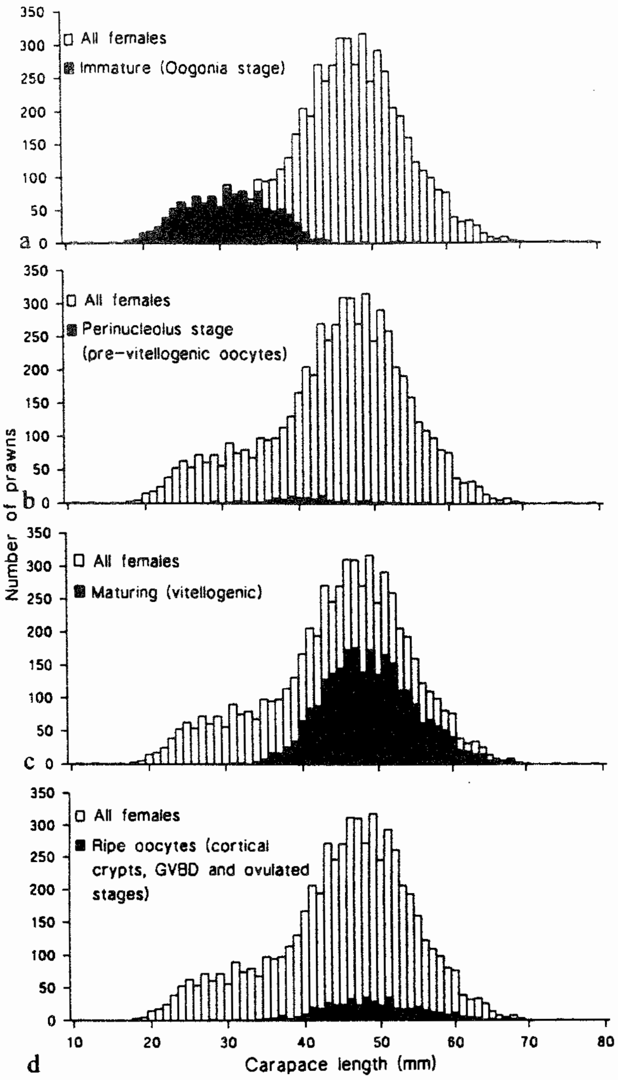

Fig. 4 *Penaeus plebejus*. Size-class frequency distributions for prawns in different stages of ovarian histological development

The cortical specialisation phase was followed by germinal vesicle break-down (GVBD, Fig. 3e). In this stage, meiotic division of the oocytes was arrested, the nucleus became indistinct, and the cortical crypts became elongated. The oocytes were entirely acidophilic and the crypts stained lighter than the cytoplasm. Basophilic follicle cells were distributed around the periphery of the oocytes. The final stage in maturation was ovulation, characterised by the disappearance of follicle cells (Fig. 3f). Because the oocyte nuclei and follicle cells disappeared, there was reduced contrast using haematoxylin and eosin, making this stage difficult to photograph. Both the GVBD and ovulation stages were rare (<2% of the total) and were included in Fig. 4d because they were considered to be in an advanced stage of development and possessed cortical crypts.

Ovaries from females in early post-moult (soft) were almost exclusively characterised by large intercellular

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Fig. 3 *Penaeus plebejus*. Histology photomicrographs of ovary development. **a** Immature ovarian lobes with scattered oogonia (26.5 mm CL); **b** perinucleolus stage oocytes (36.8 mm CL); **c** vitellogenic stage oocytes (52.4 mm CL); **d** cortical specialisation phase (48.0 mm CL); **e** germinal vesicle breakdown (GVBD, 45.4 mm CL); **f** ovulation (41.6 mm CL); **g** early post-moult ovary thought to be representative of recent spawning, resorption or re-maturation (54.1 mm CL); **h** undeveloped ovary from female (48.9 mm CL) parasitised by bopyrid isopod (*OO* oogonia; *OD* oviduct; *OV* ovary; *OW* ovary wall; *CT* connective tissue; *N* nucleus; *NI* nucleoli; *P* perinucleolus stage oocytes; *FC* follicle cells; *Y* yolk; *CC* cortical crypts) spaces, scattered basophilic follicle cells and perinucleolus-stage oocytes (Fig. 3 g). No post-vitellogenic oocytes were discerned at this stage, which was thought to represent recent spawning, resorption of mature oocytes, an early stage of re-maturation, or a combination of these.

