Variation in banana prawn catches at Weipa:

a comprehensive regional study

FRDC Project No. 2004/024

Final Report: Appendices

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CSIRO

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APPENDIX I. INTELLECTUAL PROPERTY

There is no intellectual property of a commercial nature arising from this Project.

Use of AFMA data in publications and presentations has constraints, largely to do with anonymity of individual fishers by agglomeration of sparse data points.

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APPENDIX III. DATA SOURCES AND ACCESS

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This project made use of numerous datasets in a variety of formats and at different stages of availability. A ‘Data Overview Page’ was created with a list of relevant datasets for this project. It provides an entry-point and a quick reference to various datasets of interest, while providing an overview of their level of location, completeness, format, and availability. Project workers outside CSIRO were granted guest access privileges with username and password. Workers in the Marine and Atmospheric Division have full access.

The Data Overview Pages are found at:
- Internet: http://www.bne.marine.csiro.au/public/weipa_bpv/WBPV01.htm
- Intranet: http://www.bne.marine.csiro.au/wwwsite/weipa_bpv/WBPV01.htm

Within the Data Overview Page the data sets are grouped under several headings: Biological, Fishery, Environmental, Trophodynamics, and Habitat. Other data that were derived from these source data sets or from outside data sets by the analytical working groups (Spatial Analysis, Fishery Modelling, Environmental Correlates, Ecopath Model, and Qualitative Model) were not included in this central data portal, but the sources of these are cited in appropriate locations throughout the report.

The following characteristics were recorded for each data set that was included in this central portal:

- Short, unique, alphanumeric code for easy identification

- Hyperlink directly to the relevant entry in MarLIN. MarLIN is the Divisional metadata system, which is web-accessible, and conforms to the relevant national and international metadata standards.

- The custodian’s name.

- Hyperlink to the data set’s folder. For some of the project’s data sets, files in Excel, Text and Access format were received. The folder contains these files.

- Hyperlink to a data progress page in HTML format, which lists details about the acquisition, documentation and extraction progress that has been made by the data workers.

- Format of the data. Common formats in which this project’s data are available are Oracle, Access, GIS and netCDF. Wherever possible a direct hyperlink to the actual data was made available. In these cases clicking on the format opens the actual data. Furthermore, symbols for access restrictions have been employed. These are:

    - Red restricted symbol - data sets listed with this symbol have restricted access. Data access requires negotiation with the data custodian.
    - Grey restricted symbol - available only to specific organizations or divisions.

- A flag labelled ‘Required’. This flag indicates whether or not the data set is required for the project. The data search phase found some data sets that were of value but that were not needed for the project. Rather than deleting references to these, they were kept in the Data Overview Page and flagged as ‘Not required’.

- A flag labelled ‘Phase 1’. Data sets are deemed to be usable for the project or in ‘Phase 1’ if the data custodian has been identified, a Marlin record has been created and the data are accessible in digital formats. A traffic light style has been employed for this flag:
    - green - high (content/relationships known)
    - yellow – medium
    - red - low (content/relationships mostly unknown)

No (46)	Data set	Years	Custodian	Marlin Id (31)	Progress	Folder	Phase 1 (28)	Format	Required
Biological									
B01	**Munro Prawn Surveys**	1963-65	Janet Bishop	6315	P	📁	✖	Non-digital	
B02	**Redfield Data, Eastern GOC**	1975-77	Janet Bishop Charis Burridge	1561	P	📁	✖	Oracle	
B03	**Norman River Juvenile Data**	1975-79	David Vance	4864	P	📁			
B04	**Juvenile Prawns Embley Estuary**	1981-82	Mick Haywood Rob Kenyon	6422	P	📁	✖	Oracle	✓
B05	**Pre-season Surveys**	1984-85	Janet Bishop	6309	P	📁			
B06	**Albatross Bay Adult**	1986-92	Janet Bishop Charis Burridge	1361	P	📁	?	Oracle	✓
B07	**Albatross Bay Repro**	1986-92	Tonya van der Velde	1361	P	📁	?	Oracle	✓
B08	**Albatross Bay Larval**	1986-92	Peter Rothlisberg	1663	P	📁	✓	Oracle	✓
B09	**Albatross Bay Juvenile**	1986-92	Mick Haywood Rob Kenyon	4875	P	📁	✖	Oracle	✓
B10	**Albatross Bay Primary Productivity**	1986-92	Michele Burford	1664	P	📁	✓	Oracle	✓
B11	**Coastal Nursery Ground Survey (Prawn)**	1992-95	Mick Haywood Rob Kenyon	6421	P	📁	✖	Oracle	✓
B12	**Embley Cast Net**	2003-onwards	Dave Vance	6454	P	📁			✓
B13	**Munro Prawn Surveys Bycatch Data**	1963-65	Margaret Miller	6334	P	📁	✖	Oracle	
B14	**Albatross Bay Copepods**	1986-88	Steve Edgar	6332	P	📁	✓	Oracle	✓
Fishery									
F01	**Logbook CPUE**	(1970)-1980-present	Bill Venables	6386	P	📁	✓	🚫 Excel	✓
F02	**VMS**	1999-03	Wayne Rochester	6424	P	📁		🚫 Oracle	✓
F03	**NPF Monitoring**	2002-present	Anthea Donovan	6314	P	📁	✖	Oracle	✓
F04	**NPF Monitoring New Catch Rates**	2003-present	Anthea Donovan	6314	P	📁	✖	Oracle	✓
F05	**Fisherman 1 Logbook**		Don Heales to contact		P	📁		🚫	
F06	**Fisherman 2 Logbook**		Mick Haywood	6420	P	📁	✖	🚫 Oracle	
F07	**Logbook Target Species**	1970-01	Janet Bishop		P	📁		🚫 Oracle	✓
Environmental									
E01	**CARS – Albatross Bay Relevant Data**		Jeff Dunn	5960	P	📁	✓	netCDF	✓
E02	**Albatross Bay Hydro**		Peter Rothlisberg	3203	P	📁	?	Oracle	✓
E03	**Albatross Bay Nutrients**	1986-92	Michele Burford	1662	P	📁	✓	Oracle	✓
E04	**Albatross Bay Phyto Abundance and Productivity**	1986-92	Michele Burford	1582	P	📁	✓	Oracle	✓
E05	**Embley Hydro**	1986-92	Mick Haywood	4875	P	📁	✖	Oracle	✓
E06	**AMEX**	1987-89	Mal Heron (JCU)		P	📁			✓
E07	**COMALCO Bore Water Levels**		Dave Vance to contact		P	📁			✓

E08	**Ports Corp - Dredging**		Dave Vance to contact		P	📁			✓
E09	**Rainfall/Catchment**		Ian McLeod		P	📁		GIS	✓
E10	**BOM/QDNR (SILO)**		Steve Edgar	6410	P	📁	✓	⊘ netCDF ArcInfo	✓
E11	**Weipa/Karumba S/T Loggers**		Bob Pendrey	6440 (6441)	P	📁		Excel and CSV	✓
E12	**Albatross Bay Current Meter Array**	2004-05	Bob Pendrey Scott Condie	6442	P	📁		unknown	✓
Trophodynamics									
T01	**Albatross Bay Predation**	1986-92	Dave Brewer	6423	P	📁	✗	Oracle	✓
T02	**Embley River Predation Data**		Dave Brewer	1701	P	📁	✗	Oracle	✓
T03	**Albatross Bay Shark**	October 1998	Don Heales	6414	P	📁	✗	Oracle	
T04	**Pelagics**	2002-03	Shane Griffiths	6412	P	📁	✗	Access	✓
T05	**Embley Prawn Predation**	1992-94	Mick Haywood	1703	P	📁	✗	Oracle	✓
T06	**Albatross Bay Nearshore Predation**		Dave Brewer	1661	P	📁	✗	Oracle	✓
Habitat									
H01	**AIMS Seagrass, Hydro Survey Embley River**	1985	Eric Wolanski (AIMS)		P	📁			✓
H02	**Seagrass**	1983-92,94	Rob Kenyon	4685	P	📁	✗	Oracle	✓
H03	**Mangrove Productivity**	1992-94	Carol Connacher	6419	P	📁	✗	Oracle	✓
H04	**Remotely Sensed Mangrove Distribution**		Fiona Manson		P	📁		GIS	✓
H05	**QDPI Seagrass**		Peter Rothlisberg to contact		P	📁			✓
H06	**Chris Jenkin's Sediments**		Ian McLeod		P	📁		GIS	✓
H07	**Albatross Bay Untrawlable Ground**		Mick Haywood	5261	P	📁	?	⊘ Coverage	✓

Column legend

No	Arbitrary, unique data set number for quick reference. Number in parentheses is number of data sets.	
Data set	Short, non-authoritative description of data set.	
Years	Year for which this data set is relevant.	
Custodian	Person responsible for the data set	
Marlin Id	Marlin Id. Can be queried in http://www.marine.csiro.au/marlin/. Number in parentheses is number of data sets which have a Marlin record.	
Progress P	State of progress in retrieving required information from this data set for the Weipa Banana Prawn Variability project. Simple HTML file	
Folder 📁	Link to the folder which contains documents for this data set on the Worgroups share.	
Phase 1	Data sets where the data custodian has been identified, a Marlin record has been created and the data is accessible in digital format. Number in parentheses is number of data sets which are at Phase 1. Knowledge about the data set is indicated as follows:	
	✓	**green** - high (content/relationships known)
	?	**yellow** - medium
	✗	**red** - low (content/relationships mostly unknown)
Format	Format which the data set is in. Usually Oracle, Access, GIS or netCDF	
	🚫	Data sets listed with this symbol have restricted access. Data access requires negotiation with the data custodian.
	⊘	Available only to CSIRO divisions which have made a commitment to share the cost (includes Marine Research). All CSIRO users of the SILO data are subject to the license conditions set out in the agreement between CSIRO and QDNR&M (currently being completed).
Required	✓	Data set is required for the Weipa BPV project.

APPENDIX IV. WORKING GROUP FULL REPORTS AND MANUSCRIPTS

IV-1. Reproductive dynamics of the banana prawn

Seasonal, spatial, and interannual variability in the reproductive dynamics of the banana prawn, *Penaeus merguiensis* de Man, in Albatross Bay, Gulf of Carpentaria, Australia

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Abstract

The reproductive dynamics of *Penaeus merguiensis* de Man were investigated in the Albatross Bay region of the Gulf of Carpentaria, Australia from March 1986 to March 1992. Approximately 1,923 trawls were carried out over 66 monthly sampling surveys, with a total of 102 497 prawns caught of which 52 418 females were examined. An index of population egg production; calculated from female abundance (no. ha^{-1}), the proportion of females spawning (% ripe), and fecundity according to body size was used as an indicator of reproductive output. Egg production was seasonal with a spring spawning (Aug-Nov) and a late summer-autumn (Jan- Mar) spawning; giving rise to two clearly apparent cohorts, annually. Egg production was highest in autumn (6-month old spawners), due to the high abundance of new recruits, with another peak in spring (12-month old spawners) after the intense fishing period from April to May. Surprisingly, the relatively small number of eggs and larvae from these large 12-month old individuals are responsible for the single annual pulse of recruitment to the commercial fishery in summer and autumn 3 to 6 months later. The high egg production in autumn is less successful in contributing to subsequent stocks because eggs and larvae are released too far offshore to be delivered to adjacent estuarine nursery grounds. The small numbers of larvae that do reach the nursery grounds during this period have poor survival because of less favorable nursery grounds conditions, mainly due to the low salinity and cooler water temperatures. However, during spring, the population of banana prawns (including the spawners) moves into very shallow waters, (8 to 15 m depth) close to nursery habitats. This spawning area within reach of the nursery habitat is defined as the “effective spawning envelope”.

Keywords: Penaeid shrimp, effective spawning, population fecundity index, egg production, abundance

Introduction

A basic understanding of the reproductive dynamics of a species and a description of the spawning stock is essential to be able to assess the factors affecting recruitment strength and for the development of spawning-stock recruitment relationships in penaeid prawn populations (Dichmont *et al.* 2003). Declines in the commercial catches of *Penaeus merguiensis* and other commercially important tropical penaeids have prompted intensive studies of the recruitment processes of these species (Rothlisberg *et al.* 1988; Somers 1988; Wang and Die 1996; Dichmont *et al.* 2003).

The banana prawn, *Penaeus merguiensis,* is widespread through the Indo-West Pacific region (Grey *et al.* 1983). In many countries throughout this range, it is of major commercial importance and is one of the most important commercial prawn species worldwide (Staples 1991). In Australia’s Northern Prawn Fishery, annual catches of *P. merguiensis* have ranged from a maximum of 12,711 t in 1974 to a low of 1,702 t in 1970. However, since the early 1980s, when most of the commercial fishing grounds had been discovered, catch has ranged from 2,157 to 7,245 t with a long term average of 4,302 t (Perdrau and Garvey 2005). *Penaeus merguiensis* comprise about 40% of the penaeid prawn catch in Australia’s Northern Prawn Fishery (NPF) (Perdeau and Garvey 2005).

In Australian prawn fisheries, a simple model had been used to describe the spawning stock of penaeids (Somers 1990). This model identified one main spawning period each year from which the next generation of adult stock is recruited. The model assumed that the abundance of the adult stock during this spawning period was a measure of the spawning-stock biomass (Somers 1990). Fifteen years ago, Somers (1990) suggested that a more detailed description of the seasonal timing and spatial distribution of spawning would enable this model to be refined. Despite recent analyses of banana prawn stocks (Vance *et al.* 2003), a fine-scale description of regional banana prawn stocks remains as important as it did then.

Previous studies have identified spawning areas for penaeids: it is generally assumed that these coincide with the distribution of adults (Dall *et al.* 1990). Crocos and Kerr (1983) showed two seasonal spawning peaks, with the spring peak being dominant. They also showed that the distribution of spawners comprised only part of the adult distribution. For any spawning activity to contribute to the next generation, the spawning areas must be close enough to the inshore nursery grounds for the larvae to reach them during the planktonic larval life stage (Rothlisberg *et al.* 1996, Condie *et al.* 1999). Hydrodynamic modeling of water currents in the south-eastern Gulf of Carpentaria has shown that most of the banana prawn larvae (*Penaeus merguiensis)* produced during the autumn fishing season (when adult banana prawns are most abundant) are lost to the population due to unfavourable currents (Rotho *et al* 1983). Rothlisberg *et al.* (1983) demonstrated the significant effects of both larval behaviour and hydrographic current regimes on penaeid larval advection patterns.

More recent research has emphasized the importance of the vertical migration behaviour of the postlarvae in enabling the postlarvae to be advected towards the coastal nursery areas leading to the concept of an “effective spawning envelope” – spawning areas in proximity to nursery habitats that ultimately contribute to stock renewal (Rothlisberg *et al.* 1995, 1996, Condie *et al.* 1999). Consideration of the spatial distribution of spawning activity is therefore a critical aspect of spawning-stock description.

Spawning output can be described in terms of a population fecundity index based on: the abundance of spawners in the population; the proportion of spawners that are ripe; and the contribution of each spawner to egg production according to their size and fecundity (Crocos and Kerr 1983).

This study describes for the first time the seasonal, spatial and interannual variability in reproductive output of *P. merguiensis* in Albatross Bay. The study seeks to explain mechanisms underlying variability in reproductive dynamics and recruitment at the life history stages and further provides a robust reproductive output as a component for future fisheries management models of commercial catches in the NPF.

Methods

Study area

The study area encompassed the geographical extent of the commercial prawn fishery and adjacent shallower inshore waters in the Albatross Bay region of the northeastern Gulf of Carpentaria (Figure 1). All species of commercially important penaeids found in this region were sampled: *Penaeus merguiensis, Penaeus semisulcatus, Penaeus esculentus, Metapenaeus endeavouri and Metapenaeus ensis.* The extent of the fishery was defined from commercial log-book data and the inshore waters were sampled to monitor recruitment of small prawns as they moved offshore from estuarine nursery habitats (see Vance *et al.* 1998). Deepwater stations to about 72 nautical miles (n. mile) offshore were established along east/west transects at 12°21’S and at 12° 30’S to describe the prawn population beyond the western boundary of the commercial fishery. Overall, the sampling stations covered a depth range of 5 to 45 m, while the commercial fishery is mostly confined to depths of 10 to 25 m.

Sampling

Prawns were sampled using a chartered commercial trawler towing commercial trawl gear. Trawl stations were established on a 6 x 6 n. mile grid (Figure 1). A total of 66 sampling surveys were made over the 6 y of the study, from March 1986 to March 1992. Surveys were typically of 3 to 5 nights duration and were centered on the date of the new moon; both for environmental consistency and as the prawns are abundant on nights with least light. Consistent and accurate position fixing for trawl stations was achieved with radar and a Global Positioning System.

Two groups of stations were sampled during the study, over depth ranges of 5 to 20 m (Group1) which was specific to the Penaeus merguiensis part of the project, 20 to 45 m (Group 2) (Figure 1). In total, 1923 trawls were completed, comprising 1161, 582, and 180 in station Groups 1 to 3, respectively.

During the first phase of the project, March 1986 to December 1987, all stations in Groups 1, 2 and 3 were sampled each lunar month. During the second phase, January 1988 to April 1992, sampling effort was increased on spawning and recruitment phases. Throughout this period only station Groups 1 and 2 were sampled and then only from August through to April. Sampling intensity was increased on shallow-water stations: the Group 1 stations were sampled three times, on separate nights, during each monthly survey between August and December, and twice per survey between January and April. The Group 2 stations were sampled once on each survey. Since banana prawns were rarely caught beyond the Group 1 stations, these 10 stations are deemed the standard stations for analysis of seasonal and interannual patterns over the 6 y.

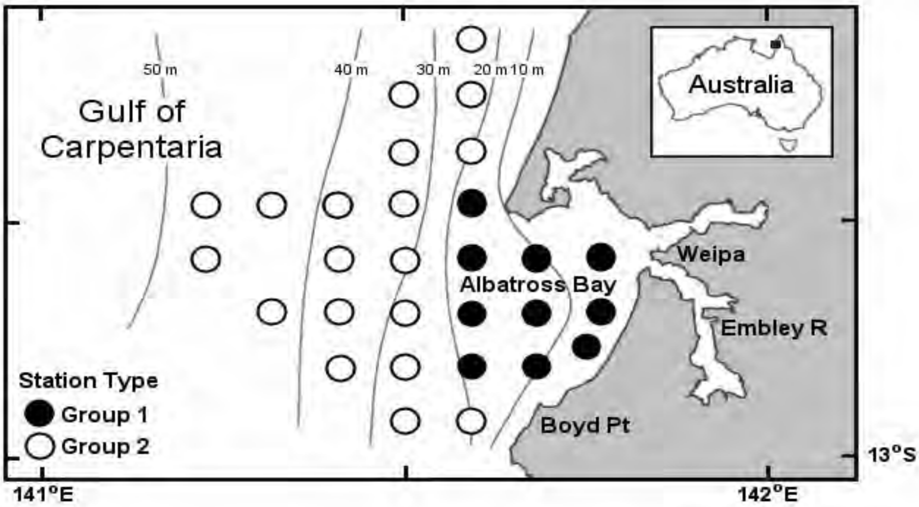


Figure 1: Study area in Albatross Bay region of northeastern Gulf of Carpentaria, Australia, showing location of sampling stations and station groups relevant to sampling stratification. Groups 1 and 2 were sampled monthly over whole 6 y period. (see “Materials and methods – Sampling” for details).

Trawls were made for 15 minutes bottom-time duration using four 9 m (headrope length) nets towed at 3.2 knots (defined as a standard trawl). The net design (Florida Flyer) and stretch mesh size (50 mm body and 44 mm cod-end) was the same for each cruise. All trawls were carried out during the hours of darkness from 1 h after sunset to 1 h before sunrise. All prawns caught were separated from the trawl bycatch, sorted to species, sexed and measured to the nearest mm of carapace length (CL). Catches from all four nets were pooled. When catches were excessively large, during peak fishing seasons, the catch was sub-sampled. The standard measure of abundance (catch per unit effort, CPUE) was defined as the number of prawns caught per standard trawl. All female *P. merguiensis* (or a random sample of up to 50 females) were collected from each trawl and frozen. In the laboratory, ovarian tissue samples were taken from adult females for an histological description of maturity. Females with ovaries developed to either Stage 4 (ready to spawn) or Stage 5 (just spawned) were deemed to be actively spawning (Crocos and Kerr 1983, Crocos 1985).

Prawn larvae were also sampled to measure the abundance of eggs and their distribution. Larvae were sampled at each trawl station in station Groups 1 and some trawls in Group 2 using stepped-oblique tows. The tows were of 5 minutes duration at each step at two depths for the shallow waters and 3 steps in the deeper waters >20m with 142 µm mesh net. All plankton samples were taken at night by a stepped-oblique tow from surface to near-bottom, with 1 or 2 intermediate steps (for full description see Jackson *et al.* 2001).

Environmental data

Temperature and salinity profiles were measured at approximately 2 m depth intervals at each sampling station with a submersible data logger (CSIRO/Yeokal SDL). Rainfall data for the Weipa area were obtained from the National Climate Centre, Melbourne, Australia.