Fewer than 1% of the prawns were parasitised by an epicaridean bopyrid parasite, most probably *Parapenaeon expansus* (Nearhos and Lester 1984). The parasites live in the gill chamber of their host. Although they do not invade the host's body tissues, they inhibit gametogenesis, indirectly sterilising the host (Abu-Hakima 1984). Ovaries from parasitised females (Fig. 3h) were invariably classed as immature, irrespective of the host's size. They were characterised by large vacant intercellular areas and were not classified as being beyond the oogonia stage.

Size at maturity

All females in post-vitellogenic stages (i.e. those in stages represented in Fig. 3c–f) were pooled and expressed as a percentage for each size class to obtain an estimate of size at maturity (Fig. 5a). About 50% of 42 mm CL females were classed as mature. The percentage mature increased with size to $\simeq$45 mm CL, and then maintained a plateau of $\simeq$75% in the size range 45 to 60 mm CL. Of the 6015 females that had their ovaries histologically staged, only 3.4% were >60 mm CL. In 60 to 65 mm CL females, there was a general decline in the percent mature with increasing carapace length, however because of the limited number of females > 65 mm CL, it is difficult to conclude whether this decline continued in these very large females (Fig. 5a). These results (particularly those for 60 to 65 mm CL females) support the results on GSI, which suggest there is some degree of ovarian senescence in females >60 mm CL.

Fecundity

The volumetric displacement of ripe ovaries ranged between 2.0 and 16.4 ml and increased with carapace length:

$$\text{Ripe ovary volume (ml)} = 0.0000749\ \text{CL}^{2.848}$$

$$(n = 104,\ r^2 = 0.53,\ p < 0.01).$$

Ripe ovary displacement was adjusted (to remove displacement due to non-oocyte structures) and then divided by the volume of a single ripe oocyte. The mean diameter of ripe oocytes (228.4 μm ± 47.3 SD, $n = 217$) was independent of carapace length, and the estimated volume of a ripe oocyte was 6.239×10^{-6} ml. Fecundity estimated in this way is expressed linearly (Fig. 5b) as:

$$\text{Log}_{(10)}\ \text{number ripe oocytes} = 0.0199\ \text{CL} + 4.7528$$

$$(n = 104,\ r^2 = 0.30,\ p < 0.01).$$

From this formula, the fecundity of 40 and 60 mm CL females was estimated to be 353 834 and 884 708 eggs, respectively.

Insemination

Very few females <30 mm CL were inseminated (Fig. 5c). The percentage inseminated increased sharply with size from 30 to 40 mm CL, and continued to rise less sharply from 40 to 55 mm CL. The highest percentage inseminated (78%) was observed in females of 55 mm CL and declined in larger (55 to 65 mm CL) females. There were only 28 individuals >65 mm CL, and of these 10 (36%) were inseminated, suggesting that the frequency of insemination continued to decline in very large females.

Relative number of fertile eggs index

The effects of the three mortality rates acting upon a population of *Penaeus plebejus* is shown in Fig. 5d. The prawns were assumed to recruit to the fishery at 20 mm CL (Glaister et al. 1990), and thereafter grow at a rate reported by Glaister et al. (1987). All three mortality rates have a dramatic effect on the number of females surviving to maturity. When the influence of these mortality rates on females of different sizes was combined with the above information on size at maturation, fecundity and insemination, the resulting RNFE indices indicated that most of the fertile eggs were produced by females ranging from 35 to 48 mm CL (Fig. 5e). All three graphs in Fig. 5e displayed two or more peaks. The first peak in each graph should be interpreted with caution, as it is strongly influenced by the relatively high proportion of females inseminated at 37 mm CL (Fig. 5c) and because fecundity was estimated by extrapolating the carapace–fecundity relationship for females <40 mm CL.

The effects of different mortality rates in the model were such that the highest rate ($Z = 1.300\ \text{mo}^{-1}$) resulted in relatively few eggs being produced, while the lowest rate resulted in the highest egg production (Fig. 5e). Each of the three graphs displayed a degree of skewness which was dependent upon the mortality rate used – the higher the mortality rate, the smaller the median size at which egg production occurred. Median sizes for egg production were 39, 40 and 42 mm CL for mortality rates of 1.300, 1.024 and 0.700 mo^{-1}, respectively. Irrespective of the mortality rate considered, females >50 mm CL contributed relatively little to the population's total fertile egg production.