Population fecundity index

The description of spawning seasonality and spawning locations was based on an index of population fecundity (PFI) that linked: the abundance of adult females; the proportion of adult females spawning and the fecundity of spawners relative to individual size. Accordingly, for a specified group of sampled stations

$$\mathrm{PFI} = \frac{1}{N}\left[\sum_{i=1}^{N} a_i p_i \frac{1}{n_i}\sum_{j=1}^{n_i} f\left(l_{ij}\right)\right]$$

where PFI is the population fecundity index, N is the number of stations in the specified area, a_i is the abundance (CPUE) of adult females in Station i, p_i is the proportion of spawning adult females in the sample from Station i, n_i is the number of spawners in the sample from station i for $i=1, 2, \ldots, N$, l_{ij} is the carapace length of the j-th spawner caught in Station i for $j=1, 2, \ldots, n_i$, i=1, 2, …N, and $f(l)$ is the fecundity of an spawner with carapace length l estimated from a fecundity-carapace length relationship. This method of estimation of the PFI first calculates the mean fecundity for each individual station:

$$\mu_i = \frac{1}{n_i}\sum_{j=1}^{n_i} f\left(l_{ij}\right).$$

Because the prawns are highly aggregated, the PFI values can be very large. For this reason the station mean fecundities were scaled to [0, 100].

The fecundity-carapace length relationship used is that given by (Crocos, 1983):

$$f\left(l\right) = 19944.7l - 441097.$$

Adult females, capable of spawning, were defined as having a carapace length ≥ 25 mm. Temporal patterns in the PFI for *P. merguiensis* in Albatross Bay were examined by pooling station data over a month, and comparing months. Spatial spawning patterns were examined by pooling the data for each survey night by station, grouped by season. The seasonal trends were examined by grouping the 'autumn' spawning, January to March; and the 'spring' spawning, August to November.

Results

Rainfall/Temperature

The climate of the Weipa region is characterized by distinct wet and dry seasons, with heavy rainfall during the summer monsoon from December to March (at least 84% of the annual rainfall falls then) (Figure 2 a). The mean annual rainfall for the 6 y of the study was 1876 mm which was close to the 26 year mean annual rainfall of 1897 mm (for more detail see Vance *et al.* 1998). The mean surface salinity in Albatross Bay ranged from a low of 32% for 2 months (February-March) at the end of the wet season, to a high of 35% in November at the end of the dry season (Figure 2 a). Between January and March, inshore surface salinities were ~ 2% lower than bottom salinities, but for the rest of the year they were generally the same. Inshore salinities (depths <15 m) showed slightly more seasonal variation than did offshore salinities, with a range of 30 to 35% (inshore) and 33 to 35% (offshore) in November and February, respectively. Surface-water temperatures also varied seasonally, with a mean peak of 30 to 31ºC in December and January, declining to 29ºC by April, and a low of 25 to 26ºC in August (Figure 2 a). Temperatures of offshore waters (>15m depth) in spring and summer (October to December) varied between the surface and the bottom (bottom temperatures were 1.5 to 2 ºC lower than at the surface). The difference was less (about 1ºC) from January to March (Figure 2 b), after which surface and bottom waters were well-mixed. Inshore waters (≤15 m) showed little surface-to-bottom difference.

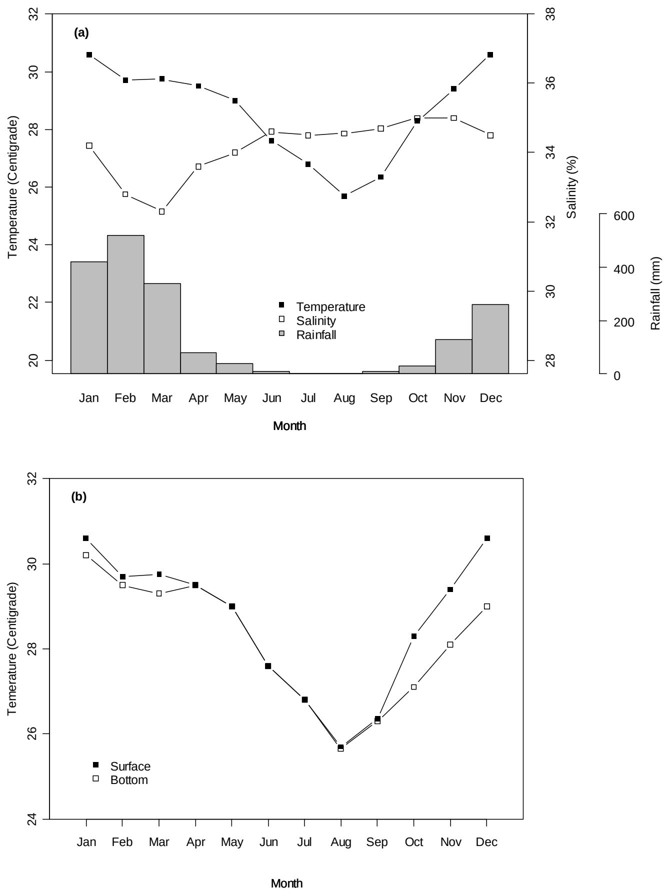


Figure 2: **a)** Mean monthly surface temperature (°C) and Salinity (%) in Albatross Bay over 6 y and mean monthly rainfall (mm) recorded at Weipa between March 1986 and March 1992; **b)** mean monthly surface and bottom temperatures at offshore stations (> 15m depth) in Albatross bay over 6y.

Seasonal variation in size structure of female population.

New recruits, prawns about 18 to 35mm CL, were most abundant during the summer months of January, February and March. A small proportion (60 %) of these recruits (~6 month old), were below the size of first maturity (Figure 3) (Crocos and Kerr (1983) suggest 25 mm CL). If they survived the fishing season in April, the females from this cohort reached spawning size and contributed significantly to the late spring/early summer spawning (September, October, November). Larger females (>30 mm CL) were relatively scarce during the early summer months (January and February) compared to the abundance of the 18 to 30 mm CL cohort. However, by August, the size of females had increased to 35 to 45 mm CL (Figure 3). From then on, these animals were present at a relatively low abundance, and persisted through the spring months and by November they had grown to 45 to 50 mm CL.

The fishing season usually commences during the month of April and up to 80% of the population is caught in the 2 months following peak recruitment (i.e. April, May). Abundance after the fishing season, from May through to October, is low. During the spring months (Sept-Nov) the potential spawning population consisted of two cohorts; ~6 month old individuals, 25 to 30 mm CL and ~12 month old individuals, 35 to 50 mm CL (Figure 3).

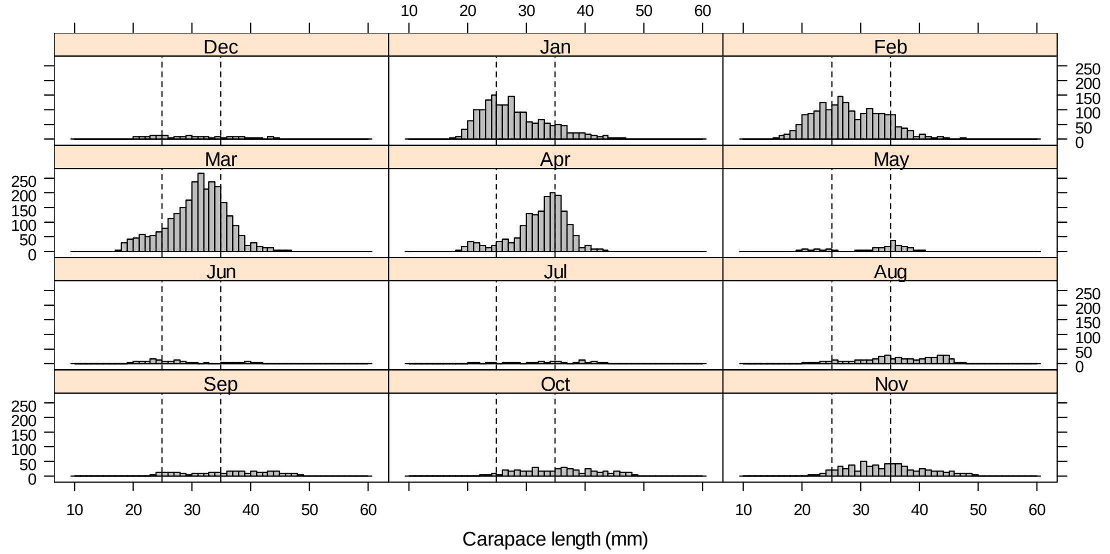


Figure 3: *Penaeus merguiensis.* Mean monthly length-frequency distribution of females over 6 yr of study (combined data) [*dashed line* at 25 *mm CL* lower size limit of females that could potentially contribute to spawning; *dashed line at 35 mm CL* arbitrary indication of upper size limit of prawns deemed to be new recruits to population].

Seasonality in spawning:

Abundance of females

Over the 6 y of the study, the mean monthly female abundance showed a strong seasonal pattern. Abundance increased in January (44.90 catch per unit effort, CPUE) due to new recruits entering the fishery, and peaked in March (438.00 CPUE), then declined steadily through to July (2.55 CPUE). There was a small increase in abundance from October (9.36 CPUE) to November (8.60 CPUE) due to the presence of the large spawners; then abundance declined slightly again in December (7.85 CPUE) (Figure 4a).

Despite the strong seasonal pattern in abundance, the average size of seasonal abundance of females varied between years. Each year, abundance increased in January or February, due to large numbers of sub-adults recruiting to the population, and continued to increase through the summer months to a high in February/March. Abundance then declined sharply from April, after the opening of the fishing season.. Over the 6 y of the study, during the period from September to November a small peak in abundance occurred, mostly large females (≥35 mm CL) (Figure 3, Figure 5a).

Proportion of spawning females

Over the 6 y period of the study, the mean monthly proportion of female prawns that were spawning also showed a strong seasonal pattern (Figure 4b). In January when prawn abundance was high, only 30.8% of the female population was spawning. The proportion decreased to as few as 7.4% in April, over a period when abundance peaked. From August, the proportion of females spawning increasing rapidly to a peak of 68% in October, followed by a decline to 40% or lower by December/January. Despite the high proportion of the population spawning in spring each year (September to November), abundance was low during this period.

Although a consistent seasonal pattern was evident, the proportion of spawners in each month varied widely from year to year over the 6 year period (Figure 5b). For example, in November 1991 88% of females were spawning, compared to 43% in September 1987. In some years the lowest proportion of spawners was in February, but in other years it was in March or April.

Population Fecundity Index

Over the 6 y study, the long term seasonal pattern of PFI showed the highest values from January to April with a peak in March (mean 2.2 units) (Figure 4c). Most of the prawns in the population at this time were small females (25 to 35 mm CL) that had newly recruited to the fishery. A smaller component were larger females (>40 mm CL) which were survivors from the previous year's stock. PFI values were lower from May (0.06) to August (0.11), due to a decrease in the abundance of females (Figure 4a) and a lower proportion of them in spawning condition (Figure 4b). From August through to December values increased slightly with a peak of 0.34 PFI units in October (Figure 4c). The small spring peak was due to the high proportion of large fecund females, even though prawn abundance at that time of year is very low.

Although a clear pattern is evident over the 6 year study, monthly Population Fecundity Index values varied from year to year and month to month. The highest PFI values were in March in most years but in January in 1991 (Figure 5c).

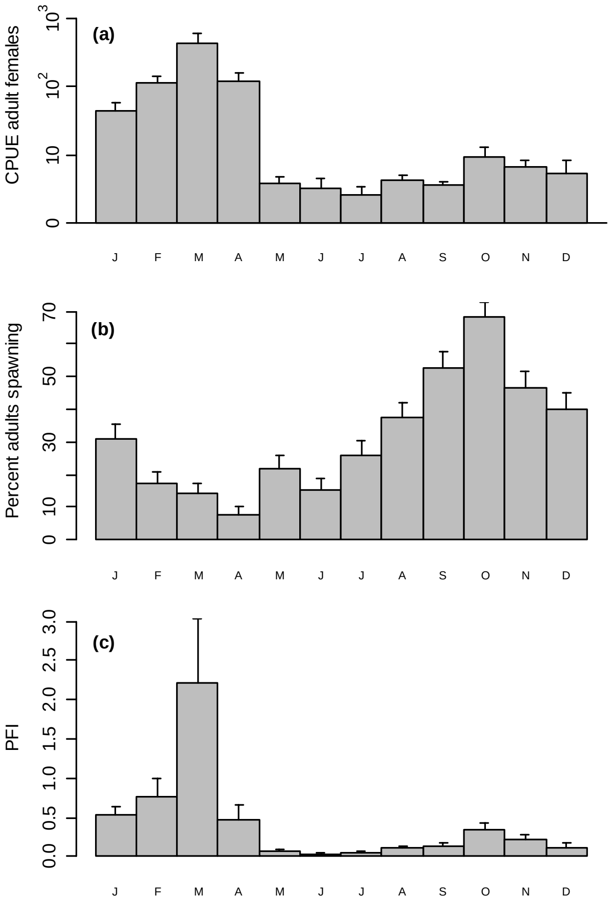


Figure 4: *Penaeus merguiensis.* Mean monthly variability in reproductive parameters for adult females over 6y. Error bars indicate one standard error of mean.

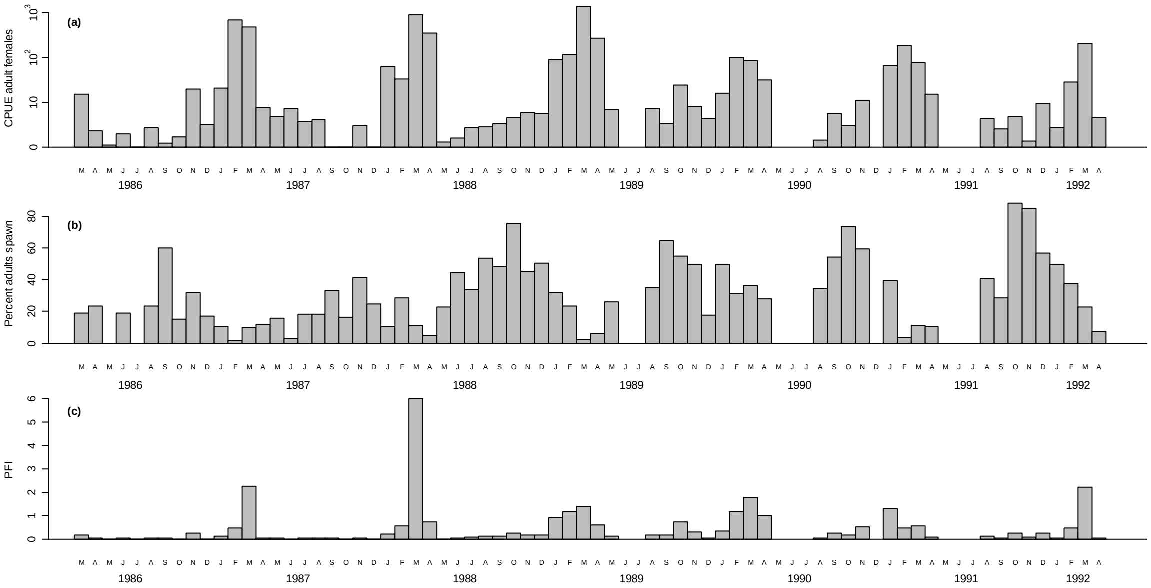


Figure 5: *Penaues merguiensis*. Monthly variability in reproductive parameters for adult females (≥25 mm CL) in each of 6 y in Albatross Bay) Mean values are for each month over 10 standard sampling stations (Group 1); **a)** Relative abundance of adult females (*CPUE* number caught per standard trawl); **b)** percentage of adult females spawning; **c)** population fecundity index (*PFI*). Data plotted according to central date of each sampling cruise; no samples were taken in June, July and December 1990 or in May, June and July 1991).

Size-class and age-class composition of spawning populations.

The size composition of the female population during the main spring spawning (August to November) is composed of two cohorts (Figure 3, Figure 6). The larger-sized cohort (median CL ~35 mm) is derived from 12 month old individuals that were spawned in spring and entered the offshore population in the following summer (Dec – Feb). The cohort of smaller size females (median CL ~25 mm) is consistent with recruitment from the peak of estuarine juveniles present in April (Vance et al 1998) which is derived from spawning in the previous late summer.

It is evident that both the spring and autumn cohorts contribute to the reproductive output during the spring spawning (August to December) each year,. However the spring cohort (12 month old animals) dominates the reproductive output: its mean PFI values ranged from 0.03 to 0.30. The reproductive output for the 6 month old spawners ranged between 0.01 to 0.05 (Figure 6). Over the six years the relative contributions of the two age classes to reproductive output varied widely from year to year. The highest value for the 6-month old cohort was in 1989 with a value of 0.05, while in 1987 it was only 0.01. The highest value for the 12 month old cohort was in 1989 with a PFI value of 0.30 and was due to the large size of the spawning females (Figure 6).

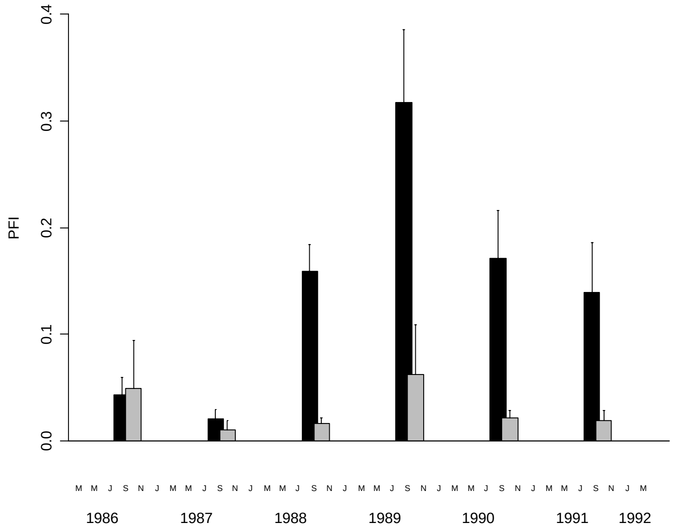
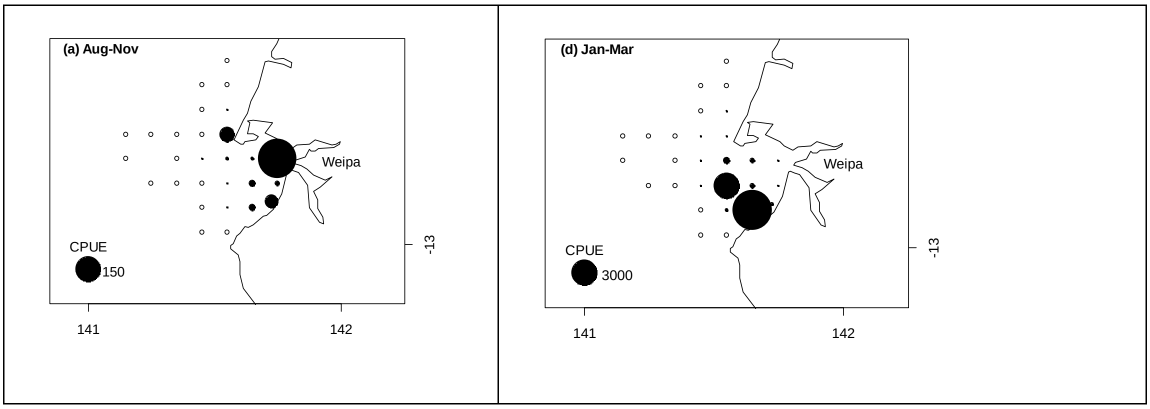


Figure 6: *Penaeus merguiensis.* Relative contributions of spring and autumn cohorts (~ 12 and ~6 month-old, black and gray histograms, respectively) to population fecundity index during major spring spawning period in each of the 6 yr. Error bars indicate one standard error of mean.

Spatial distribution of spawning.

Throughout spring (August to November) the abundance of adult females was highest in shallow depths of less than 10 m (74 CPUE units) adjacent to the estuary mouth. Abundance was lower in depths >15 m (10.5 CPUE units) with no prawns present beyond 20 to 25 m depth (Figure 7a). A high percentage (50 to 69%) of females were in spawning condition throughout Albatross Bay in waters < 20 m deep (Figure 7b). Spawning output (as measured by the PFI) varied; it had the highest values in depths of less than 10m adjacent to the estuary mouth. Inshore stations had values of 0.1-0.5 PFI. In waters deeper than 10m the PFI values were markedly lower 0.01 to 0.08 PFI. There was no evidence of significant spawning beyond the 20m depths (Figure 7c).

During autumn (January to March), adult females were most abundant in shallow waters in the southeast of Albatross Bay 10 to 20 m (1116 CPUE units) and lower in depths over 20 m (84 CPUE units) (Figure 7d). The highest percentage of females that were spawning (29%) were in very shallow waters (~6 m, in the south east). Offshore (>20 m), the percentage of females in spawning condition was low (<5 %) (Figure 7e). PFI values were highest (1.11) in waters less than 10 m depth in the south east of Albatross Bay (Figure 7f).



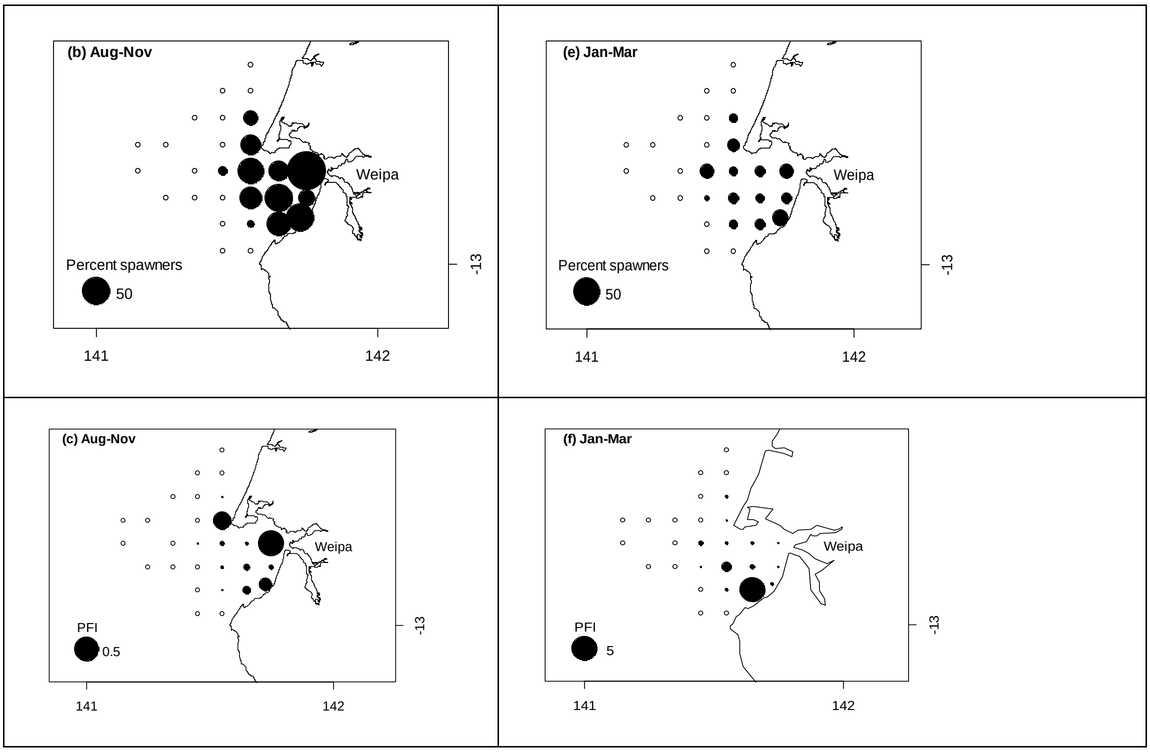


Figure 7: *Penaeus merguiensis.* Spatial distribution of population spawning attributes for August to November (**a, b, c,**) and January to March (**d, e, f,**) spawning periods. Mean of 6 y, 1986 to 1991. **a, d.** abundance of adult females, CPUE; **b, e.** proportion of adult females spawning, %; **c, f.** population fecundity index, PFI **.** Data circles scaled according to key in each graph (*open circles* zero values). For depth contours see Figure 1.

Discussion

Life history patterns

Penaeid prawns have complex life-history dynamics that vary markedly both with species and between species. For all known members of the family, 4 types of life cycles have been distinguished with some overlap. This includes whether they are predominantly estuarine, inshore or offshore and whether they are demersal or pelagic. The FAO/OSLR Penaeid Recruitment Project (PREP) (Staples and Rothlisberg 1990) used a comparative geographic approach to enhance the understanding of the effects of fishing and environmental impacts on annual recruitment of penaeid prawns. PREP demonstrated a clear latitudinal trend; from a bimodal recruitment pattern near the equator to a unimodal pattern at each of the regions of higher latitude. Rothlisberg *et al.* (1985) also suggested that the basic life-history for *P. merguiensis* throughout its range consists of two populations of approximately equal size (spring and autumn populations) with a life-cycle duration of 6 months. In the Gulf of Carpentaria, they proposed that a variation of this pattern was imposed by the short wet season; so that the two populations were of unequal size and only the autumn or early-dry season population supported the offshore commercial fishery (Rothlisberg *et al.* 1985).

Although a significant proportion of females may be capable of spawning all year round, the reproductive output of the population is determined by the seasonal cycles of prawn abundance and the size of the spawners (which affects fecundity), as well as the proportion of females actually spawning (Garcia 1977, Crocos 1985, 1987a). Moderating this ‘biological potential’ for effective spawning are limitations imposed by key environmental processes: (1) availability of phyto- and zooplankton that support prawn larvae during life stages; (2) hydrodynamic circulation patterns that facilitate the inshore advection of postlarvae; and (3) the availability of suitable inshore nursery habitats. If the postlarvae reach the nursery habitats, other biological and environmental process determine their immigration, survival and emigration offshore to reach the fishery (Vance *et al.* 1998).

Defining effective spawning

The effectiveness of spawning may be defined as the subset of the reproductive output that ultimately contributes to stock renewal. Effective spawning is a critical parameter for input controls and effective management of commercial fisheries (Dichmont *et al.* 2003). The notion of effective spawning encompasses seasonal spawning patterns, spawning areas, spawner age, and even spawner performance components (Crocos and van der Velde 1995, Crocos and Coman, 1997). A measure of the critical periods of seasonal spawning, or "effective spawning", therefore combines observed seasonal patterns in spawning output and observed seasonal patterns of abundance of larvae and estuarine juveniles that result from these spawnings. Comparisons of the critical spawning times in each year can then be used to examine interannual differences in the effective reproductive output of the *P. merguiensis* populations.

The use of an index of population fecundity provides a more meaningful account of reproductive output than a simple measurement of the percentage of ovigerous females in crustacean populations (Crocos and Kerr 1983). The simple method of a percentage measurement can give a biased measure of population reproduction in *P .merguiensis* populations; as demonstrated by Munro (1975), Thubthimsang (1976) and Chong (1980). On the basis of the percentage of ripe and spent females observed, Munro (1975) suggested that most of the spawning of *P. merguiensis* in the southeastern Gulf occurred in spring and early summer. However, this approach did not take account of variable population size across seasons, or prevailing currents that determine whether larvae can actually reach the estuarine nursery ground.

In the 1980s hydrodynamic modeling of water currents and larval behaviour studies in the south-eastern Gulf of Carpentaria showed that most of the *P. merguiensis* larvae produced during the autumn fishing season (when adult prawns are most abundant) are lost to the population due to unfavourable currents (Rothlisberg 1982, Rothlisberg *et al.* 1983). The combination of hydrodynamics and behaviour of larvae and postlarvae define the spatial extent of effective spawning (i.e. the effective spawning envelope) for the banana prawns in Albatross Bay (Rothlisberg *et al.* 1996, Condie et al 1999). The interplay of biological and physical parameters demonstrates a more complex system of recruitment for penaeids with an estuarine juvenile phase than envisaged by researchers in the 1970s and 1980s.

Seasonal and interannual variation in spawning patterns

In the present 6-y study in the northeastern Gulf of Carpentaria, the measurement of the population fecundity index found a bimodal annual pattern with a small but critical peak of reproductive activity in spring (August-November); and a larger peak in autumn(February-April) (Figure 4c). However, there was variability between years. Each of the 6 years had large late summer or early autumn peaks with one year (1987) having an extraordinary large peak which was due to the proportion of large size females in spawning condition (Figure 5c).

The clearest way to demonstrate which of the spawning peaks is the effective one is a comparative analysis of the abundance of larval and estuarine juvenile stages (Crocos and van der Velde 1995). Rothlisberg *et al.* (unpublished) found two seasonal peaks of larval abundance similar in relative size to the PFI peaks – a large peak during the summer months (January to April) and a much smaller peak during the spring months (September to November). However, Vance *et al.* (1998) found two seasonal peaks of estuarine juvenile abundance, but they were out of phase with the offshore egg and larval peaks. In November to January there is a large peak of postlarvae and early juveniles in the estuary and another smaller peak during autumn. Vance *et al.* (1998) felt that this mismatch was caused by both differential postlarval delivery and seasonal and interannual changes in suitability of the nursery ground (i.e. variable periods of low salinity in the wet season) which prevented postlarval ingress and juvenile settlement.. Therefore, the spawning period during spring (September –November), which gives rise to the major estuarine juvenile peak in November, is the critical one that contributes to offshore stock renewal in early summer and autumn (January to March).

Relative contribution of spring and autumn cohorts to spring spawning.

The effective spring spawning consists of two cohorts of females: 12-month old prawns spawned the previous spring and 6-month old prawns spawned the previous autumn. The older spring cohort was the major contributor to the spawning period (Figure 7). During spring a high proportion of large females (>35mm CL) were in spawning condition compared to the smaller sized prawns in the autumn cohort. During the spring spawning the smaller prawn size cohort was less significant as a smaller proportion of females were in spawning condition. This smaller size cohort did contribute consistently over the six years though. Lucas *et al.* (1979) suggested that ≈ 85% of the population is removed during the intensive March-April fishing season. It is therefore, the small proportion of the stock remaining after the fishing ceases that contributes to the spring spawning. This is a critical factor for the long-term sustainability of the banana prawn fishery and also an important factor in contributing to annual variation of prawn catches (Dichmont *et al* 2006*).* Although the abundance of 12-month old spawners was always very low, these were largely responsible for the single annual pulse of recruitment to the commercial fishery in autumn.

Crocos and van der Velde (1995) determined for the first time a two-cohort composition of spring spawners in *Penaeus semisulcatus* in Albatross Bay and Crocos and Kerr (1983) also observed a two-cohort composition in *Penaeus merguiensis* in the southeastern Gulf of Carpentaria*.*

Laboratory trials have demonstrated that the older and significantly larger females produce higher rates of spawning, larval survival and therefore larval production than the younger individuals (Crocos and Coman 1997). The age-class composition of spawners together with PFI values influences the overall reproductive output during the spring spawning. The production of larvae, and the subsequent contribution to the next year's stock, would be higher from the older 12 month old cohort; i.e. the remnant of the commercial fishing earlier in the year. The effects of this age-class structure, is important when developing models for stock recruitment relationships and fishery-management strategies on the basis of life history dynamics (Somers 1990; Somers and Kirkwood 1991, Dichmont *et al.* 2003).

Spatial distribution of spawning activity.

Seasonal and inter-annual variation in spatial distribution of spawning activity is complex, and a critical part of spawning studies given its impact on defining the effective spawning population. Crocos and Kerr (1983) observed a tendency for more spawning activity of *P. merguiensis* in deeper waters and increased egg production in spring in the southeastern Gulf of Carpentaria. Their spatial findings are in contrast to the current study; we found consistently higher densities of spawners in shallow depths. Crucially, the abundance of spawners was greatest adjacent to the mouth of the estuary in spring, but not in autumn when they were dominant to the south-west of the estuary entrance. Most reproductive activity occurred within the depth band of 8-10 m during the spring spawning and within 10 to 20 m during the late-summer-autumn spawning. The sampling during this study was more intense and for a longer period of time than the Crocos and Kerr study, hence giving us a better understanding of the distribution of the species.

It cannot be assumed that all spawners contribute equally to subsequent recruitment to the fishery even if the spatial distribution of spawners is known. Eggs spawned are only effective if they are in a suitable hatching environment and the larvae are successful at catching food to support growth and at reaching a suitable nursery habitat. This is dependent on prevailing hydrographic regimes that determine the direction, extent and rate of larval advection. Although little is known about hatching environment there is a significant amount known on larval advection dynamics. Rothlisberg (1982), Rothlisberg *et al.* 1983, 1995, and 1996) used data on the vertical migratory behaviour of larvae and the hydrography to estimate how far penaeid prawn larvae in the southeastern Gulf of Carpentaria could be advected, and found a seasonal change in the direction of advection. There was strong evidence that the transport of prawn larvae to coastal nursery habitats in northern Australia is controlled by interactions between tidal flows and the vertical migration of the larvae. The seasonal variable advection pattern demonstrates dramatic consequences to postlarval recruitment to nursery grounds. It showed that the larvae were actually transported away from the nursery grounds into waters were they could not naturally survive during the warmer months (summer/ early autumn) This therefore resulted in very low numbers of postlarvae reaching the nursery ground; hence a major spawning peak had very little contribution to the adult population. Therefore, it is important to determine the location of spawning in relation to local larval advection regimes to determine effective spawning populations. Rothlisberg *et al.* (1996) modeled larval behaviour scenarios in Albatross Bay that provided estimates of the size of the spawning area from which larva and postlarvae are drawn to their estuarine nursery grounds populations – referred to as advection envelope.

Our results show that a majority of *P. merguiensis* in spring spawn close to the nursery grounds, near the entrance to the Embley River estuary. This is in contrast to the species *Penaeus semisulcatus* which has an intensive offshore migration and spawns over a much wider geographical area (Crocos and van der Velde 1995).

Conclusions

Sustainability of any fishery can only be successful if stringent management procedures are followed (Dichmont *et al.* 2003). Stock assessment models provide information on stock levels to develop and implement management strategies. Prior to this study, population models that have been used to assess spawning stock recruitment relationships assumed one effective spawning per year which we have confirmed. The surviving spring stock contributes the effective spawning each year; the more abundant autumn stock (which is fished earlier that year) does not. The model had correctly assumed that the abundance and distribution of the adult population directly represented the spawning stock.

The confirmation of one effective spawning stock, which aggregate close inshore during the critical times of the year, contrasts to the South East Gulf where the spawning is carried out in deeper waters (Crocos and Kerr 1983). Together with the seasonal direction of advection of larvae, these factors have led to regional closures to ensure the stocks are protected and the fishery well-managed. This study has clearly defined a more detailed estimate of spawning stock (as a subset of the population) and demonstrates the importance of the “effective spawning stock” for *Penaeus merguiensis* in the Albatross Bay region.

The findings of this study, namely: a clearer definition of the different spawning cohorts’ performance; their spatial distribution; and their contribution to the subsequent fished stock are incorporated into the management regimes of the banana prawn component of the Northern Prawn Fishery. This approach can then be applied to other species of penaeids and possibly to other fisheries.

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IV-2. Qualitative Modelling of the Weipa Banana Prawn Ecosystem and Fishery

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Introduction

The goal of the overall study has been to better understand why the commercial catch of banana prawns has declined in the Weipa region of Australia's northern prawn fishery. An array of possible explanations has been considered over the course of this study, and three main hypotheses remain as viable explanations for a decline in catch (Okey and Dichmont 2005):

H1. Prawn recruitment has collapsed due to overfishing.
H2. Recruitment has collapsed due to a change in the prawn's environment.
H3. Adult banana prawns are still present, but fishers cannot find or catch them because:
    a. The searching power of the fishing fleet has declined.
    b. Adult banana prawns are staying inshore away from fishing grounds.
    c. Adult banana prawns are no longer schooling.

The purpose of this work has been to draw together what is known about the banana prawn's biology, ecosystem, and fishery within a qualitative modelling framework that, in a rigorous manner, allows us to organize our thinking about how the system works. From this knowledge relatively simple models are developed that are used to the explore possible dynamics of the system, and from which we can hopefully increase our understanding of the system, distinguish what is likely behaviour of the system from what is not, and to pose new and testable hypotheses for future management and research efforts. Another purpose of qualitative modelling is to provide a means to juxtapose and compare results from other modelling techniques, such as those with statistical and quantitatively derivations, so as to better distinguish what is a general and emergent property of the system from what is merely an artefact of a specific modelling assumption. A useful attribute of the qualitative modelling approach is the ability to quickly develop and combine sub-models for different elements of a system e.g. biology, fishery, economics, environmental influences. The behaviour of the overall model can be evaluated, as well as the behaviour of its component sub-models, and compared with the behaviour of models with a simplified structure.

Our conception of the Weipa banana prawn ecosystem and fishery evolved from simple models, with only a few variables, to more complicated models with many variables. During the process of building models, there can be an impetus to include a large number of variables and interactions. This may lead to large, unwieldy models, which offer only a limited potential to understand the basic dynamics of the system. However, it is possible to identify a core of relevant variables, or a subsystem, that encompasses essential feedbacks and dynamics, and from which we can build alternative models that inform and lead our research.

Qualitative models: from growth equations to community matrices and signed digraphs

The relationships between variables can be represented by equations, matrices, and also graphically. The simplest model of the Weipa banana prawn ecosystem could be portrayed through three population variables in a system of Lotka–Volterra-type growth equations

$$\begin{aligned}
&\text{Prawn food}: \frac{\mathrm{d}N_1}{\mathrm{d}t} = N_1\left(-\alpha_{1,1}N_1 - \alpha_{1,2}N_2 + \beta_1\right), \\
&\text{Prawns}: \quad \frac{\mathrm{d}N_2}{\mathrm{d}t} = N_2\left(\alpha_{2,1}N_1 - \alpha_{2,3}N_3 - \delta_2\right), \\
&\text{Predators}: \frac{\mathrm{d}N_3}{\mathrm{d}t} = N_3\left(\alpha_{3,2}N_2 - \delta_3\right) + R,
\end{aligned} \qquad (1)$$

where variable N_1 is prawn food and prey, N_2 is the banana prawn population, and N_3 is a guild of predators. The alpha terms are the density-dependent interaction coefficients, which describe the effect of one species upon another, or the effect of a species on itself (*e.g.* as in density dependent mortality). The beta and delta terms respectively denote density-independent rates of birth and death, and R is a birth rate of the top predator supported by consumption of a resource external to the model system. The purpose of these equations is simply to account for the births and deaths in each population and also the effect that one population has on the rate of birth or death of another.

When the system is at or near equilibrium, direct effects between species are formally defined from the first partials of the per capita form (*i.e.* $\mathrm{d}N/N\mathrm{d}t$) of the growth equations

$$a_{ij} = \partial\left(\tfrac{\mathrm{d}N_i}{N_i\mathrm{d}t}\right)\Big/\partial N_j \,. \qquad (2)$$

These are organized in the community matrix **A**, which for the above system is:

$$\mathbf{A} = \begin{bmatrix} -\alpha_{1,1} & -\alpha_{1,2} & 0 \\ \alpha_{2,1} & 0 & -\alpha_{2,3} \\ 0 & \alpha_{3,2} & -R/N_3^2 \end{bmatrix}. \qquad (3)$$

The community matrix in Eq. (5) corresponds to the signed digraph (i.e. sign directed graph) of Figure 8, where interaction terms are shown as links between variables. These

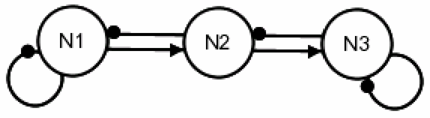


Figure 8: Signed digraph of minimum complexity model for Weipa banana prawn ecosystem, corresponding to variables in Eq. (1); where banana prawns (N_2) are sustained by a food resource (N_1) and are consumed by a guild of generalist predators (N_3). Links between variables denote direct effects, as described by the community matrix of Eq. (3). Links ending in an arrow denote a positive effect, those ending in a filled circle denote a negative effect, and links connecting a variable to itself denote self-effects.

Links have sign values according to the direct effect of one variable upon another. For instance, predators impart a rate of death to their prey, which corresponds to a negative link, ending in a filled circle (—•). The nutritional benefit of prey consumption contributes a positive effect to the predator's rate of birth, and is depicted as a link ending in an arrow (→). Links originating and ending in the same variable (↻,↻) describe self-effects.

Often elements of the community matrix are simply the α_{ij} interaction coefficients of the system, but they can also include terms that are less obvious. For instance, consumption by the top predator of a prey resource from outside the model system imparts a negative self-effect to the predator of the form $-R/N_3^2$, such that predators exhibit self-damping feedback. Within the context of the model then, the top predator here behaves as though it is self-regulated. Thus external resources will act as though they are intrinsic to the variable through which they enter the system.

In developing qualitative models for the Weipa banana prawn ecosystem and fishery, we started with simple models for the prawn life cycle and then built in links to environmental influences, and subsystems involving food resources, predators, and fishery harvest.

Life-stage models

Since juvenile and adult prawns live in different habitats (*i.e.* estuary and ocean), and are subjected to different sources of mortality and regulation, we can split a single population variable into a multiple life-stages (Figure 9), and corresponding equations could take the following form

$$\begin{aligned}\text{Juvenile}: \frac{\mathrm{d}J}{J\mathrm{d}t} &= f_A \frac{A}{J} - f_J\ ,\\ \text{Adult}: \frac{\mathrm{d}A}{A\mathrm{d}t} &= f_J \frac{J}{A} - \delta_A\ .\end{aligned} \tag{4}$$

Here variable J is juvenile prawns in the estuary, variable A is adult prawns in the ocean, f_J is the rate of maturation and migration of juveniles from the estuary, f_A is the rate of reproduction and larval transport into the estuary and δ_A is the rate of loss of adults from the population *i.e.* total mortality from fishing and natural causes. While there are no specific self-regulation coefficients in the above equations, they do in fact emerge when we construct the community matrix **A**, which for Eq. (4) is

$$\mathbf{A} = \begin{bmatrix} -f_A \dfrac{A}{J^2} & \dfrac{f_A}{J} \\ \dfrac{f_J}{A} & -f_J \dfrac{J}{A^2} \end{bmatrix}. \tag{5}$$

Note the sign structure of this matrix and the corresponding signed digraph of Figure 9*b*, here the mutualistic relationship between juvenile and adult prawns is non-trophic, rather it is based on life-stage development and reproduction.

The division of a single variable into multiple variables is valid as long as the sign of the feedback of the single variable is matched by the overall feedback of the larger system. In this case, the single variable for prawns in Eq. (1) and Figure 8 has no self-regulation, *i.e.* $\mathbf{A}_{2,2} = 0$, and the overall feedback of the system of equations in Eq. (4) is also zero—*i.e.* the determinant of matrix **A** in Eq. (5) defines overall feedback, and has algebraic terms that cancel out, such that $(f_A A/J^2)(f_J J/A^2)-(f_A/J)(f_J/A) = 0$. Additional life stages can also be incorporated within this basic framework and the criteria for zero overall feedback will always be met.