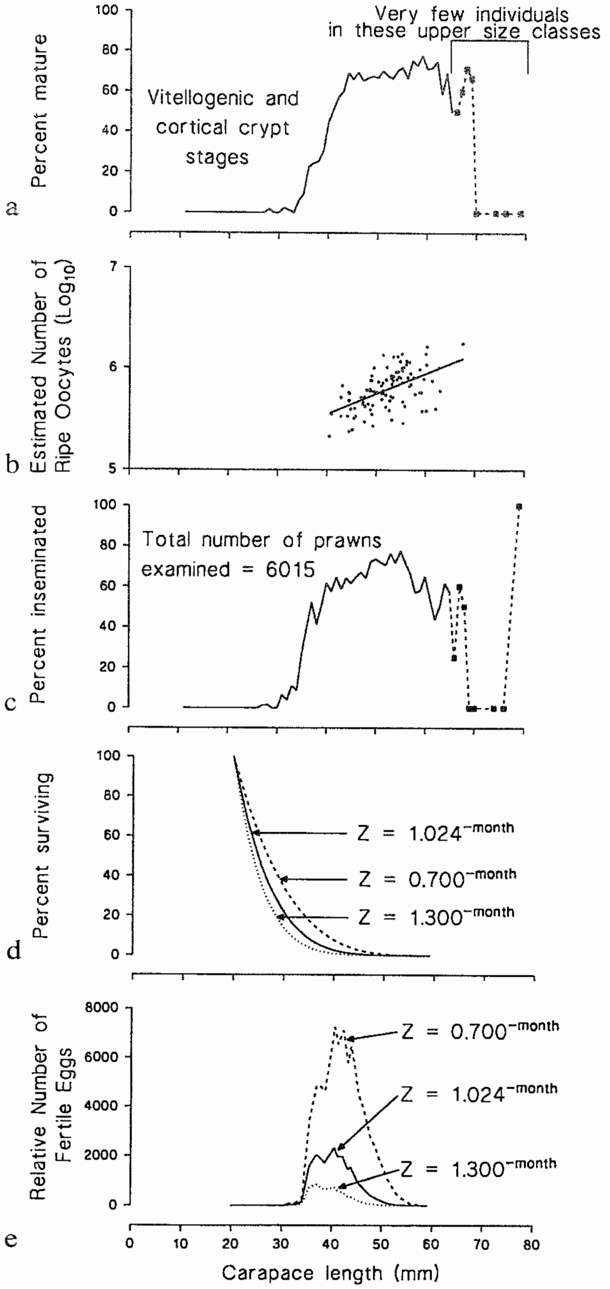

Fig. 5 *Penaeus plebejus*. Factors influencing egg production in different size classes. **a** Percent mature in each size class; vitellogenic stages and stages with cortical crypts present were used as measure of maturity. **b** Estimated fecundity against carapace length. **c** Percent inseminated against carapace length. **d** Percent of post-recruits (≥ 20 mm CL) surviving in population; range of total mortality (Z) rates, including Lucas' (1974) estimate, were used; percent surviving at a given time was converted to percent surviving at size using Glaister's (1987) growth curve. **e** Relative number of fertile eggs produced for each size class. Each graph represents a different estimate of total mortality (Z)

Discussion and conclusions

The gonosomatic index

The main purpose of using an index in reproductive studies is to take into account variation due to the size of the individual. GSIs have been used extensively in marine prawn reproductive studies (e.g. O'Connor 1979; Abu-Hakima 1984; Anderson et al. 1985; Shlagman et al. 1986; Potter et al. 1989; El Hady et al. 1990; Gab-Alla et al. 1990). However, results from the present study indicate that GSI is not independent of prawn size in *Penaeus plebejus* and, therefore, unless the size of the prawns is considered, GSIs are likely to be poor indicators of reproductive activity in penaeid prawns. If use of the GSIs is continued, then cautious interpretation of the results is required and the influence of female size within and between samples should be considered. The simplest and most logical alternative would be to use a measure of mean ovary weight for specific size classes of females. In practice this is sometimes difficult due to the lack of control over the size range of the females being sampled.