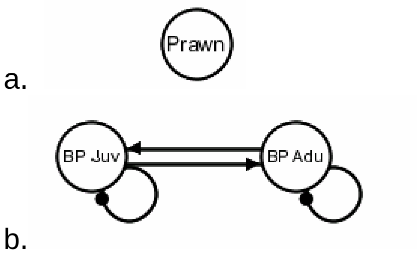


Figure 9: Signed digraph of a) the banana prawn (BP) variable from Figure 8 and b) an equivalent multiple life-stage model split into juvenile (Juv) and adult (Adu) variables corresponding to the community matrix of Eq. (5).

Harvest subsystem

An interest in harvest dynamics leads to a detailed treatment of harvest as a subsystem of catch, effort, and market price (Figure 10). In Figure 10*a* the harvest variable is self-damped, reflecting limitation from a variety of management and market forces, such as statutory fishing rights, seasonal closures, gear restrictions, access to markets, and market price of prawns, all of which ultimately limit the number of boats joining the fishery. In Figure 10*b* fishery harvest is depicted as a three variable subsystem composed of prawn catch, fishing effort (boat days), and market price of banana prawns. Here catch suppresses market price via a supply-demand relationship, and the influence of market sectors external to the processing of catch of wild prawns imparts self-damping to their price. Market price is the primary driver of fishing effort, which is also self-regulated through statutory limitations imposed by the Australian Fisheries Management Authority. Prawn catchability is implicit within the interactions associated with the banana prawn stock and its fishery. In Figure 10*c* and 3*d* the price paid for prawns is set by a global market. Here market price is insensitive to the amount of catch and the link from catch to market price is severed. In 3*d* effort expended in the fishery follows catch. The product of this mutualistic relationship constitutes a positive feedback cycle between catch and effort, such that lower catch will lead to reduced effort, which in turn results in lower catch, etc.

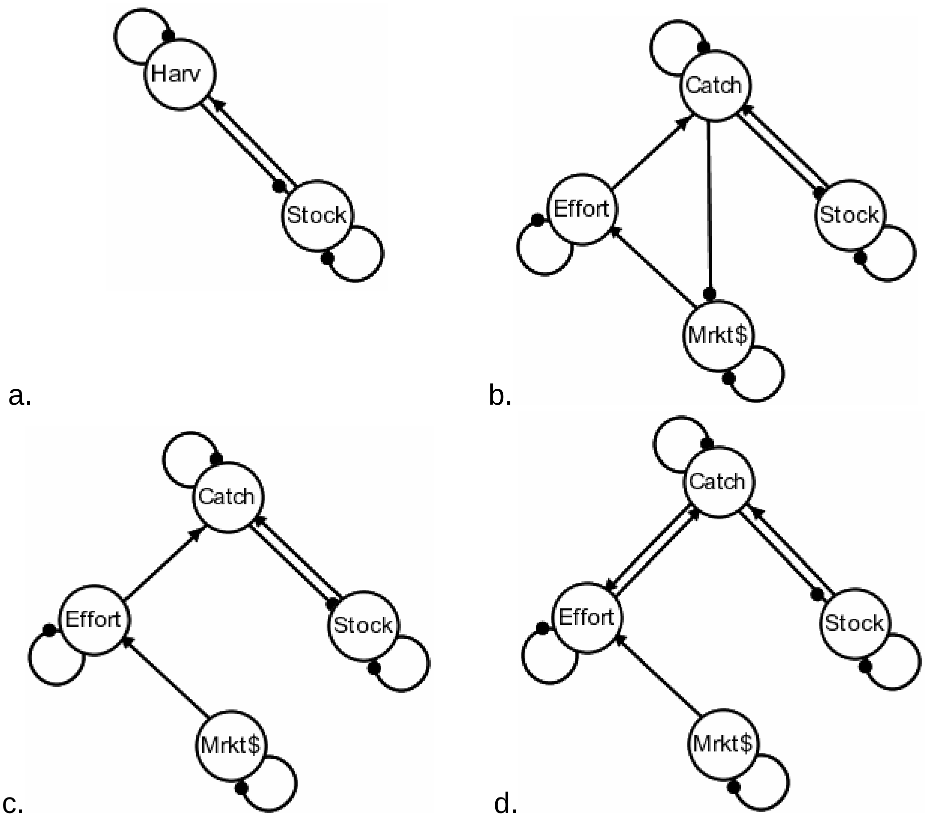


Figure 10: Signed digraph of a) local harvest (Harv) variable and fishery stock, and b–d) alternative models where the harvest variable is split into a subsystem of catch, effort (boat days) and market price (Mrkt$). In b) market price is affected by local catch, while in c) and d) it is not, but rather controlled by a global market. In d) fishing effort follows catch.

The overall feedback of the harvest subsystems in Figure 10*b* and Figure 10*c* is negative and composed of the product of the links between effort, catch, and market price. As such these subsystems will exhibit self-damped dynamics and can be taken as equivalent representations of the self-damped harvest variable in Figure 10*a*. The harvest subsystem in Figure 10*b*, however, is not equivalent, as there is positive feedback between the catch and the effort variables. The sign of the overall feedback of this subsystem is ambiguous, and can be either positive, negative, or zero.

The above models are based on a level of fishery harvest that is sustainable and allows for a sufficient level of recruitment in the stock to offset its losses to harvest mortality. Here the stock can respond to a perturbation with stabilizing, self-damped feedback, such that its rate of recruitment will increase when its population is decreased, allowing for stock recovery. However, this response can be diminished by excessive harvest to the point that the feedback properties of the stock variable are reversed and the system is destabilized. For example, a stock that forms dense aggregations that can be targeted by the fishery is vulnerable to excessive levels of harvest. This can then create a relationship of “hyperstability” between catch per unit effort (CPUE) and stock size (Hilborn and Walters 2003), i.e. the fishery can maintain a relatively high level of exploitation and CPUE even while the overall abundance of the stock declines. This relationship is likely to apply to banana prawns in the Northern Prawn Fishery, which form dense “balls” that are targeted by bottom trawls. Consider a fishery for a stock that follows logistic growth, with a carrying capacity K_2 equal to its pre-harvest or virgin biomass, and where r is the stock’s intrinsic rate of growth

$$\begin{aligned} \text{Harvest}: \frac{\mathrm{d}N_1}{N_1\mathrm{d}t} &= -\alpha_{1,1}N_1 + \alpha_{1,2}N_2\left(1+\frac{N_2}{K_2}\right)^{-1} \\ \text{Stock}: \quad \frac{\mathrm{d}N_2}{N_2\mathrm{d}t} &= r_2\left(1-\frac{N_2}{K_2}\right) - \alpha_{2,1}N_1\left(1+\frac{N_2}{K_2}\right)^{-1}. \end{aligned} \tag{6}$$

Here the standard per capita rate of harvest, $\alpha_{ij}N_j$, is modified by the function $(1+N_2/K_2)^{-1}$; accordingly, as harvest lowers the population below its virgin biomass the per capita rate of fishing mortality increases. Within the community matrix this function introduces positive feedback to the self-regulation of the stock in $\mathbf{A}_{2,2}$

$$\mathbf{A} = \begin{bmatrix} -\alpha_{1,1} & \alpha_{1,2}\dfrac{K_2^2}{(K_2+N_2)^2} \\ -\alpha_{2,1}\dfrac{K_2}{K_2+N_2} & -\dfrac{r}{K_2} + \alpha_{2,1}\dfrac{N_1K_2}{(K_2+N_2)^2} \end{bmatrix}. \tag{7}$$

When the level of harvest mortality is sufficiently high, such that

$$\alpha_{2,1}N_1 > r\frac{(K_2+N_2)^2}{K_2^2}, \tag{8}$$

then the positive term in $\mathbf{A}_{2,2}$ dominates and the stock gains self-enhancing feedback; the signed digraph for the system will then be as in Figure 11.

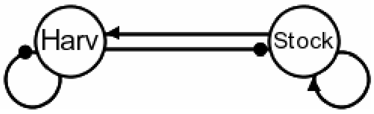


Figure 11: Signed digraph of fishery where there is over-harvest of an aggregating stock; Harv: harvest variable N1 in Eq (6).

The rate of recruitment of a stock regulated by a positive self-effect will not increase in the face of low population density; instead it declines with stock abundance. This destabilizes the system, and creates problems for monitoring and management because even when the stock has been reduced to a mere remnant of its former biomass, CPUE can appear relatively stable over time.

Since the price paid for banana prawns caught in the Weipa fishery is set by a global market, the harvest subsystem of Figure 10*c* was chosen to represent the dynamics of the fishery within the Weipa ecosystem.

Weipa banana prawn ecosystem and fishery

The model in Figure 12 is built around four prawn life-stages, conforming to what Dall *et al.* (1990) classify as a Type II life history — i.e. spawning takes place in marine waters and the juveniles live in estuarine waters. Banana prawn postlarvae settle in mangrove-lined estuaries and juveniles are euryhaline and can tolerate low salinities (down to 5 ppt) in the upper reaches of rivers (Vance *et al.* 1990, 1998). Near the end of their juvenile stage, banana prawns migrate to inshore demersal habitats, and as adults live in deeper offshore areas. The migration of juveniles is influence by prawn size, but can be triggered or accelerated by rainfall and associated effects on river flow and salinity (*i.e.* low salinities stimulate the migration of smaller prawns) (Staples and Vance 1996, Vance *et al.* 1998, Loneragan and Bunn 1999). Spawning adults appear to move to shallow inshore areas near river mouths, but when early summer rains reduce inshore salinities, they move offshore to where they become available to the prawn fishery.

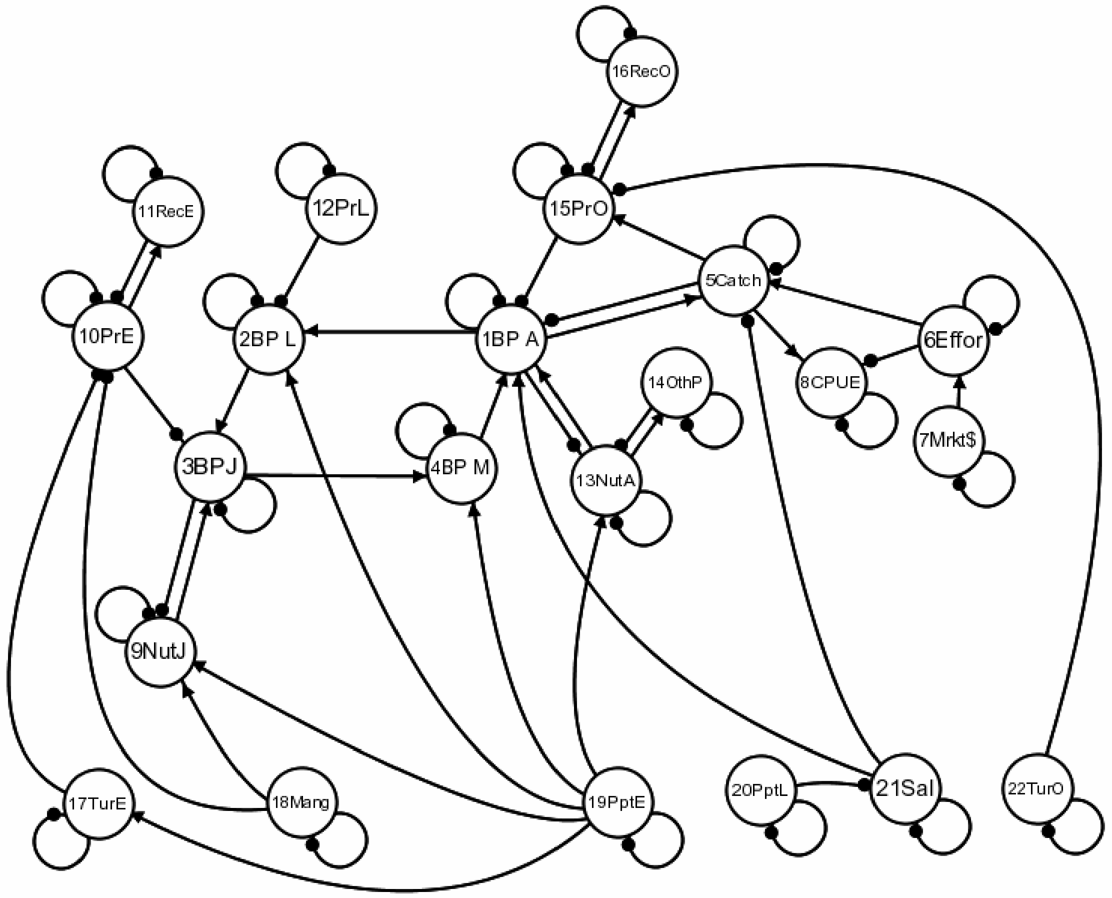


Figure 12: Signed digraph of Weipa banana prawn ecosystem, where numbers 1–16 represent biological and fishery harvest variables and numbers 17–22 are direct effects of physical and biological factors; 1: adult banana prawn, 2: juvenile banana prawn, 3: larval banana prawn, 4: migrant banana prawn, 5: catch of banana prawn, 6: fishery effort, 7: market price for banana prawn, 8: catch per unit effort, 9: juvenile banana prawn nutrition or food, 10: predation pressure in estuary, 11: recreational estuarine fishing, 12: predators of larval banana prawn, 13: adult banana prawn nutrition or food, 14: other prawn species, 15: predation pressure in ocean, 16: recreational ocean fishing, 17: estuarine turbidity, 18: mangrove habitat, 19: early or summer rainfall, 20: late or autumn rainfall, 21: near-shore salinity, 22: ocean turbidity.

The model includes specific resources and predators for individual life stages, and recreational fisheries for top predators in both the estuary and ocean. Since banana prawns constitute a relative minor portion of the system's biomass and an equally minor portion of the total annual food resource of their predators (Salini et al. 1990), changes in their abundance are assumed to have a negligible effect on the biomass of their predators. Therefore the model omits a positive link between banana prawn life-stages and their predator variables (Figure 12, Table 1). Other prawn species (e.g. tiger prawns) have been included as a potential competitor for food resources.

The banana prawn fishery is included as shown in Figure 10*b*, with the added effect of discarded bycatch increasing local predation pressure on adult prawns, primarily through sharks (Hill and Wassenberg 1990, 1992, 2000). A response variable CPUE (no. 8) has been added to track changes in catch per unit effort. Variable no.'s 17–22 represent an array of environmental and biological effects that are known or suspected to influence the banana prawn ecosystem (Table 1). Strictly speaking, these are not variables but factors, and are connected to the system by one-way linkages and do not receive feedback from the system. They are therefore not involved with the essential dynamics of the systems. However, as will be seen below, they permit one to consider how the system responds to changes in one or more factors. For instance, early rainfall (no. 19) directly influences variables 2, 4, 9, and 13, and indirectly affects variable 10 via estuarine turbidity (no. 17) (Figure 12, Table 1). Next we consider the general stability properties of the model system, and then its response to external perturbations.

Table 1: Links between environmental factors and biological variables in the Weipa banana prawn ecosystem model of Figure 12, where effects are listed as "from" and "to" the factor or variable.

Factor or variable no.		
From	To	Effect
1	15	Adult prawns are a minor component of predator diet in marine waters, positive effect negligible.[†]
2	12	Postlarval prawns minor are a component of predator diet in the estuary, positive effect negligible.[†]
3	10	Juvenile prawns are a minor component of predator diet in the estuary, positive effect negligible.[†]
5	15	Shark consumption of discards increases local predation pressure.[‡]
17	10	Turbidity interferes with predator foraging in the estuary.[*, ††]
18	9	Mangroves trap and retain nutrients.[§]
18	10	Mangroves provide refuge from predators and cover in the estuary.[§]
19	2	Summer rainfall increases larval prawn food supply in marine waters.[*]
19	4	Summer rainfall increases prawn migration from estuary.[*, ††]
19	9	Summer rainfall increases juvenile prawn food supply.[*]
19	13	Summer rainfall increases adult prawn food supply.[*]
19	17	Summer rainfall increases turbidity.[*]
20	21	Autumn rainfall decreases near-shore salinity.[*]
21	5	Decreased near-shore salinity increases movement of prawns to fishing grounds, which influences prawn catchability.[*]
21	1	
22	15	Turbidity interferes with predator foraging in marine waters.[*, ††]

[†]: Salini *et al.* (1990).

[‡]: Hill and Wassenberg (1990, 1992, 2000).

[*]: Vance *et al.* (2003).

[§]: Manson *et al.* (2005).

[††]: Dall *et al.* (1990).

Qualitative Stability

The stability of the model was assessed by omitting environmental factors from the full model in Figure 12, and considering only variables 1–16 (Figure 13*a*). While the environmental factors can act as avenues of input and perturbation, they do not receive feedback from the system and thus do not contribute to, or affect, its inherent stability. Rather, it is the feedback among variables 1–16 that determine the essential dynamics of the model ecosystem.

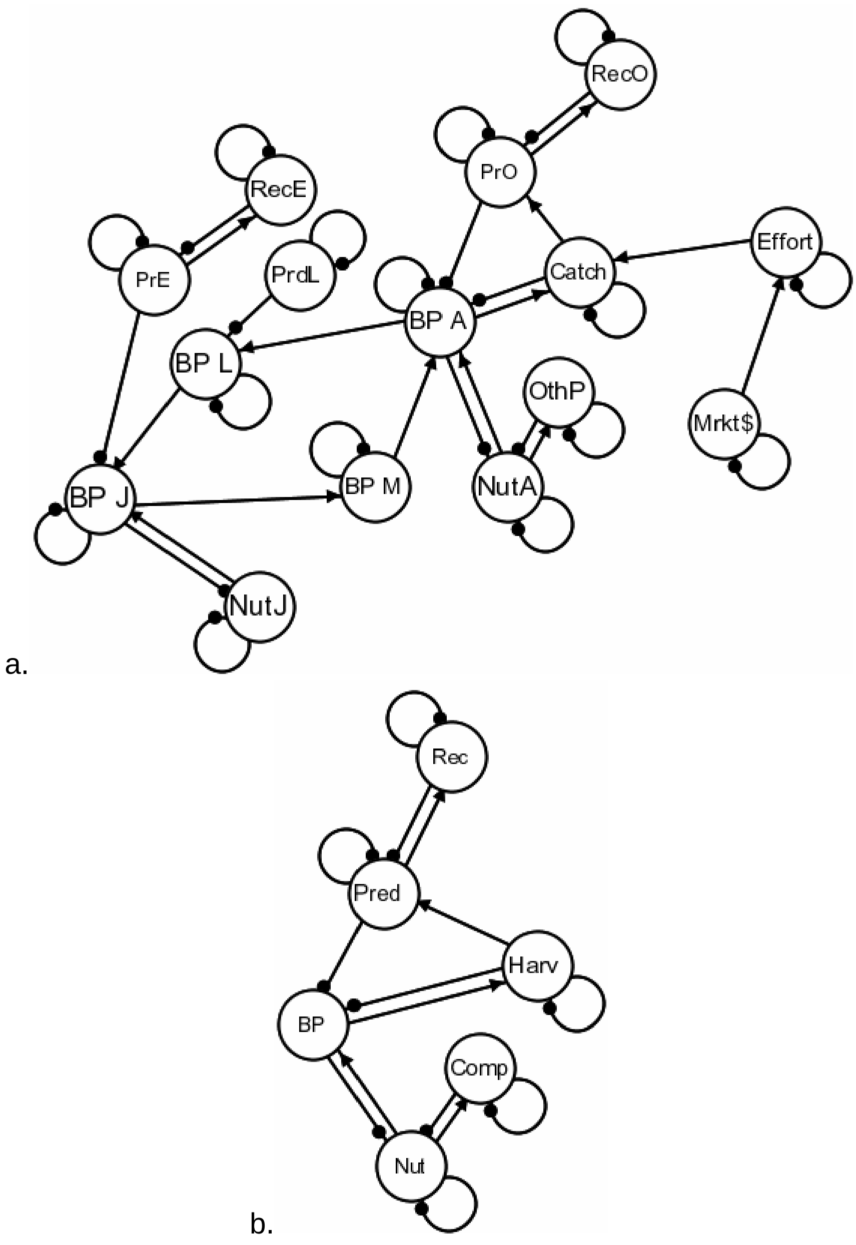


Figure 13: Model of Weipa banana prawn ecosystem and fishery a) with the effects of physical factors omitted, and b) the core system of reduced dimension. Variable definitions in a) are same as those in Figure 12; in b) BP: banana prawns, Comp: competitor for banana prawn food, Harv: banana prawn fishery, Pred: predator, Rec: recreational fisheries, Nut: banana prawn food or nutrition.

While we can conduct an analysis of stability for this system, we can more easily consider an equivalent model of reduced dimension by decomposing the system into independent subsystems. Since we have chosen to omit the positive link to predators from larval and juvenile prawns, we can assess the stability of these predator's subsystems independently of the system coupled to prawns. In the case for both predators, their subsystems are *sign stable*, meaning that given the sign pattern of their interactions, they will be stable for all possible values of interaction strengths in the system. However, the same cannot be done for predators of adult prawns, as they receive feedback through the harvest variable. The prawn life-stage subsystem can now be collapsed back to its equivalent unregulated single variable by combining juvenile and adult food sources (Figure 13*b*). Similarly, the harvest subsystem can be reduced to a single variable with a negative self-effect, which leaves a six variable core model (Figure 13*b*) that has stability properties equivalent to the model system of Figure 13*a*.

The assessment of qualitative stability can be understood in terms of system feedback where stability depends on two criteria describing the overall sign and balance of feedback at each level of the system (Dambacher *et al.* 2003*a*). A system with *n* variables will have *n* levels of feedback. Feedback at the lowest level is composed of the self-effects of each variable, which for all models considered thus far have been either negative or zero. Level two feedback is composed of products of conjunct or disjunct links between pairs of variables, as in the products of predator-prey relationships but also the products of self-effects. Level three feedback incorporates long loops connecting three variables, as well as the products of feedback from lower levels, and so on. The two criteria of stability are that (i) the feedback at each level of the system is negative, and (ii) the feedback at lower levels is greater than feedback at higher levels of the system. Systems that fail criterion (i) are driven from equilibrium by a self-enhancing series of interactions, creating what is commonly described as a vicious cycle. A system that is unstable due to this self-enhancing feedback will diverge from, and never return to, the levels of population abundance of a former equilibrium state. Systems failing criterion (ii) do so by over-correcting in response to a perturbation. This over-correction is caused by the system being controlled more by feedback from long loops than by feedback from shorter loops, leading to undamped oscillations of increasing amplitude.

In Figure 13*b*, only negative feedback is found at all levels of the system, and thus this system can never be unstable due to failure of criterion (i). For the second criterion, however, there is a feedback cycle, or long loop, of length three that is of potential concern. It comes from interactions between banana prawns, their fishery, and their ocean predators (*i.e.* BP→ Harv→ PrO—• BP) (Figure 13). Stability by criterion (ii) requires that the product of these interactions be less than the product of self-effects and predator-prey interactions. In practical terms, instability in this system will arise when discarded bycatch from the prawn fishery supports a relatively high level of predation pressure on banana prawns and when the statutory limitation of the fishery is weak. These conclusions are equally valid for the more detailed models of Figure 12 and Figure 13*a*.

Perturbation response

Perturbations to a system at or near equilibrium can be considered in two general ways. Pulse perturbations are an instantaneous increase or decrease in the level of one of the system variables, say N_j, after which N_j is released. The response through time of all N_i variables in the system is determined by the a_{ij}'s, or the direct interactions between the variables

$$\frac{\mathrm{d}N_i^*}{\mathrm{d}t} = \sum_{j=1}^{n} a_{ij} N_j \,, \tag{9}$$

which in matrix form is

$$\frac{\mathrm{d}\mathbf{N}^*}{\mathrm{d}t} = \mathbf{AN} \,, \tag{10}$$

and where asterisks denote the system is at or near equilibrium. From these equations it is evident that the response of a system variable to a pulse perturbation is determined solely by direct effects between variables, as specified in the community matrix **A**. Thus the direction of change of a variable can be ascertained simply from the sign pattern of **A**, or by extension, its corresponding signed digraph.

Press perturbations, on the other hand, arise from a sustained change to a system parameter, such as a density-dependent interaction (a_{ij}), or a density-independent rate of birth (β_i) or death (δ_i). In general we want to know the change in the equilibrium level of any N_i population, due to the sustained change of a specific parameter, say p_h. An important difference here is that press perturbations are determined by both direct and indirect effects; they therefore can produce complex and unexpected responses. To a large extent responses are determined by the network properties of a system, thus allowing for a qualitative interpretation of expected system behavior. The change in any N_i due to change in parameter p_h, is obtained through the inverse of the negative community matrix

$$\mathrm{d}\mathbf{N}^* = -\mathbf{A}^{-1}\frac{\partial\left(\dfrac{\mathrm{d}\mathbf{N}}{\mathbf{N}\mathrm{d}t}\right)}{\partial p_h}\mathrm{d}p_h . \tag{11}$$

In qualitative analyses we are only concerned with the sign (sgn) or direction of change of a variable, which in general can be obtained through the adjoint (adj) of the negative community matrix (Dambacher *et al.* 2002, 2005)

$$\operatorname{sgn}\Delta\mathbf{N}^* = \operatorname{sgn}[\operatorname{adj}(-\mathbf{A})]. \tag{12}$$

This formulation is useful because the adjoint matrix provides a summary of the positive and negative feedback cycles that propagate through the system as a result of press perturbations.

Weipa model predictions

Eq. (13) gives qualitative predictions for responses to press perturbations for the full model of the Weipa banana prawn ecosystem and fishery in Figure 12.

$$\operatorname{sgn}\Delta\mathbf{N}^* = \begin{array}{l|cccccccccccccccccccccc|}
 & 1 & 2 & 3 & 4 & 5 & 6 & 7 & 8 & 9 & 10 & 11 & 12 & 13 & 14 & 15 & 16 & 17 & 18 & 19 & 20 & 21 & 22 \\
\text{1 BP A} & + & + & + & + & - & - & - & 0 & + & - & + & - & + & - & - & + & + & + & + & - & + & + \\
\text{2 BP L} & + & + & + & + & - & - & - & 0 & + & - & + & - & + & - & - & + & + & + & + & - & + & + \\
\text{3 BP J} & + & + & + & + & - & - & - & 0 & + & - & + & - & + & - & - & + & + & + & + & - & + & + \\
\text{4 BP M} & + & + & + & + & - & - & - & 0 & + & - & + & - & + & - & - & + & + & + & + & - & + & + \\
\text{5 Catch} & + & + & + & + & (+) & (+) & (+) & 0 & + & - & + & - & + & - & - & + & + & + & + & ? & ? & + \\
\text{6 Effort} & 0 & 0 & 0 & 0 & 0 & (+) & (+) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\text{7 Mrkt\$} & 0 & 0 & 0 & 0 & 0 & 0 & (+) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\text{8 CPUE} & + & + & + & + & (+) & ? & ? & (+) & + & - & + & - & + & - & - & + & + & + & + & ? & ? & + \\
\text{9 Nut J} & - & - & - & - & + & + & + & 0 & (+) & + & - & + & - & + & + & - & + & ? & ? & + & - & - \\
\text{10 Pr E} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & (+) & (-) & 0 & 0 & 0 & 0 & 0 & (-) & (-) & (-) & 0 & 0 & 0 \\
\text{11 Rec E} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & (+) & (+) & 0 & 0 & 0 & 0 & 0 & (-) & (-) & (-) & 0 & 0 & 0 \\
\text{12 Pr L} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & (+) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\text{13 Nut A} & - & - & - & - & + & + & + & 0 & - & + & - & + & (+) & (-) & + & - & - & - & ? & + & - & - \\
\text{14 Oth P} & - & - & - & - & + & + & + & 0 & - & + & - & + & (+) & (+) & + & - & - & - & ? & + & - & - \\
\text{15 Pr O} & + & + & + & + & (+) & (+) & (+) & 0 & + & - & + & - & + & - & (+) & (-) & + & + & + & ? & ? & (-) \\
\text{16 Rec O} & + & + & + & + & (+) & (+) & (+) & 0 & + & - & + & - & + & - & (+) & (+) & + & + & + & ? & ? & (-) \\
\text{17 Ter E} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & (+) & 0 & (+) & 0 & 0 & 0 \\
\text{18 Mang} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & (+) & 0 & 0 & 0 & 0 \\
\text{19 Ppt E} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & (+) & 0 & 0 & 0 \\
\text{20 Ppt L} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & (+) & 0 & 0 \\
\text{21 Sal} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & (-) & (+) & 0 \\
\text{22 Tur O} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & (+)
\end{array} \tag{13}$$

In interpreting the adjoint matrix, the responses of each variable to a change in a parameter are read down the column of the variable directly controlled by that parameter. In Eq. (13) ambiguous responses are shown by question marks or are enclosed in parentheses, and occur where both positive and negative feedback cycles contribute towards a response. Ambiguous predictions can be treated in a probabilistic manner by considering the number of feedback cycles of each sign. Here a ratio is taken of the net to the total number of cycles, creating a "weighted prediction". Weighted predictions greater than 0.5 (*i.e.* greater than a 1:2 ratio of the net to total number of feedback cycles) have been shown to have a high degree of sign determinacy in both empirical studies (Dambacher *et al.* 2002) and computer simulations (Dambacher *et al.* 2003*b*). In Eq. (13) and below, ambiguous responses with predictions weights ≥ 0.5 are enclosed in parentheses and those <0.5 are given as question marks. From this matrix we can infer two useful indicators of system response due to change in any parameter or factor in the Weipa system. One is the direction of change in abundance for each variable, and the other is correlations of change among variables.

While there are a total of 484 possible responses to consider in Eq. (13), those relevant to our investigations are much fewer. Of particular interest are responses associated with high levels of rainfall either in the early wet-season (summer, column 19), or the late wet-season (autumn, column 20). A high level of early season rainfall is predicted to increase the abundance of all life stages and also to increase CPUE in the fishery. Conversely, high levels of late season rainfall are predicted to suppress the abundance of all life stages of prawn, although the direction of change in CPUE is ambiguous. Thus the model predicts that the correlation between prawn abundance and CPUE will be positive when the perturbation is through increased early rainfall, but it can be either negative or positive for an increase in late season rainfall.

Another perturbation scenario of interest to this study is a possible decrease in fishing effort in the Weipa region. Where we want to consider a negative input to a biological variable, or a decrease in a physical factor, then elements of the adjoint matrix are simply reversed. Reduced fishing effort can thus be seen as a sign reversal in column 6 of Eq. (13), and as one would expect, it will benefit the prawn stock, however the prediction for change in CPUE (variable 5) is highly ambiguous and could be either positive or negative, or neutral if the opposing effects are of similar strength. Identical predictions are obtained for a decrease in the market price of prawns (column 7).

While a change in population abundance is a primary means of monitoring ecosystem response and can be used to validate model predictions, we can gain additional insight into system dynamics by considering the sign of correlations among variables. If, for a given perturbation, two variables both increase, or both decrease, then their response predictions are positively correlated, and if change is in an opposing direction, they are negatively correlated. Variables are neutrally correlated if there is no change in one or both variables. Looking across all columns of the adjoint matrix in Eq. (13) one can identify general patterns of predicted responses among variables. The correlation of responses between banana prawns and other prawn species (variable 14) are generally negative, with the exception of a positive correlation for change in adult prawn nutrients (variable 13).

Correlations among each banana prawn life stage are positive in all columns of Eq. (13), indicating that no information has been gained by splitting the banana prawn variable. Apart from the benefits of this detailed depiction for conceptualization of the system, one could gain the same level of understanding of the system’s dynamics by using a model with fewer life stages, as in the six variable core model of Figure 13*b*.

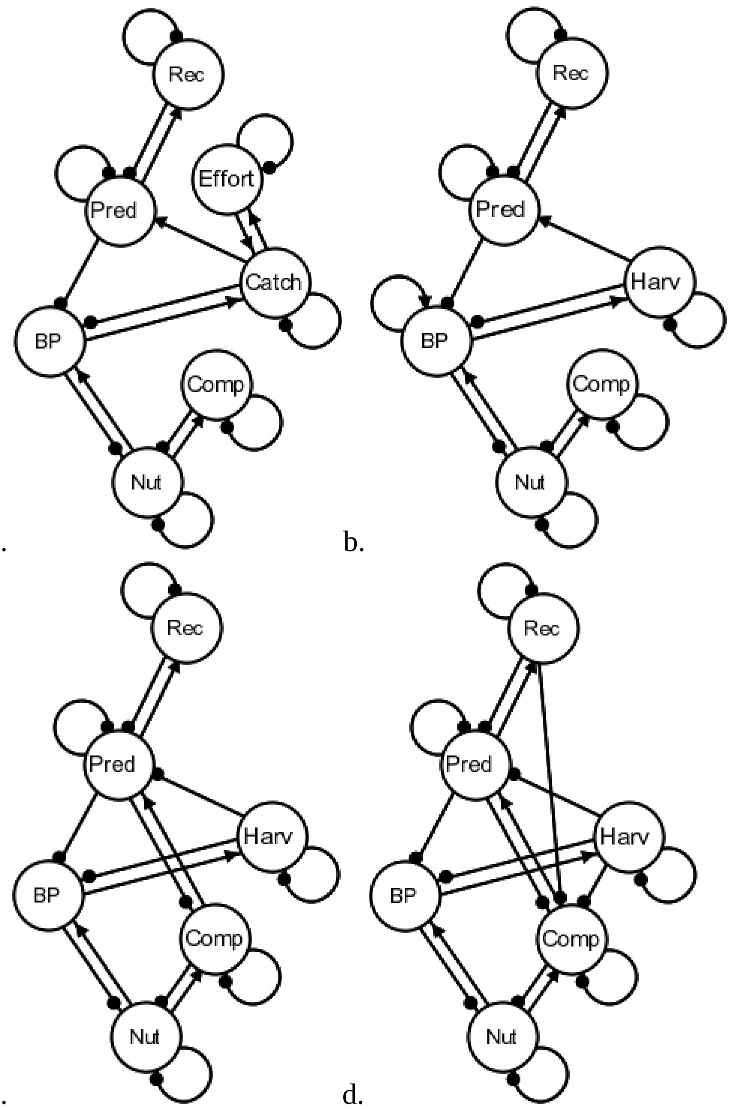
Adjoint matrix predictions for this reduced system are equivalent to those of the full model in Eq. (13).

$$\operatorname{sgn}\Delta\mathbf{N}^* = \begin{array}{l|cccccc|} & \multicolumn{6}{c}{\text{Model of Fig. } 6b} \\ & 1 & 2 & 3 & 4 & 5 & 6 \\ \hline 1:\text{BP} & + & - & + & - & - & + \\ 2:\text{Harv} & + & + & + & - & - & + \\ 3:\text{Nut} & - & + & + & - & + & - \\ 4:\text{Comp} & - & + & + & + & + & - \\ 5:\text{Pred} & + & + & + & - & + & - \\ 6:\text{Rec} & + & + & + & - & + & + \\ \hline \end{array} \qquad (14)$$

Alternative hypotheses and model structures

The core model of Figure 13*b* represents an intermediate level of complexity, yet it preserves the essential dynamics and feedback properties of the larger more detailed model of Figure 12. Hence, it can be used as a basis to more simply and easily investigate the consequences of different hypotheses regarding system structure. In Figure 14 are four alternative models that incorporate different hypotheses about the effects of the prawn fishery and trophic interactions in the system. Figure 14*a* treats fishing effort as following or increasing with the banana prawn catch of the Weipa region, as in the model of Figure 10*d*. Figure 14*b* considers the case for an over harvest of an aggregating stock, with a positive self-effect for banana prawns, as in the model of Figure 11. In Figure 14*c* and Figure 14 *d* are models considering the effect of ocean predators of banana prawns (*e.g.* sharks) also consuming species that compete for food with banana prawns (*i.e.* other prawn species such as tiger prawns but also various fishes, such as juvenile flathead). In these latter two models, the fishery is depicted as having a negative effect on sharks, and presumes the level of shark mortality, from fishery bycatch, is high and out weighs the effect of fishery discards in attracting sharks to the area. The model of Figure 14*d* includes impacts from the recreational and commercial fisheries to the resource competitors of banana prawns.

There is considerable difference in the stability properties of the models in Figure 14 due to the effect of positive feedback variously introduced as self-effects, pair-wise interactions, and interaction chains involving 3 or more species. In the model of Figure 14*a*, stability requires that self-regulation of the fishery be strong enough to counter the positive feedback between catch and effort. A more severe condition exists in the model for Figure 14*b*, where the positive self-effect on the banana prawn variable compromises each of the 7 levels of feedback for the model system. Stability in this case requires that the positive feedback not be too great, and from Eq. (8) we gain the insight that the strength of the positive feedback will be high when the stock of banana prawns (N_2) is low. When this occurs, then maintaining system stability



a. b.
c. d.

Figure 14: Alternative model structures for the Weipa banana prawn ecosystem and fishery.

requires that effort (N_1) or catchability ($\alpha_{2,1}$) be reduced. In the models of Figure 14*c* and Figure 14*d* positive feedback is occurs at higher feedback levels with complex trophic interactions involving predators and resource competitors of banana prawns, as well as the prawn fishery. Conditions for stability are most severe in the model for Figure 14*d*, which includes multiple effects from recreational and commercial fisheries. Stability in either of these model systems depends in large part on the effects of the fishery being regulated, such that effort or catchability is not too great.

The following equations give the adjoint matrix predictions for the four models in Figure 14.

$$\text{Model of Fig. }7a$$

$$\operatorname{sgn}\Delta\mathbf{N}^{*}=\begin{array}{rc} & \begin{array}{ccccccc}1&2&3&4&5&6&7\end{array}\\ \begin{array}{r}1:\text{BP}\\2:\text{Catch}\\3:\text{Effort}\\4:\text{Nut}\\5:\text{Comp}\\6:\text{Pred}\\7:\text{Rec}\end{array} & \begin{bmatrix}?&-&-&?&?&?&?\\+&+&+&+&-&-&+\\+&+&+&+&-&-&+\\?&+&+&+&-&?&?\\?&+&+&+&?&?&?\\+&+&+&+&-&(+)&(-)\\+&+&+&+&-&(+)&(+)\end{bmatrix}\end{array}$$

$$\text{Model of Fig. }7b$$

$$\operatorname{sgn}\Delta\mathbf{N}^{*}=\begin{array}{rc} & \begin{array}{cccccc}1&2&3&4&5&6\end{array}\\ \begin{array}{r}1:\text{BP}\\2:\text{Harv}\\3:\text{Nut}\\4:\text{Comp}\\5:\text{Pred}\\6:\text{Rec}\end{array} & \begin{bmatrix}+&-&+&-&-&+\\+&?&+&-&-&+\\-&+&?&?&+&-\\-&+&?&?&+&-\\+&?&+&-&?&?\\+&?&+&-&?&?\end{bmatrix}\end{array}$$

$$\text{Model of Fig. }7c$$

$$\operatorname{sgn}\Delta\mathbf{N}^{*}=\begin{array}{rc} & \begin{array}{cccccc}1&2&3&4&5&6\end{array}\\ \begin{array}{r}1:\text{BP}\\2:\text{Harv}\\3:\text{Nut}\\4:\text{Comp}\\5:\text{Pred}\\6:\text{Rec}\end{array} & \begin{bmatrix}+&(-)&(+)&-&?&?\\+&(+)&(+)&-&?&?\\-&(+)&(+)&?&+&-\\?&(+)&(+)&(+)&?&?\\-&?&?&+&+&-\\+&?&?&+&+&?\end{bmatrix}\end{array}$$

$$\text{Model of Fig. }7d$$

$$\operatorname{sgn}\Delta\mathbf{N}^{*}=\begin{array}{rc} & \begin{array}{cccccc}1&2&3&4&5&6\end{array}\\ \begin{array}{r}1:\text{BP}\\2:\text{Harv}\\3:\text{Nut}\\4:\text{Comp}\\5:\text{Pred}\\6:\text{Rec}\end{array} & \begin{bmatrix}+&?&(+)&-&?&(+)\\+&(+)&(+)&-&?&(+)\\(-)&?&?&?&(+)&?\\?&?&?&(+)&?&?\\-&?&?&+&(+)&(-)\\-&?&?&+&(+)&?\end{bmatrix}\end{array} \tag{15}$$

Of interest in all four models of Figure 14 is a predicted negative response of banana prawns from an input to the fishery say, through increased effort. This prediction in the first and second models is unambiguous, while in the third it comes with a high prediction weight (equal to 0.5), and in the forth with a low prediction weight (equal to 0.23). In the model of Figure 14*d*, the complex interactions between the fishery, and the predators and competitors of banana prawns, create multiple indirect effects that act to lessen the effects of predation and resource competition. Making a reliable prediction of whether an input to the fishery will have net positive or negative effect on the banana prawn stock requires quantification of the system's interaction strengths.

A positive input to banana prawn food is predicted to increase the abundance of banana prawns and fishery catch in the models of Figure 14 *b*, *c* and *d*. But in the model of Figure 14*a*, where fishing effort follows catch, fishery catch and effort are both predicted to increase, although the sign for change in banana prawns is completely ambiguous with a weighted prediction equal to zero. This ambiguity arises from the positive feedback between catch and effort, and it is possible that change in CPUE could be positively, negatively or even neutrally correlated with change in stock size, depending on the strength of self-regulation in the system versus the strength of the effects of catch on effort and effort on catch.

Opportunity cost and effort allocation in the Weipa fishery

Allocation of fishing effort in the Northern Prawn fishery has been described as possibly being a case where fishing effort follows change in local catch (Figure 10*d*), but is also determined by relative differences in benefit-cost ratios between fishing in different regions of the Gulf of Carpentaria. We next seek to encompass the dynamics between the prawn fishery in the Weipa region and other regions in the gulf by expanding the two variable model of Figure 10*d* to an eleven variable model (Figure 15) that examines the effect of opportunity costs for fishing “here” versus “there”—*i.e.* with “here” being the Weipa region and “there” being elsewhere in the Gulf of Carpentaria. Since Weipa is the most northerly fishing region in the gulf, relocation to another region exacts a relatively long travel time and high fuel cost. In addition, ocean turbidity in Weipa is usually too great to permit use of spotter planes to locate prawn aggregations, a technique commonly used to great advantage by the fishery in other regions. Hence, a boat operator deciding to remain in the Weipa region must weigh the benefit and cost of its catch in Weipa against opportunity costs for not fishing elsewhere.