The analysis of variance using carapace length as a covariate also demonstrated that GSI was not independent of histological stage, moult stage, bopyrid parasitism or insemination status. As histological development progresses in an individual, it is also likely that there is a concurrent increase in the mass of the ovary; therefore, the lack of independence between histological stage and GSI was not entirely unexpected. Similarly, the relationship between reproduction and moulting in decapods is also synchronised and usually antagonistic (Emmerson 1980; Adiyodi 1985). In closed-thelycum penaeid prawns such as *Penaeus plebejus*, spawning occurs at a specific stage in the moult cycle (Dall et al. 1990). It was therefore suspected that GSI would not be independent of moult stage. The GSIs of soft (early post-moult)-cuticle females were significantly lower than those of hard (post-moult, inter-moult and pre-moult)-cuticle females. In order to account for this influence on ovary weight or GSI during a reproductive study, it would be prudent to record the moult stage of each female, or the incidence of females with soft cuticles in each sample. Alternatively, only females with hard cuticles, or females in a particular moult stage (which would have to be readily identifiable) should be used in the analysis.

The sterilising effects of bopyrids upon their penaeid prawn hosts is well known (Abu-Hakima 1984), and so the difference in GSI between parasitised and non-parasitised females was expected. Females with bopyrid parasites had significantly lower GSIs than those without. These results are consistent with the histological results, which showed that development of the ovary is suspended in parasitised prawns (Fig. 3h). Because bopyrids influence ovary weight and are therefore a source of variation in ovary weight, it would also be prudent to note presence or absence of bopyrid parasites on female prawns whenever measures of ovary weight are used to study spawning patterns. In some penaeid prawn fisheries, the incidence of bopyrid parasitism can be quite high (>30%, Owens and Glasebrook 1985; Mathews et al. 1988). Under such circumstances it would be difficult to explain the variation in ovary weight without considering the incidence of parasitism.

Females that were inseminated had a significantly higher GSI than non-inseminated females. The relationship between spermatophore insemination and ovarian development is not clearly understood in penaeid prawns, and therefore the lack of independence between insemination and GSI is difficult to explain. Female penaeid prawns with the closed-type thelycum are inseminated in early post-moult while the cuticle is still soft (Dall et al. 1990). Ovarian maturation occurs after insemination, during inter-moult and early premoult, and individuals lose their spermatophore at ecdysis (Emmerson 1980). Shlagman et al. (1986) noted a positive correlation between histological developmental stage and the proportion inseminated in *Penaeus semisulcatus*. Similarly, Potter et al. (1989) noted that female *Metapenaeus dalli* in early stages of ovarian development were rarely (<3%) inseminated while those in late stages of development were frequently (20 to 35%) inseminated. We speculate that an absence of spermatophore (i.e. through failure to copulate) is partially responsible for the low GSI observed. This could be an energy-saving mechanism, as it appears futile to develop ovaries, which can account for as much as 13% of total body weight, if no sperm is present to fertilise spawned eggs.

Ovarian histological development

Development of oocytes in *Penaeus plebejus* was similar to that described for other penaeid prawns (Tuma 1967; Anderson et al. 1984; Yano 1988; Clark and Pillai 1991). Some stages of oocyte development were rare, while others were common. If it can be assumed that catchability is independent of maturation stage, the variation in the incidence of different stages is most probably attributable to the duration of each stage. The low incidence (<2%, Fig. 4b) of perinucleolus-stage females was therefore probably due to the short duration of this stage. In contrast, the vitellogenic stage was common (Fig. 4c), and probably due to females remaining in this stage for long periods, possibly in readiness to mature and spawn.

The incidence of cortical crypt, GVBD and ovulation stages was also low, indicating a short period between cortical specialisation and spawning. The cortical specialisation stage (Fig. 3d) of *Sicyonia ingentis* occurred ≃90 h prior to spawning in the laboratory, GVBD (Fig. 3e) commenced more than 24 h prior to spawning, and the longest period recorded between ovulation (Fig. 3f) and spawning was 4 h (Anderson et al. 1984). If the timing of spawning is similar for wild-caught *Penaeus plebejus*, then each of these three stages is likely to be indicative of spawning activity, and thus can be used to provide temporal and spatial information on the fishery's spawning stock. This is the first report and description of the occurrence of ovulation in a natural population of penaeid prawns. All other published references to this stage of development have emanated from laboratory studies of maturation where the prawns were held in captivity (Anderson et al. 1984; Yano 1988; Clark and Pillai 1991). Although the incidence of both the GVBD and ovulation stages was low (<2%), it could be used to provide very detailed information on temporal and spatial spawning activities in natural populations. For example, the incidence of these stages during short-term, frequent sampling of a population could reveal relationships between spawning activity and lunar, or even diel, phases.