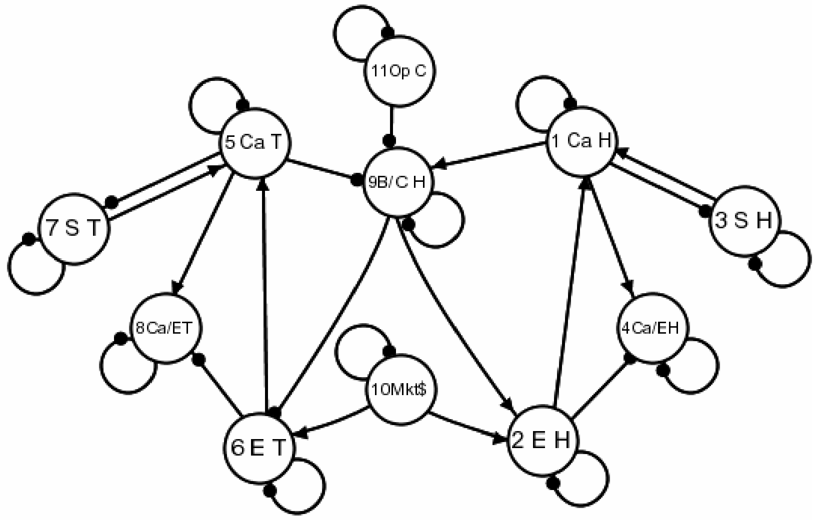


Figure 15: Qualitative model of effort allocation and opportunity cost for the Weipa region of Australia’s Northern prawn fishery. Effort (E), in boat days, is allocated to the Weipa region, i.e. “here” (H) vs. other regions, i.e. “there” (T), in the Gulf of Carpentaria, depending on a benefit-to-cost ratio (B/C) for the Weipa region. This ratio is suppressed by an opportunity cost (Op C) for staying in Weipa region. Local prawn stocks (S) positively affect the level of catch (Ca) in each region, but catch in Weipa has a positive effect on the benefit/cost ratio, while catch from “there” suppresses this ratio. Effort in both regions is uniformly controlled by a global market price (Mkt$) for both domestic and wild caught prawns. Catch per unit effort (Ca/E) is included as a response variable for each region.

This model has a positive feedback cycle between catch and effort, but here via an intermediate variable (no. 9: B/CH) that allocates effort based on the benefit-cost ratio for the Weipa region. The sign of the overall feedback of this model is ambiguous, like that of the model in Figure 10*d*. From the model in Figure 15, we have the following qualitative predictions

$$\operatorname{sgn}\Delta\mathbf{N}^{*} = \begin{array}{l|ccccccccccc|}
 & 1 & 2 & 3 & 4 & 5 & 6 & 7 & 8 & 9 & 10 & 11 \\
\hline
1\,\text{Ca H} & ? & ? & ? & 0 & - & - & - & 0 & + & ? & - \\
2\,\text{E H} & + & ? & + & 0 & - & - & - & 0 & + & ? & - \\
3\,\text{S H} & ? & ? & ? & 0 & + & + & + & 0 & - & ? & + \\
4\,\text{Ca/E H} & ? & ? & ? & ? & ? & ? & ? & 0 & ? & ? & ? \\
5\,\text{Ca T} & - & - & - & 0 & ? & ? & ? & 0 & - & ? & + \\
6\,\text{E T} & - & - & - & 0 & + & ? & + & 0 & - & ? & + \\
7\,\text{S T} & + & + & + & 0 & ? & ? & ? & 0 & + & ? & - \\
8\,\text{Ca/E T} & ? & ? & ? & 0 & ? & ? & ? & ? & ? & ? & ? \\
9\,\text{B/C H} & + & + & + & 0 & - & - & - & 0 & + & ? & - \\
10\,\text{Mkt\$} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & ? & 0 \\
11\,\text{Op C} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & ? \\
\hline
\end{array} . \tag{16}$$

An increase in opportunity cost, read down the eleventh column of Eq. (16), gives unambiguous predictions for a decrease in effort (E H) and an increase in stock size (S H) for the Weipa region, and an increase in effort (E T) and a decrease in stock size (S T) for other regions. Environmental input to the Weipa stock produces a similar response. For instance, a decrease in rainfall in the Weipa region that diminishes the productive capacity of the stock, read as a negative input to the third column of Eq. (16), will move fishing effort out of the Weipa region to other regions in the Gulf of Carpentaria. The predicted change in stock abundance in the Weipa however, is ambiguous, as the reduction in harvest mortality has the potential to offset the diminishment of recruitment. In general, any cause acting to reduce the catch of prawns in Weipa will be reinforced by the positive feedback between effort and catch embedded in the harvest subsystem, thereby causing a shift in the location of fishing effort away from the Weipa region. In this system a change in CPUE will not necessarily be correlated with a change in local stock size, as CPUE can either increase or decrease with change in stock size depending on the system's interaction strengths.

Discussion

This work has been aimed at providing a general representation of the Weipa banana prawn ecosystem and fishery. In the course of model development we have arrived at an intermediate level of complexity with an array of alternative models that appear to capture the essential dynamics of the system. While the qualitative models incorporate what is known about the system, the different models also reflect a degree of uncertainty about relationships among the system variables.

Predictions from the models are generally consistent with the hypotheses considered as potential explanations of why the catch of banana prawns has declined in the Weipa region. The first hypothesis, that catches are low because of over harvesting banana prawns, is accounted for in the model in Figure 14*b*; and of any of the models considered, it has the least potential for stability. The second hypothesis, that of an environmental effect was responsible for the low catches, can be considered through specific perturbations to the full model in Figure 12, or more simply through input to the biological variables for the five alternative models in Figure 13*b* and Figure 14. The three hypotheses that catch has declined because the fishery can no longer find or catch prawns can be addressed in a number of ways. A decline in the searching power of the fleet is implied in the models of Figure 14*a* and Figure 15, which incorporate a positive feedback between effort and catch. The latter model accounts for this phenomenon as a trade-off in opportunity cost and catch levels in the Weipa region versus other regions in the gulf.

The hypothesis that adult prawns are staying inshore and are less available to the fishery can be accounted for in the full model of Figure 12 through a negative input to autumn rainfall, and in the five alternative models simply as a negative input to the harvest variable or subsystem. The hypothesis that banana prawn adults no longer aggregate is equivalent to the hypothesis that prawns are remaining inshore, as both deal with effects that reduce prawn catchability, thereby increasing prawn abundance and decreasing prawn catch.

A general conclusion from the analyses of all of the models is that system stability requires that the fisheries behave in a self-regulated manner, either through limitations in effort or catchability. This requirement is most important for the model of Figure 14*b*, where there is an over harvest of an aggregating stock, and in the model of Figure 14*d*, where both recreational and commercial fisheries impart multiple effects through the trophic web.

Another important conclusion from this study is that a change in CPUE will not necessarily be correlated with a change in the size of the banana prawn stock. This was observed most clearly from input to environmental variables in the full model of Figure 12, and in the effort allocation model of Figure 15. Thus, interpretations of long term changes in catch and effort data should consider whether there has been a change in prawn catchability, and whether effort has fallen in the Weipa fishery as a result of regional economic pressures.

Conclusions from the stability analyses and response predictions lead to and support questions critical to the management of the Weipa banana prawn stock, namely: 1) has the banana prawn stock collapsed due to an over harvest?, 2) are prawns abundant but now remaining inshore or no longer schooling?, and 3) are prawns abundant but too expensive to catch compared to elsewhere? These three basic questions form the core of the management decision support framework submitted to NORMAC (Okey and Dichmont 2005), and intensive recruitment surveys and experimental fishing are suggested as the means to answer them.

The models developed within this work can be viewed as a first attempt to provide a conceptual framework for understanding the dynamics of the Weipa banana prawn ecosystem and fishery. The simple models developed are not meant to be an endpoint, but rather a first means of comparison and a basis for future work. As more information is collected it will undoubtedly be instructive to consider model structures based on different hypotheses, or to delve into greater detail and expand the resolution of certain aspects or subsystems not considered thus far.

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IV-3. Assessment of the potential effects on recruitment to the stock of banana prawns at Weipa of exploitation and environment

The potential impacts of exploitation and environment on recruitment to the stock of banana prawns at Weipa

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Abstract

Estimates of daily catch per unit of effort (CPUE) for the banana prawn stock at Weipa were calculated using logbook data for two core regions containing grid cells that had been consistently fished during the history of the fishery. The daily catch data for each year were subjected to virtual population analysis (VPA), under the assumption that no prawns survived at the end of each year and the correlations between the resulting population estimates and the daily CPUE data were calculated. Applying the Bonferroni correction, fifteen of the resulting 34 correlation coefficients were statistically significant, suggesting that the daily CPUEs could be employed as an index of abundance. However, very considerable variation in CPUE at any population size was evident in many of the results. It is likely that such variation is due to the aggregating behaviour of the banana prawns and the ability of fishers to detect and fish aggregations. Thus, although the CPUEs could be employed as a proxy for abundance, they would be likely to be highly imprecise.

The daily catch and CPUE data were subjected to a tuned VPA, with both catchability and terminal biomass being estimated as parameters of the model. The resulting estimates of recruitment and spawning biomass were used, in combination with time series of environmental data, to explore whether recruitment was affected by spawning biomass and/or the effects of those environmental variables. The data provided strong support for the hypothesis of constant recruitment, considerably weaker support for the hypothesis that recruitment was affected by spawning biomass and essentially no support for hypotheses that recruitment was affected by the environmental variables either separately or in combination with spawning biomass. The analysis suggested that recruitment had declined since the early 1970s, remained highly variable but stable till 1997, before declining to low levels between 2000 and 2003 and possibly showing a slight recovery in 2004. No obvious trend was discernable in spawning biomass estimates.

A depletion analysis, based on similar assumptions to the tuned VPA, was fitted simultaneously to the daily CPUE data for all years. This model provided estimates of the parameters of a Beverton and Holt stock-recruitment relationship and of the coefficients of a linear combination of the environmental variables used as the exponent of a term which modulated predicted recruitment by the effects of those environmental variables. The results from this model confirmed the finding of the tuned VPA that spawning biomass and the environmental variables appeared to contribute little towards improving the fit of the model to the data beyond that obtained by assuming constant recruitment.

The fact that there was insufficient information in the data to demonstrate a relationship between recruitment and spawning biomass and/or the environmental variables cannot be used as evidence that no such relationship exists. The imprecision of the CPUE data for banana prawns is likely to mask any signal of such a relationship in the data. Accordingly, in accordance with the precautionary principle, it would be prudent to manage the fishery under the assumption that such a relationship

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[1] Modelling of the fishery benefited greatly from the input and criticism of the Working Group, however the Group has not had the opportunity to critically review the final modelling results. Errors and inadequacies of this section remain the responsibility of the compiler, N. G. Hall. For membership of the Fishery Impact Group see Workshop 1 Report.

between spawning biomass and recruitment exists and may have produced the apparent decline in recruitment observed in the banana prawn stock at Weipa since 2000.

Introduction

The decline in catches from the Albatross Bay (Weipa) stock of prawns reported in 2000 to 2004 by vessels from the Northern Prawn Fishery led to concerns that either changes to the ecosystem or environmental factors or due to fishing itself had led to reduced recruitment. This study explores whether the decline in banana prawn catches at Weipa might be the result of one of the following.

1. An artifact of the reduced area fished;
2. A decline in recruitment resulting from
    a. the reduction in spawning stock caused by exploitation; and/or
    b. the influence of environmental variables.

Methods

Processed daily logbook data for each vessel that fished in the NPF from 1970 to 2003 were obtained from Janet Bishop, CSIRO, and subsequently for 1970 to 2004 from Roy Deng, CSIRO. These latter data had been processed using the new effort split algorithm developed by Bill Venables, and included the gear type (“Gtype”), latitude and longitude (in decimal degrees), total banana prawn catch (kg) and, for banana prawns, the identity of the banana prawn stock to which the catch had been attributed. The data were filtered to extract the logbook data for banana prawns (*i.e.* Gtype = “Banana”) and for the Albatross Bay (*i.e.*, Weipa) stock.

A preliminary exploration of alternative fishery models for the banana prawn fishery at Weipa was undertaken using age-structured and biomass dynamics models that employed annual catch and effort data, delay-difference and depletion models based on weekly catch and effort data, and a virtual population analysis (VPA) that was applied to both daily and weekly catch data and which assumed a terminal abundance of zero and constant size of prawns. Examination of the results derived from analysis of the newly-extracted banana prawn data revealed that the results from an earlier stock assessment of the banana prawn data (Vance et al., 2003, Chapter 7) had been influenced strongly by an adjustment for fishing power that had been made to those data. Thus, the stock-recruitment relationships reported previously were likely to be artifacts of these fishing power adjustments. Further consideration of the data requirements for the new assessment indicated that an estimate of an abundance index derived from the annual catch and the annual nominal fishing effort would be unreliable due to the highly seasonal nature of relative prawn abundance and the changes in fishing pattern and spatial distribution of fishing since 1970. An abundance index calculated from daily or weekly catch and nominal fishing effort would overcome the first two of these problems, but calculation of such an index would still need to account for changes in the spatial distribution of fishing.

Using the filtered data from the 1970-2003 data set (*i.e.*, from the data that were derived using the earlier effort-split algorithm), the total catch and number of vessel-days within each 6” × 6” geographical grid cell were calculated for each week within each year. Examination of these data indicated that, while a core group of grid cells had been consistently fished; many cells had been infrequently or never visited. To ensure that estimates of the average catch per unit of effort (CPUE) were not biased through the influence of the data from such infrequently-fished cells, it was decided to base estimates of abundance indices on the data for only those grid cells within a core region of the Weipa fishery that had been the basis of most catches and the majority of fishing. Two core regions of grid cells were identified. Core region 1 comprised 26 grid cells in which the average annual catch had exceeded ~5,000 kg, and core region 2 was based on a smaller subset of 19 of these in which the average annual catch had exceeded ~7,000 kg (Table 2).

Table 2: Latitude and longitude values associated with core regions 1 and 2 of the Weipa banana prawn fishery.

	Core region 1		Core region 2	
Cell number	Lat	Long	Lat	Long
1	-12.35	141.25	-12.85	141.45
2	-12.65	141.35	-12.75	141.45
3	-12.45	141.35	-12.65	141.45
4	-12.95	141.45	-12.55	141.45
5	-12.85	141.45	-12.45	141.45
6	-12.75	141.45	-12.35	141.45
7	-12.65	141.45	-12.85	141.55
8	-12.55	141.45	-12.75	141.55
9	-12.45	141.45	-12.65	141.55
10	-12.35	141.45	-12.55	141.55
11	-12.85	141.55	-12.45	141.55
12	-12.75	141.55	-12.35	141.55
13	-12.65	141.55	-12.25	141.55
14	-12.55	141.55	-12.85	141.65
15	-12.45	141.55	-12.75	141.65
16	-12.35	141.55	-12.65	141.65
17	-12.25	141.55	-12.35	141.65
18	-12.85	141.65	-12.25	141.65
19	-12.75	141.65	-12.65	141.75
20	-12.65	141.65		
21	-12.45	141.65		
22	-12.35	141.65		
23	-12.25	141.65		
24	-12.65	141.75		
25	-12.65	141.85		
26	-12.55	141.85		
Bounds				
Lower left	-12.95	141.25	-12.85	141.45
Upper right	-12.25	141.85	-12.25	141.75

An estimate of the total banana prawn catch (kg) for the entire Weipa region was calculated using the data from all grid cells and the 1970-2004 data set (i.e., the data based on the revised effort-split algorithm). The total daily banana prawn catch (kg) and fishing effort (vessel-days) were also calculated for each grid cell, and used to derive an estimate of the daily catch per unit of effort (CPUE) for that cell. An average of these daily CPUEs was then calculated for each core region using (a) only data for grid cells that had been fished, thereby producing an "optimistic" estimate of CPUE (i.e., assuming fishers detect and fish in the grid cells containing the greatest abundance of prawns), (b) all grid cells with the assumption that the CPUE in the non-fished cells was zero, thereby producing a "pessimistic" estimate of CPUE, and (c) all grid cells with the assumption that the CPUE in the non-fished cells was equal to the minimum of the CPUEs recorded in the fished cells, thus producing an estimate that is "intermediate" between the optimistic and conservative estimates.

Virtual Population Analysis

A virtual population analysis was undertaken using the daily catch data recorded in the logbooks and the optimistic catch rates derived from core region 1. For this, it was assumed that the instantaneous coefficient of natural mortality M (day^{-1}) was constant,

$$B_{d-1,y} = B_{d,y} \exp[M] + C_{d-1,y} \exp[0.5M] \text{ (Pope, 1972, 1984),}$$

body size of prawns remained constant throughout the year, and the biomass at the end of the year was zero. $C_{d\,y}$ is the mass of prawns caught on day d of year y. Following Lucas *et al.* (1979), the estimated value of M is set to 0.05 week^{-1}, *i.e.* M=0.05/7 day^{-1}. The resulting daily biomass estimates were compared with the observed CPUEs to assess whether it was appropriate to use CPUE as an index of abundance.

The VPA was repeated, but allowing for an unknown terminal biomass and tuning to match the available CPUE data. Thus, this terminal biomass was estimated, together with catchability, by minimizing for each year the sum of squared deviations between the natural logarithms ($\log_e(x+1)$) of the CPUEs ($I_{d,y}$) and the estimates of those CPUEs, where the latter were derived using the assumption of constant catchability within each year and the observation model relating the estimated daily CPUE ($\hat{I}_{d,y}$) to the corresponding biomass

$$\hat{I}_{d,y} = q_y B_{d,y} \,.$$

As limited data were available for more recent years, the models for 2000 to 2004 were fitted simultaneously to estimate the terminal biomasses and an assumed common catchability for these years.

After subjectively filtering to eliminate parameter estimates resulting from several extremely poor fits of the model to the CPUE data, the resulting estimates of recruitment were regressed against the estimates of spawning biomass and environmental variables. Following Somers and Wang (1997), who calculated an index of spawning biomass as the average number of female prawns in the population between August 1 and October 31, a period that represented the peak of the Spring spawning, an index of total spawning biomass (*i.e.* both sexes) was calculated as average weight of prawns over days 213 to 304 of the year

$$S_y = \frac{1}{92} \sum_{d=213}^{304} B_{d,y} \,.$$

Recruitment was assumed to be related to spawning biomass through a model of the form described by Beverton and Holt, modulated by the impact of the environmental variables $X_{j,y}$, *i.e.*

$$R_y = \left\{ \frac{aS_{y-1}}{b + S_{y-1}} \right\} \exp\left[\sum_j c_j X_{j,y} \right],$$

where a, b and c_j are parameters estimated by minimizing the sum of squared deviations between the values of recruitment and the estimates derived from the above equation.

Four models were fitted and compared, *i.e.* (1) constant recruitment; (2) recruitment related to spawning biomass alone; (3) recruitment related to environmental variables alone; and (4) recruitment related to both spawning biomass and environmental variables. Models were compared by calculating and comparing the small sample version of Akaike's Information Criterion (Burnham and Anderson, 2002), AIC$_c$, where

$$AIC = n \log_e \left(\frac{SS}{n} \right) + 2p$$

and

$$AIC_c = AIC + \frac{2p(p+1)}{n-p-1}$$

and where SS is the sum of squares, n is the number of observations, and p is the number of parameters (including the estimate of the variance of the residuals). AIC differences were calculated as

$$\Delta_j = AIC_{c_j} - AIC_{c_{\min}}$$

where the subscript j refers to model number j. Akaike weights were then calculated as

$$w_j = \frac{\exp(-0.5\Delta_j)}{\sum_k \exp(-0.5\Delta_k)}.$$

Depletion model with non-informative priors

It is assumed that banana prawns at Albatross Bay recruit to the stock at the beginning of the year, although recruitment to the fishery occurs later that year. The recruitment for year y is denoted by R_y. Noting that the fishery now operates over a very short period, it is assumed that recruitment is measured as the biomass of the recruits which would be available to the fishery if all had survived to recruit to the fishery. Thus, at day 1 of year y, the biomass of prawns recruiting to the stock is

$$B_{1,y} = R_y \, .$$

At the start of each subsequent day, d, the biomass of prawns that were available may be calculated using the equation

$$B_{d,y} = B_{d-1,y} \exp[-M] - C_{d,y} \exp[-0.5M].$$

As in the VPA described earlier, the estimated value of M is set to 0.05 week^{-1}, *i.e.* M=0.05/7 day^{-1}. The above equation represents Pope's (1972) approximation, where catches are assumed to be taken at the mid-point of the period (see also Pope, 1984).

An index of total spawning biomass (*i.e.* both sexes) was calculated as the average weight of prawns over days 213 to 304 of the year, as described earlier for the VPA, *i.e.*

$$S_y = \frac{1}{92} \sum_{d=213}^{304} B_{d,y} \, .$$

Two assumptions regarding the relationship between recruitment and spawning stock in the previous year are considered, (1) recruitment is constant, *i.e.*

$$R_y = a\,,$$

and (2) the expected recruitment for year *y* is calculated from the spawning biomass in the previous year, *i.e.*

$$R_y = \left\{ \frac{aS_{y-1}}{b + S_{y-1}} \right\},$$

where this represents the recruitment that would be expected to result from the spawning biomass if the stock-recruitment relationship is of the Beverton and Holt form. The constant recruitment case is a particular instance of the Beverton and Holt equation in which $b = 0$.

For each of these two recruitment-spawning stock scenarios, the effect of environmental variables is explored by considering recruitment as (1) independent of the environmental variables, *i.e.* as represented by the above equations, or (2) dependent on the values of the environmental variables $X_{j,y}$ such that

$$R_y = a \exp\left[\sum_j c_j X_{j,y} \right]$$

if recruitment is independent of spawning biomass, otherwise

$$R_y = \left\{ \frac{aS_{y-1}}{b + S_{y-1}} \right\} \exp\left[\sum_j c_j X_{j,y} \right].$$

Thus, these equations reflect the expected recruitment that would result from the spawning biomass in the previous year, modulated by the effect of the environmental variables. The recruitment scenarios in which recruitment is independent of environmental variables represent the special case of the latter relationship in which the coefficient of the *j*'th environmental variable, $X_{j,y}$ is set to zero, *i.e.* $c_j = 0$ for each *j*.

A further two options were considered for each of the above four recruitment-spawning stock-environment relationships. Recruitment was assumed to be either (1) a deterministic function of spawning biomass, taking into account environmental factors, as described by the relationships above, or (2) a stochastic variable with the median value of recruitment determined by the above deterministic equations and log-normally distributed error η_y where $\eta_y \sim N\left(0, \frac{1}{\tau_\eta}\right)$. Thus, recruitment for these stochastic relationships is represented by

$$R_y = \left\{ \frac{aS_{y-1}}{b + S_{y-1}} \right\} \exp\left[\sum_j c_j X_{j,y} \right] \exp\left[\eta_y\right],$$

where $b = 0$ for the cases in which recruitment is independent of spawning biomass, and $c_j = 0$, for all *j*, for the cases in which recruitment is independent of the environmental variables.

The estimated catch per unit of effort was calculated as

$$\hat{I}_{d,y} = q_y B_{d,y}\,,$$

where the catchability in year y is denoted by q_y. Three scenarios were explored, in which (1) q_y was set to a common value q for all years, (2) separate (independent) values of q_y were fitted for 1970 to 2000, and q_y for 2001 to 2004 was set to the value of q_y for 2000, and (3) the values of q_y from 1970 to 2000 were assumed to undergo a random walk, and q_y for 2001 to 2004 was set to the value of q_y for 2000. In the last case, the deviations between successive values of q_y were assumed to be normally distributed, *i.e.*

$$q_y = q_{y-1} + \upsilon_y$$

where $\upsilon_y \sim N\left(0, \frac{1}{\tau_\upsilon}\right)$.

The sum of squared deviations of the observed from the expected catches per unit of effort, SS_{cpue}, were calculated as

$$SS_{\text{cpue}} = \sum_y \sum_{d=81}^{213} \left(I_{d,y} - \hat{I}_{d,y}\right)^2 .$$

Note that the selection of the period from day 81 to 213 (*i.e.*, from 20 March to 31 July) was arbitrary, but was intended to include the period that is now considered to represent the banana prawn fishing season in the Northern Prawn Fishery.

The log-likelihood of the observation errors was calculated as

$$\lambda_{\text{cpue}} = -\frac{n_{\text{cpue}}}{2}\left\{\log_e[2\pi] + \log_e\left[\frac{1}{\tau_{\text{cpue}}}\right]\right\} - \left(\frac{\tau_{\text{cpue}}}{2}\right) SS_{\text{cpue}}$$

where τ_{cpue} is an estimate of the precision (=1/variance) of the observation errors and it is assumed that the prior probability distribution of τ_{cpue} is a gamma distribution with parameters 0.001 and 1000 (using the Microsoft Excel syntax, and which correspond to the WinBugs' parameters 0.001 and 0.001).

The log-likelihood of the process errors η_y was calculated as

$$\lambda_\eta = -\frac{n_\eta}{2}\left\{\log_e[2\pi] + \log_e\left[\frac{1}{\tau_\eta}\right]\right\} - \left(\frac{\tau_\eta}{2}\right)\sum_y \eta_y^2 .$$

The log-likelihood of the deviations υ_y in the random walk undertaken by the catchabilities was calculated as

$$\lambda_\upsilon = -\frac{n_\upsilon}{2}\left\{\log_e[2\pi] + \log_e\left[\frac{1}{\tau_\upsilon}\right]\right\} - \left(\frac{\tau_\upsilon}{2}\right)\sum_y \upsilon_y^2 .$$

The following prior probability distributions were assumed for the various (free) parameters:

$$\log_e a \sim N(0.,25.)$$

$$b \sim N(0., 10000.)$$

$$\log_e R_{1970} \sim N(0.,25.)$$

$$q_y \sim N\left(0.,\frac{1}{\tau_q}\right) \text{ (if not a random walk, but see discussion)}$$

$$c_j \sim N(0.0, 10000.0)$$

τ_{cpue}, τ_η, τ_q and τ_υ were assumed to have gamma prior probability distributions with parameters 0.001 and 1000 (in Excel syntax)

Two approaches to fitting the model were considered. Initially a MCMC approach, using the Metropolis algorithm, was applied. However, with 144 analyses to be undertaken (two sets of core grid cells, three sets of CPUE (*i.e.* optimistic, conservative and intermediate), and 24 scenarios), it was recognized that an alternative, less computer-intensive approach would be required. Accordingly, the models were fitted using simulated annealing (Press *et al.*, 1992).

The model was fitted by maximizing the penalized log-likelihood equation, *i.e.* by calculating the combined log-likelihood of the data given the parameters and of the parameters given the prior probability distributions (Cooper *et al.*, 2003; Maunder, 2004; Hoyle and Maunder, 2004; Porch *et al.*, 2006). Without knowledge of the ratio of the variances of process to observation errors, simultaneous fitting of both forms of error is inappropriate (Hilborn and Walters, 1992, p. 226). In effect, the prior probability distributions that are assumed for the process errors allocate error among processes and observations to allow estimation of both the model parameters and the process errors. Thus, the assumptions regarding the prior probability distributions determine the ratio of the variances of process to observation error.

The parameters that are required to be estimated by the model depend upon which of the 24 scenarios is being examined (Table 3).

Table 3: Scenarios considered in the study.

Scenario	**Catchability**	**Stock-recruitment relationship**	**Recruitment deviations**	**Environment**	**Free parameters**
1	q free $q_y=q$	$b=0$	$\eta_y=0$	$c_j=0$	a, q, τ_{cpue}
2	q free $q_y=q$	$b=0$	η_y free	$c_j=0$	a, q, η_y, τ_{cpue}, τ_η
3	q free $q_y=q$	b free	$\eta_y=0$	$c_j=0$	a, b, q, τ_{cpue}
4	q free $q_y=q$	b free	η_y free	$c_j=0$	a, b, q, η_y, τ_{cpue}, τ_η
5	q_y free	$b=0$	$\eta_y=0$	$c_j=0$	a, q_y, τ_{cpue}, τ_q
6	q_y free	$b=0$	η_y free	$c_j=0$	a, q_y, η_y, τ_{cpue}, τ_q, τ_η

Scenario	Catchability	Stock-recruitment relationship	Recruitment deviations	Environment	Free parameters
7	q_y free	b free	$\eta_y=0$	$c_j = 0$	a, b, q_y, τ_{cpue}, τ_q
8	q_y free	b free	η_y free	$c_j = 0$	a, b, q_y, η_y, τ_{cpue}, τ_q, τ_η
9	q_{1970} free υ_y free	b=0	$\eta_y=0$	$c_j = 0$	a, q_{1970}, υ_y, τ_{cpue}, τ_υ
10	q_{1970} free υ_y free	b=0	η_y free	$c_j = 0$	a, q_{1970}, υ_y, η_y, τ_{cpue}, τ_υ, τ_η
11	q_{1970} free υ_y free	b free	$\eta_y=0$	$c_j = 0$	a, b, q_{1970}, υ_y, τ_{cpue}, τ_υ
12	q_{1970} free υ_y free	b free	η_y free	$c_j = 0$	a, b, q_{1970}, υ_y, η_y, τ_{cpue}, τ_υ, τ_η
13	q free $q_y=q$	b=0	$\eta_y=0$	c_j free	a, q, c_j, τ_{cpue}
14	q free $q_y=q$	b=0	η_y free	c_j free	a, q, c_j, η_y, τ_{cpue}, τ_η
15	q free $q_y=q$	b free	$\eta_y=0$	c_j free	a, b, q, c_j, τ_{cpue}
16	q free $q_y=q$	b free	η_y free	c_j free	a, b, q, c_j, η_y, τ_{cpue}, τ_η
17	q_y free	b=0	$\eta_y=0$	c_j free	a, q_y, c_j,

Scenario	Catchability	Stock-recruitment relationship	Recruitment deviations	Environment	Free parameters
					τ_{cpue}, τ_q
18	q_y free	$b=0$	η_y free	c_j free	a, q_y, c_j, η_y, τ_{cpue}, τ_q, τ_η
19	q_y free	b free	$\eta_y=0$	c_j free	a, b, q_y, c_j, τ_{cpue}, τ_q
20	q_y free	b free	η_y free	c_j free	a, b, q_y, c_j, η_y, τ_{cpue}, τ_q, τ_η
21	q_1 free υ_y free	$b=0$	$\eta_y=0$	c_j free	a, q_{1970}, c_j, υ_y, τ_{cpue}, τ_υ
22	q_1 free υ_y free	$b=0$	η_y free	c_j free	a, q_{1970}, c_j, υ_y, η_y, τ_{cpue}, τ_υ, τ_η
23	q_1 free υ_y free	b free	$\eta_y=0$	c_j free	a, b, q_{1970}, c_j, υ_y, τ_{cpue}, τ_υ
24	q_1 free υ_y free	b free	η_y free	c_j free	a, b, q_{1970}, c_j, υ_y, η_y, τ_{cpue}, τ_υ, τ_η

Results

Vessels fishing in the Northern Prawn Fishery are constrained each year to operate within two fishing seasons, the first of which has typically fallen between April/May and June and the second between August and November (AFMA, 2003). In 2005, the first (banana) season extended from 9 April to 21 May, while the second (tiger) season was 1 August to 15 November (Haine and Garvey, 2005). Prior to 1984, an increasing percentage of the annual catch was taken before 1 April (Figure 16). Since 1984, other than in 1994 when the season opened on 13 March, the season has opened on or after that date. By the end of June, virtually the entire annual banana prawn catch for Weipa has been taken. Although the period from 20 March to 31 July was subjectively selected for use when fitting the models in this study, it encompasses a slightly greater proportion of the daily catch data in the period prior to 1984 and in 1994.

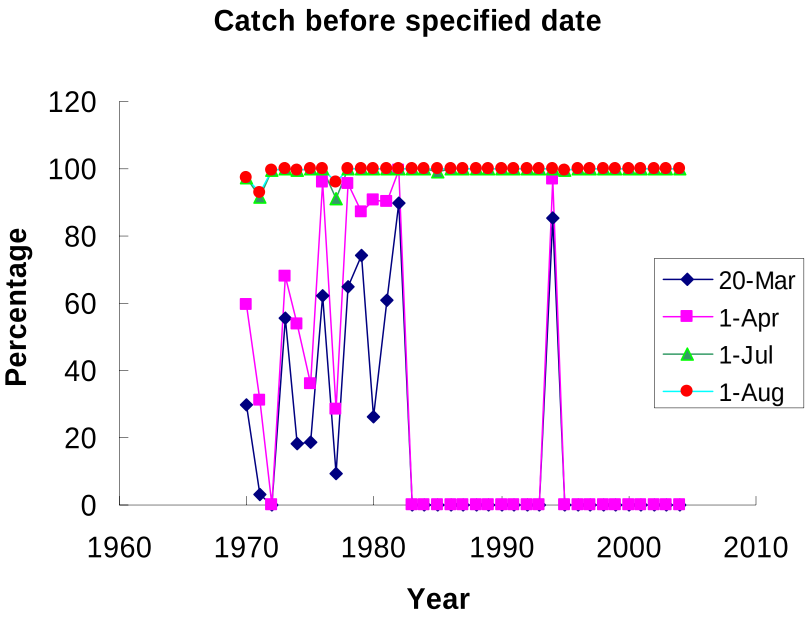


Figure 16: The percentage of the annual banana prawn catch taken from waters off Weipa before 20 March, 1 April, 1 July and 1 August. The period used in the study was 20 March to 31 July, and the banana season typically extends from April/May to June.

Prior to 1980, the number of days on which non-zero catches of banana prawns from Weipa were recorded in logbooks typically exceeded 60 per year (Figure 17). In the subsequent period, to 1997, the number on non-zero catch days had reduced to approximately 30 per year. However, the number of such days declined to approximately 11 between 1998 and 2000, before falling to 4 in 2001, 5 in 2002 and 1 in 2003, then recovering slightly to 10 in 2004. The duration of the period over which the majority of the annual catch of banana prawns at Weipa were caught, calculated as the number of days required to take an additional 90% of the annual catch following the capture of the first 5% of the annual catch, followed essentially the same trend as the number of non-zero catch days. It should be noted that both variables are constrained by the opening and closing dates imposed by fishery managers.

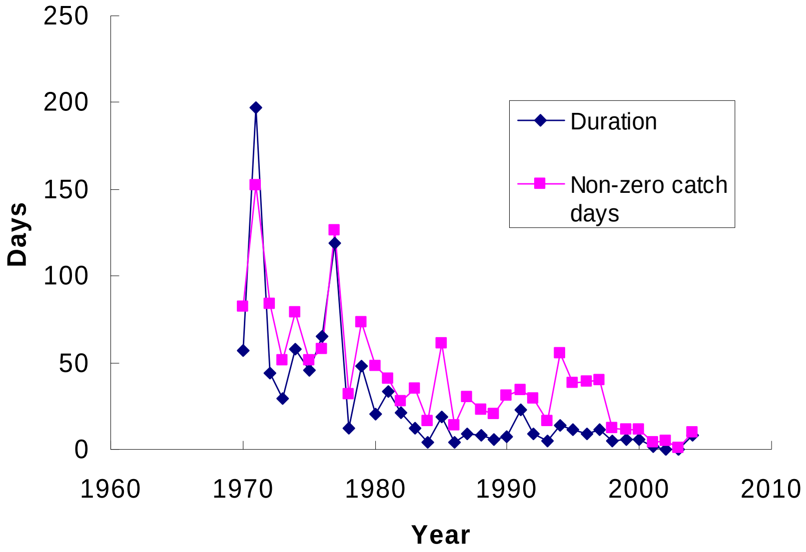


Figure 17: The period following the capture of the first 5% of the catch required to take the next 90%, and the number of non-zero catch days recorded in the logbook data.

Virtual population analysis using assumption of zero terminal biomass

For earlier years, the estimates of abundance calculated using the virtual population analysis show a relatively slow decline at the start of each season before the prawns become vulnerable to the fishery (Figure 18). Noting that it was assumed for the VPA that body size of prawns is constant; this decline reflects the impact of natural mortality. Subsequently, as the prawns become vulnerable to fishers, the abundance declines rapidly as a result of relatively heavy exploitation. The rate of decline decreases towards the end of the banana season, presumably as fishing effort is reduced. The initial portion of the curve is considerably truncated from 1984 onward, due to the change in opening date of the banana season to approximately 1 April. The decline that occurs when the prawns become vulnerable to the trawlers appears to have become more rapid in the 1980s and 1990s, as is reflected in the reduced number of days required to take the major portion of the catch (Figure 17).

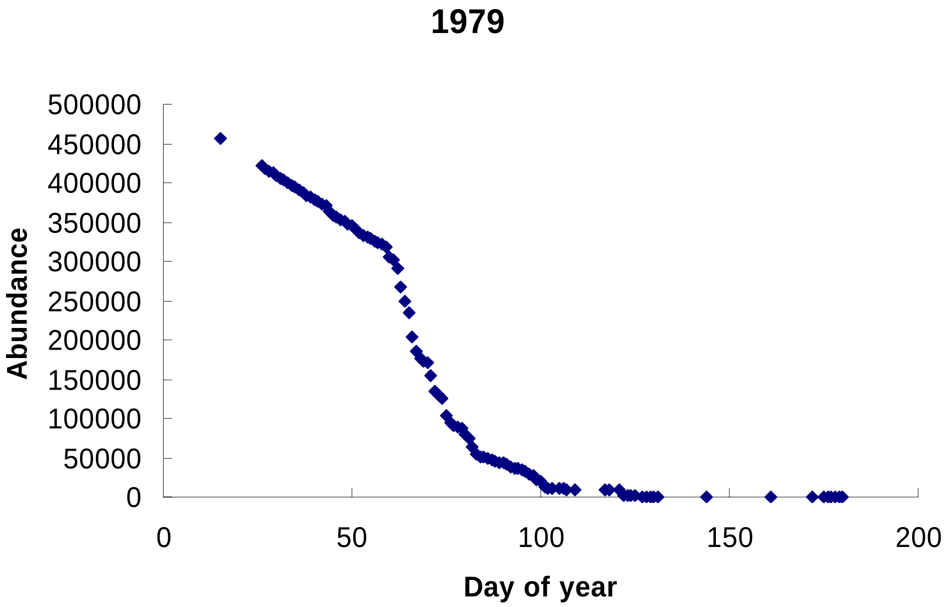


Figure 18: Abundance (kg) of banana prawns at Weipa at each day of the 1979 fishing season, calculated using virtual population analysis and assuming constant mortality and body size and no prawns surviving at the end of the year.

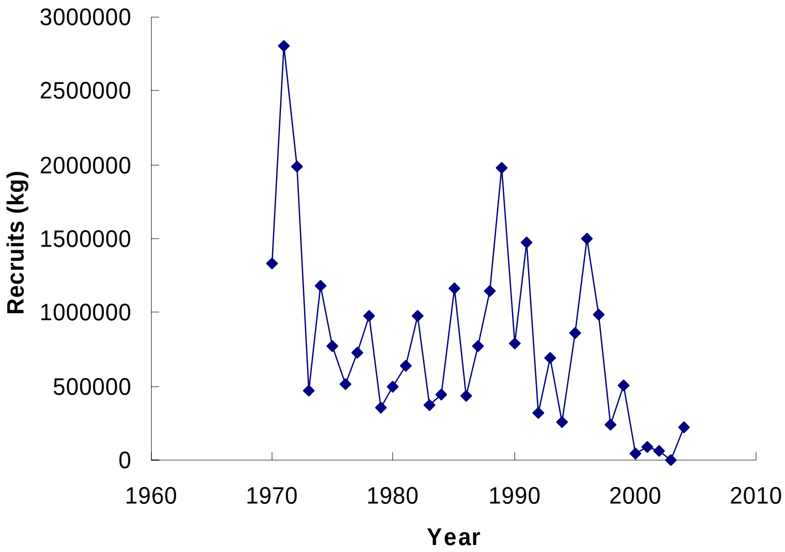


Figure 19: Annual recruitment (kg) of banana prawns at Weipa, calculated using virtual population analysis and assuming constant mortality and body size and no prawns surviving at the end of the year.

Apart from very high values for 1971, 1972 and 1989, estimates of annual recruitment (kg) of banana prawns to the Weipa stock, calculated using virtual population analysis, have remained relatively stable although highly variable in the period till 1997 (Figure 19). Because of the low number of non-zero catch days, estimates of abundance produced by the VPA for 1998 to 2004 are highly uncertain as they are particularly sensitive to the assumption that the terminal abundance of the Weipa banana prawn stock is zero. Thus, the apparent decline in recruitment since 1997 in the results produced by this VPA should be viewed with caution as it may simply be an artifact of low fishing effort and inappropriate assumptions.

The highly variable nature of the catch per unit of effort (CPUE) data for banana prawns is characteristic of the fishery at Weipa, reflecting searching for and capture of individuals of a species that are often highly aggregated. The population estimates obtained from the virtual population analysis were plotted against estimates of daily CPUE to assess the adequacy of the assumption that CPUE could be used as an index of abundance, *i.e.* whether CPUE is linearly correlated with the intra-annual population estimates. Although there appeared to be a general tendency for CPUE to increase with population abundance, the data frequently exhibited considerable scatter, *e.g.* Figure 20. While for some years the correlation appeared relatively strong, *e.g.* Figure 21, for many, it was poor. In years in which recruitment to the fishery may have been delayed, a number of low values of CPUE were recorded for days in which a large population was estimated to be present. In others, high CPUEs were recorded later in the season when the predicted abundance was low, presumably resulting from the detection by fishers of an aggregation of banana prawns that was subsequently fished.