Fecundity

Our estimates of fecundity were comparable with those for other large *Penaeus* species (Dall et al. 1990). *P. plebejus* is Australia's largest endemic prawn in the *Penaeus* genus, and is the second (to *P. monodon*) largest penaeid prawn in Australian coastal waters. Females reach 300 mm CL (Grey et al. 1983) and can exceed 150 g in weight. However, our estimates were considerably higher than those of Kelemec and Smith (1984), who studied egg production in *P. plebejus* under laboratory conditions. Kelemec and Smith derived a regression based upon counts of spawned eggs from females of different sizes. They estimated that females from 45 to 60 mm CL spawned ≃76 000 to 604 000 eggs, respectively – well below those of the present study, particularly for females ≲50 mm CL. The regression derived by Kelemec and Smith included only females that had spawned completely, and therefore the difference between their estimates and those of the present study cannot be attributable to unspawned eggs remaining in the ovary. Part of the difference may be attributable to the relatively few spawnings upon which their regression was based. For example, the estimates of egg production in females equal to 45 mm CL are extremely low, and for females <42 mm CL egg production is nil.

Insemination

The plot of the percent inseminated in each size class has typically resulted in an S-shaped, or sigmoidal relationship in closed-thelycum prawns (Crocos and Kerr 1983; Crocos 1987a, b; Courtney and Dredge

1988). Our results suggest that a sigmoidal relationship may not be appropriate for *Penaeus plebejus*, as there is a distinct decline in the proportion inseminated in females >55 mm CL (Fig. 5c). The reason for this decline is unknown, but two hypotheses can be put forward to account for this. The first is that there is some form of selective mating behaviour favouring smaller (<55 mm CL) females; this may be due to the relatively large size differences between sexes in adult *P. plebejus* ($L_\infty = 45.4$ and 59.5 mm CL for males and females, respectively, Glaister et al. 1987). The second hypothesis is that there is some degree of spatial segregation based upon size which reduces the likelihood of large females being inseminated. Whatever the reason, our results suggest that these large females will not contribute to the population's total fertile egg production as much as would otherwise be expected.

Relative number of fertile eggs index

Previous studies (Tuma 1967; Crocos and Kerr 1983; Crocos 1987a,b; Courtney and Dredge 1988) have described the relationships between female size and (a) maturation, (b) fecundity, and (c) insemination as separate and discrete aspects of reproductive development. In this study, we have considered the combined influences from these and other factors (mortality and growth rates) which influence the number of viable eggs produced in different size classes of females. Because the index provides an indication of the relative importance of different size classes of females to the population's total egg production, it could be of some value to the fishery's management. For example, the index suggests that large (>50 mm CL) females contribute little to total egg production. If recruitment overfishing is suspected, management could mistakenly reduce effort on these large females in the belief that this will increase egg production. However, this would result in little, or no increase in egg production as the bulk of eggs are produced by 35 to 48 mm CL females. These smaller size classes are equivalent to ages of ~5.0 to 8.5 mo, respectively.

The limitations of the index are that it is heavily reliant upon the assumptions made about (a) size at recruitment, (b) the lack of individual variability in growth rate, and (c) the accuracy of the mortality rates. The assumptions about size at recruitment and growth rate are consistent with those made by Glaister et al. (1990), who modelled yield-per-recruit in the fishery. Size at recruitment was assumed to be knife-edged (occurring at 20 mm CL) and growth was deterministic (after Glaister et al. 1987). Although the current mortality rate (Z) in the fished population is unknown, the range of rates considered included one measure of total mortality by Lucas (1974), as well as other estimates that have been used to model the fishery (Glaister et al. 1990; Courtney et al. 1991). The range of mortality rates considered was therefore likely to reflect the actual mortality rate currently experienced by the population.

The reason large (>50 mm CL) size classes contributed little to total egg production was mainly that very few females surviving long enough to grow to such large sizes. Even for the lowest mortality rate considered (0.700 mo^{-1}), only ~2% of female recruits survived through to ages corresponding to ≥ 50 mm CL. However, other factors, including (a) the decline in the percentage inseminated in females >55 mm CL, and (b) the declines in mean GSI and the percentage mature in females >60 mm CL, would have also resulted in a reduced capacity in large(old) females to produce and fertilise eggs. The declines in mean GSI and the percentage mature in females >60 mm CL may be indicative of ovarian senescence and has not been reported previously for penaeid prawns.

Acknowledgements This work was funded by the Australian Fishing Industry Research and Development Council (FIRDC Grant #90/4) and the Queensland Fish Management Authority (QFMA). We thank skippers D. Trama, M. Coglan, K. Walker, P. Seib, S. Wood, W. Sterling and the McIlwain family for assisting in the collection of samples. We also thank D. Green and P. Peters for carrying out the laboratory dissections.

References

Abu-Hakima R (1984) Preliminary observations on the effects of *Epipenaeon elegans* Chopra (Isopoda; Bopyridae) on reproduction of *Penaeus semisulcatus* de Haan (Decapoda; Penaeidae). Int J Invert Reprod Dev 7: 51–62

Adiyodi RG (1985) Chapter 3. Reproduction and its control. In: Bliss DE, Mantel LH (eds) The biology of Crustacea. Vol. 9. Integument, pigments and hormonal processes. Academic Press, Inc., London, pp 147–215.

Anderson SL, Chang ES, Clark WH (1984) Timing of postvitellogenic ovarian changes in the ridgeback prawn *Sicyonia ingentis* (Penaeidae) determined by ovarian biopsy. Aquaculture, Amsterdam 42: 257–271

Anderson SL, Clark WH, Chang ES (1985) Multiple spawning and molt synchrony in a free spawning shrimp (*Sicyonia ingentis*: Penaeidae). Biol Bull mar biol Lab, Woods Hole 168: 377–394

Clark WH, Pillai MC (1991) Egg production, release and activation in the marine shrimp, *Sicyonia ingentis*. In: Wenner A, Kuris A (eds) Crustacean egg production. A.A. Balkema, Rotterdam, pp 3–8 (Crustacean Issues Vol. 7)

Courtney AJ, Dredge MCL (1988) Female reproductive biology and spawning periodicity of two species of king prawns, *Penaeus longistylus* Kubo and *Penaeus latisulcatus* Kishinouye, from Queensland's east coast fishery. Aust J mar Freshwat Res 39: 729–41

Courtney AJ, Masel JM, Die DJ (1991) An assessment of recently introduced seasonal prawn trawl closures in Moreton Bay, Queensland. Queensland Department of Primary Industries, Deception Bay, Qd (Inf Ser No. QI91037)

Crocos PJ (1987 a) Reproductive dynamics of the grooved tiger prawn, *Penaeus semisulcatus*, in the north-western Gulf of Carpentaria, Australia. Aust J mar Freshwat Res 38: 79–90

Crocos PJ (1987 b) Reproductive dynamics of the tiger prawn, *Penaeus esculentus*, and a comparison with *P. semisulcatus*, in the north-western Gulf of Carpentaria, Australia. Aust J mar Freshwat Res 38: 91–102

Crocos PJ, Kerr JD (1983) Maturation and spawning in the banana prawn *Penaeus merguiensis* de Man (Crustacea: Penaeidae) in the Gulf of Carpentaria, Australia. J exp mar Biol Ecol 69: 37-59

Dakin WJ (1938) The habits and life-history of a penaeid prawn (*Penaeus plebejus* Hesse) Proc zool Soc Lond 108A: 163–183

Dall W (1985) A review of prawn biological research in Australia. In: Rothlisberg PC, Hill BJ, Staples DJ (eds) Second Australian National Prawn Seminar. NPS2 Cleveland, Queensland, Australia, pp 11–21

Dall W, Hill BJ, Rothlisberg PC, Staples DJ (1990) Chapter 7. Reproduction. In: Dall W, Hill BJ, Rothlisberg PC, Staples DJ (eds) The biology of the Penaeidae. Academic Press, London, pp 251–275 (Adv mar Biol 27)

El Hady HA, Abdel Razek FA, Ezzat A (1990) Reproduction of *Penaeus semisulcatus* de Haan in Dammam Water (Arabia Gulf), Kingdom of Saudi Arabia. Arch Hydrobiol 118: 241–251

Emmerson WD (1980) Induced maturation of prawn *Penaeus indicus*. Mar Ecol Prog Ser 2: 121–131

Gab-Alla A A-FA, Hartnoll RG, Ghobashy A-F, Mohammed SZ (1990) Biology of penaeid prawns in the Suez Canal lakes. Mar Biol 107: 417–426

Garcia S (1983) The stock-recruitment relationship in shrimps: reality or artefacts and misinterpretations? Océanogr trop 18: 25–48

Glaister JP, Lau T, McDonall VC (1987) Growth and migration of tagged eastern Australian king prawns, *Penaeus plebejus* Hess. Aust J mar Freshwat Res 38: 225–242

Glaister JP, Montgomery SS, McDonall VC (1990) Yield-per-recruit analysis of eastern king prawns, *Penaeus plebejus* Hess, in eastern Australia. Aust J mar Freshwat Res 41: 175–197

Gracia A (1991) Spawning stock-recruitment relationships of white shrimp in the southwestern Gulf of Mexico. Trans Am Fish Soc 120: 519–527

Grey DL, Dall W, Baker A (1983) A guide to the Australian penaeid prawns. Department of Primary Production of the Northern Territory, Darwin, Australia

Gulland JA (1984) Introductory guidelines to shrimp management: some further thoughts. In: Gulland JA, Rothschild BJ (eds) Penaeid shrimps – their biology and management. Fishing News Books Limited, Surrey, England, pp 290–299

Kelemec JA, Smith IR (1984) Effects of low temperature storage and eyestalk enucleation of gravid eastern king prawns, *Penaeus plebejus*, on spawning, egg fertilisation and hatching. Aquaculture, Amsterdam 40: 67–76

Lucas C (1974) Preliminary estimates of stocks of the king prawn, *Penaeus plebejus*, in south-east Queensland. Aust J mar Freshwat Res 25: 35–47

Mathews CP, El-Musa M, Al-Hossaini M, Samuel M, Abdul Ghaffar AR (1988) Infestations of *Epipenaeon elegans* on *Penaeus semisulcatus* and their use as biological tags. J Crustacean Biol 8: 53–62

Montgomery SS (1990) Movements of juvenile eastern king prawns, *Penaeus plebejus*, and identification of stocks along the east coast of Australia. Fish Res 9: 189–208

Neal RA (1975) The Gulf of Mexico research and fishery on penaeid prawns. In: Young PC (ed) First Australian National Prawn Seminar. Australian Government Publishing Service, Canberra, pp 2–7

Nearhos SP, Lester RJG (1984) New records of Bopyridae (Crustacea: Isopoda: Epicaridea) from Queensland waters. Mem Qd Mus 21: 257–259

O'Connor C (1979) Reproductive periodicity of a *Penaeus esculentus* population near Low Islets, Queensland, Australia. Aquaculture, Amsterdam 16: 153–162

Owens L and Glazebrook JS (1985) The biology of bopyrid isopods parasitic on commercial penaeid prawns in northern Australia. In: Rothlisberg PC, Hill BJ, Staples DJ (eds) Second Australian National Prawn Seminar. NPS2, Cleveland, Queensland, Australia, pp 105–113

Penn JW, Caputi N (1986) Spawning stock-recruitment relationships and environmental nfluences on the tiger prawn (*Penaeus esculentus*) fishery in Exmouth Gulf, Western Australia. Aust J mar Freshwat Res 37: 491–505

Potter IC, Baronie FM, Manning RJG, Loneragan NR (1989) Reproductive biology and growth of the western school prawn, *Metapenaeus dalli*, in a large Western Australian estuary. Aust J mar Freshwat Res 40: 327–40

Potter MA (1975) Movements of the eastern king prawn (*Penaeus plebejus*) in southern Queensland waters. In: Young PC (ed) First Australian National Prawn Seminar. Australian Government Publishing Service, Canberra, pp 10–17

Racek AA (1959) Prawn investigations in eastern Australia. Res Bull St Fish NSW 6: 1–57

Ruello NV (1975) Geographical distribution, growth and breeding migration of the eastern Australian king prawn *Penaeus plebejus* Hess. Aus J mar Freshwater Res 26: 343–354

Shlagman A, Lewinsohn C, Tom M (1986) Aspects of the reproductive activity of *Penaeus semisulcatus* de Haan along the southeastern coast of the Mediterranean. Mar Ecol Prog Ser 7: 15–22

Tuma DJ (1967) A description of the development of primary and secondary sexual characteristics in the banana prawn, *Penaeus merguiensis* de Man (Crustacea: Decapoda: Penaeinae). Aust J mar Freshwat Res 18: 73-88

Yano I (1988) Oocyte development in the kuruma prawn *Penaeus japonicus*. Mar Biol 99: 547–553