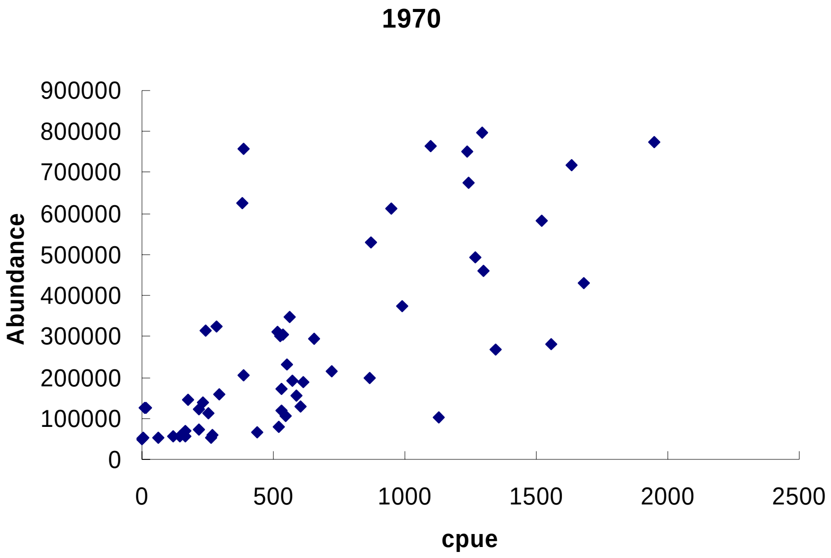


Figure 20: Relationship between the abundance of banana prawns at Weipa estimated using virtual population analysis of daily catch data for 1970 and the recorded daily CPUEs.

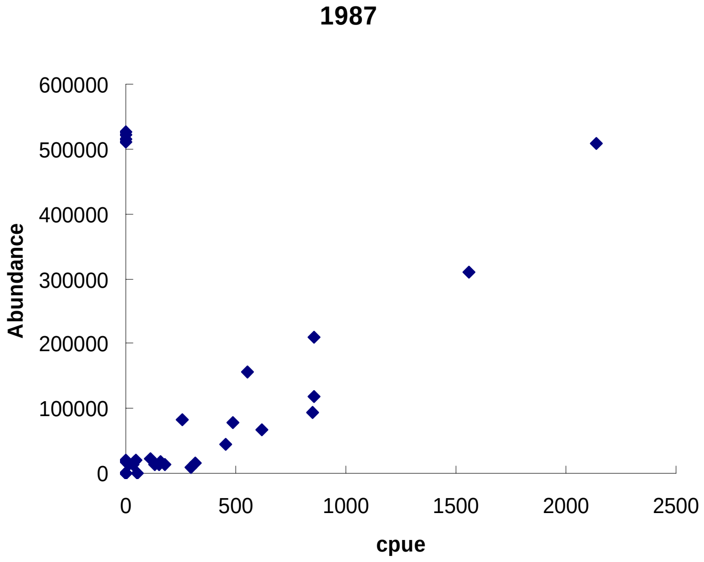


Figure 21: Relationship between the abundance of banana prawns at Weipa estimated using virtual population analysis of daily catch data for 1987 and the recorded daily CPUEs.

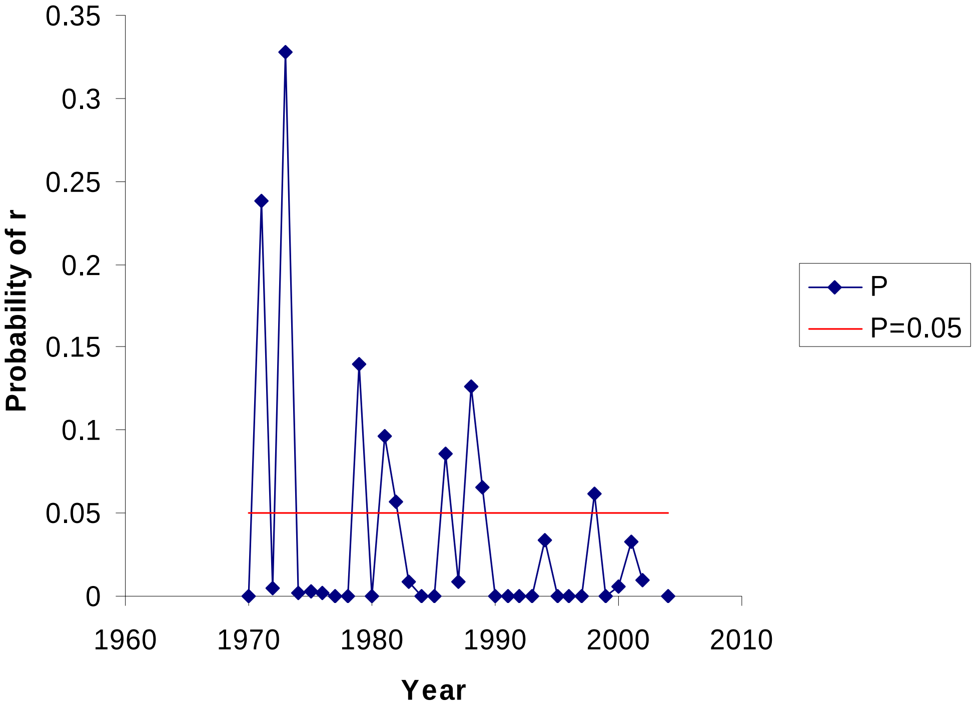


Figure 22: Probabilities associated with the tests of significance of the correlation coefficients r of the relationships between the abundances estimated from the virtual population analysis and the recorded daily CPUEs.

Twenty five of the 34 correlation coefficients for the years 1970 to 2002 and 2004 calculated using the predicted daily abundances and the recorded daily CPUEs were found to be statistically significant ($P < 0.05$), and 15 of these were less than $P = 0.05/34$, the critical level calculated using the Bonferroni correction for multiple comparisons (Figure 22). It should be noted, however, that the data for the two variables used when calculating the correlation coefficients are not independent.

Tuned virtual population analysis using estimate of terminal biomass

The results obtained from the virtual population analysis that estimated the terminal biomass rather than assuming it to be zero were mixed, presumably reflecting the adequacy of the CPUEs as indices of abundance. While reasonable results were obtained for some years, *e.g.* 1970 (Figure 23), those for other years, *e.g.* 1975 (Figure 24) illustrated the difficulty associated with fitting the model to CPUE data that contain a mixture of both low and high values over a relatively short period during which the abundances of prawns should have been approximately similar. For several years, the estimates of terminal biomass were so high and the catchability so low as to be infeasible. Such years were filtered from the estimates of recruitment and spawning biomass before attempting to fit the various stock-recruitment relationships.

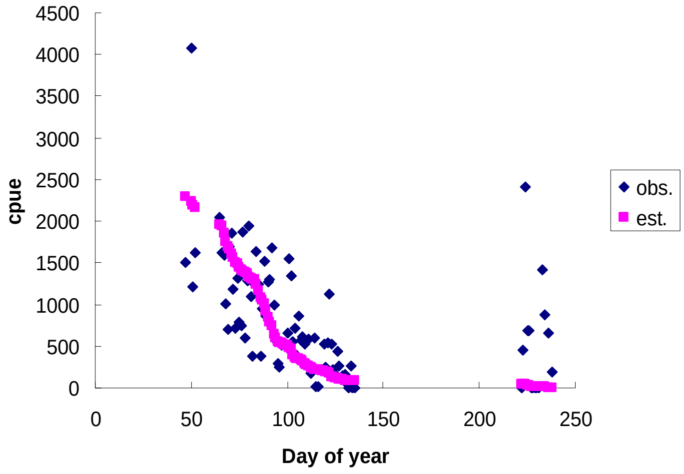


Figure 23: Observed and estimated CPUEs for banana prawns at Weipa in 1970.

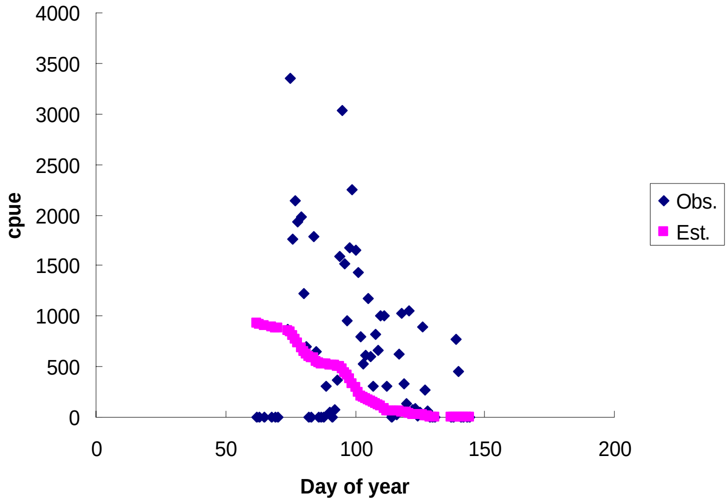


Figure 24: Observed and estimated CPUEs for banana prawns at Weipa in 1975.

The results obtained from the virtual population analysis indicated that recruitment had declined from the high values experienced in the early 1970s to become variable but relatively stable in the period to 1997 (Figure 25). Subsequently, it had declined to very low values between 2000 and 2003, but appeared to be indicating a slight recovery in 2004. Estimates of spawning biomass revealed no obvious trend (Figure 26).

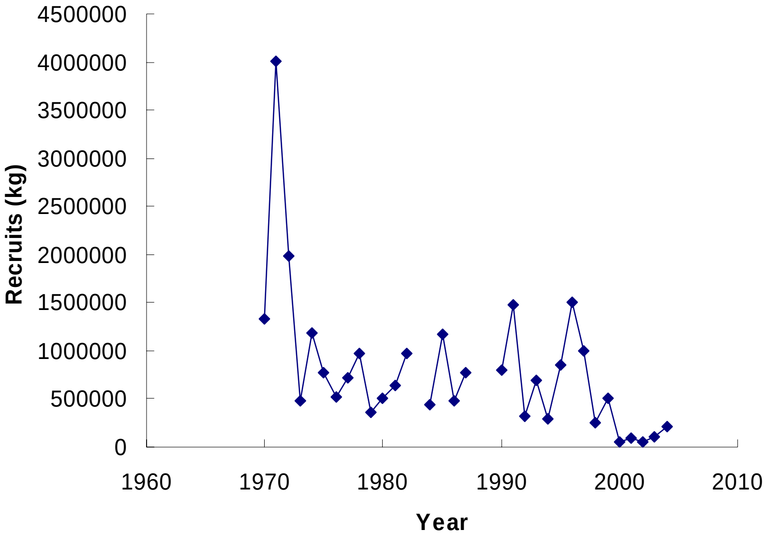


Figure 25: Estimates of recruitment of banana prawns at Weipa derived from the tuned VPA.

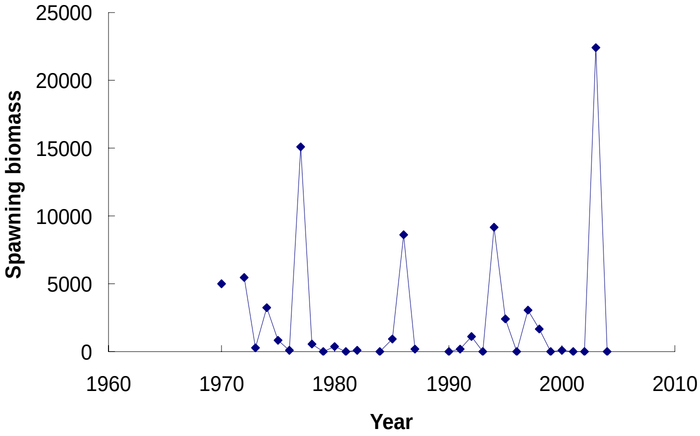


Figure 26: Estimates of spawning biomass of banana prawns at Weipa derived from the tuned VPA.

The model that produced the lowest value of AIC_c was the constant recruitment model. The data provided essentially no support for the models that incorporated the effects of the environmental variables, however there was some support for the model which assumed recruitment to be related to spawning biomass ($\Delta = 2.12$). The weight of evidence in favour of the constant recruitment model ($w = 0.74$) was, however, almost three times greater than that for the model that assumed a relationship with spawning biomass ($w = 0.26$).

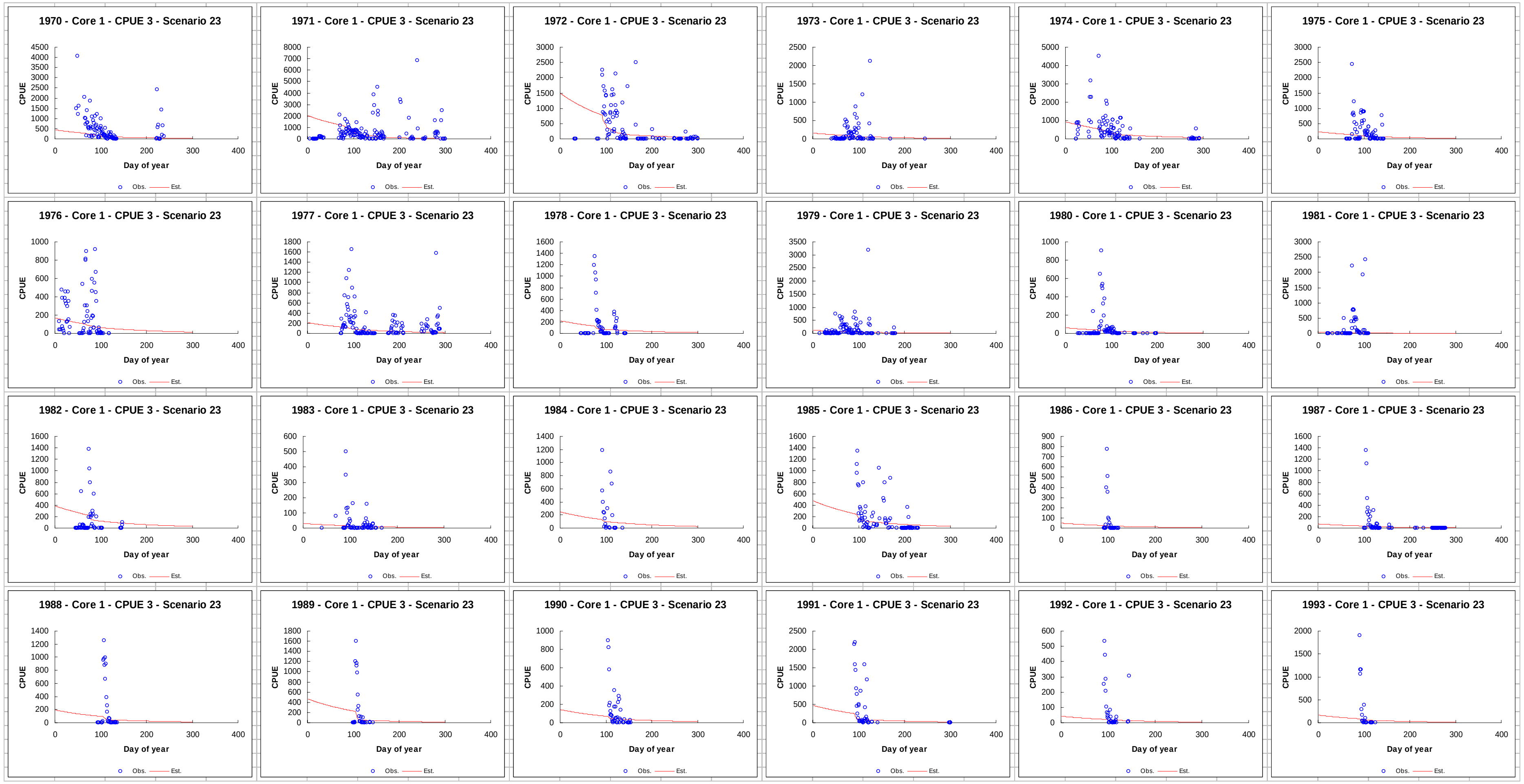
Depletion model with non-informative priors

The estimates of the daily CPUEs for banana prawns from Weipa, produced under Scenario 23 by the depletion model fitted to CPUEs calculated from logbook data using the intermediate hypothesis regarding the values in non-fished grid cells, displayed similar trends when the calculations were based on grid cells from core region 1 or 2. (Figure 27 & Figure 28 vs Figure 29 & Figure 30). Although the estimates of recruitment resulting from calculations based on the two core regions differed slightly in magnitude, trends were similar and the differences appeared to relate more to the Scenario being explored than the core region used (Figure 31 to Figure 36). Trends in the relationship between recruitment and spawning stock, with or without the effects of environmental variables, were again similar and differences in magnitude again appeared to be related more to the Scenario employed than the core region used when calculating the CPUEs at Weipa (Figure 37 to Figure 42).

As with the tuned VPA, the depletion model produced relatively poor fits to the CPUE data (Figure 27 to Figure 30), which again appeared to be related to the mix of high and low CPUEs encountered at each level of prawn abundance. The weights given to the deviations when fitting the depletion model differed from those of the tuned VPA. The former model employed a sum of squares calculated using raw CPUE data and fitted the model simultaneously to the data for all years, whereas the latter modified the data using a log(x + 1) transformation prior to calculating the sum of squares and first fitted the models to the daily data for the years to produce the data required for exploration of the relationship between recruitment and spawning biomass and/or environmental variables. Values of CPUE that fell outside the fitted region, *i.e.* day 81 to 213, were poorly predicted by the depletion model. The poor prediction prior to day 81 was, however, not unexpected, as these prawns would not yet have become fully recruited to the fishery.

The estimates of annual recruitment of banana prawns from Weipa, calculated using the CPUEs derived from logbook data using the grid cells from core regions 1 and 2 with the optimistic (“CPUE 1”), pessimistic (“CPUE 2”) and intermediate (“CPUE 3”) assumptions regarding CPUEs in non-fished grid cells, differed in response to the Scenario that was being explored (Figure 31 to Figure 36). While the magnitude of recruitment often differed among the results from the different Scenarios, so too did the estimates of catchability associated with those recruitment estimates, thus the impact on predicted CPUEs was minimal. While the estimates from Scenarios that allowed for non-constant recruitment suggest a decline in recruitment from the early 1970s, subsequent estimates of recruitment are highly variable and indicate no consistent trends. Although for some Scenarios and data sets there was a suggestion of a further decline in more recent years, this was not evident for other scenarios.

Invariably, when the parameter b was free and fitted by the model (Scenarios 3, 4, 7, 8, 11, 12, 15, 16, 19, 20, 23 and 24), a low value was estimated, suggesting little evidence of a relationship between recruitment and spawning biomass (Figure 37 to Figure 42). The recruitment estimates obtained by allowing for the effect of environmental variables had negligible impact except when considered in the constant catchability Scenarios without interannual recruitment variability, *i.e.* Scenarios 13 and 15. In these cases, high levels of recruitment were predicted for some years in the early 1970s and in 1999.



1970 - Core 1 - CPUE 3 - Scenario 23
1971 - Core 1 - CPUE 3 - Scenario 23
1972 - Core 1 - CPUE 3 - Scenario 23
1973 - Core 1 - CPUE 3 - Scenario 23
1974 - Core 1 - CPUE 3 - Scenario 23
1975 - Core 1 - CPUE 3 - Scenario 23
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1991 - Core 1 - CPUE 3 - Scenario 23
1992 - Core 1 - CPUE 3 - Scenario 23
1993 - Core 1 - CPUE 3 - Scenario 23

Figure 27: Daily CPUEs for banana prawns from Weipa from 1970 to 1993, calculated from logbook data using the grid cells from core region 1 with the intermediate rather than optimistic or pessimistic assumption regarding CPUEs in non-fished grid cells. The values of CPUE predicted by the model when fitted using Scenario 23 are also presented.

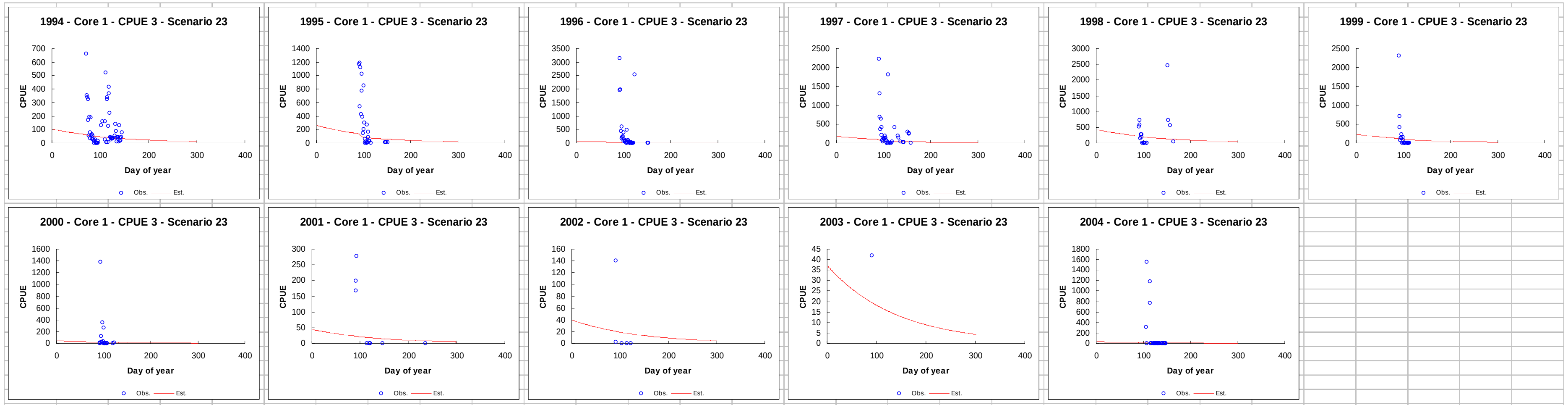


Figure 28: Daily CPUEs for banana prawns from Weipa from 1994 to 2004, calculated from logbook data using the grid cells from core region 1 with the intermediate rather than optimistic or pessimistic assumption regarding CPUEs in non-fished grid cells. The values of CPUE predicted by the model when fitted using Scenario 23 are also presented.

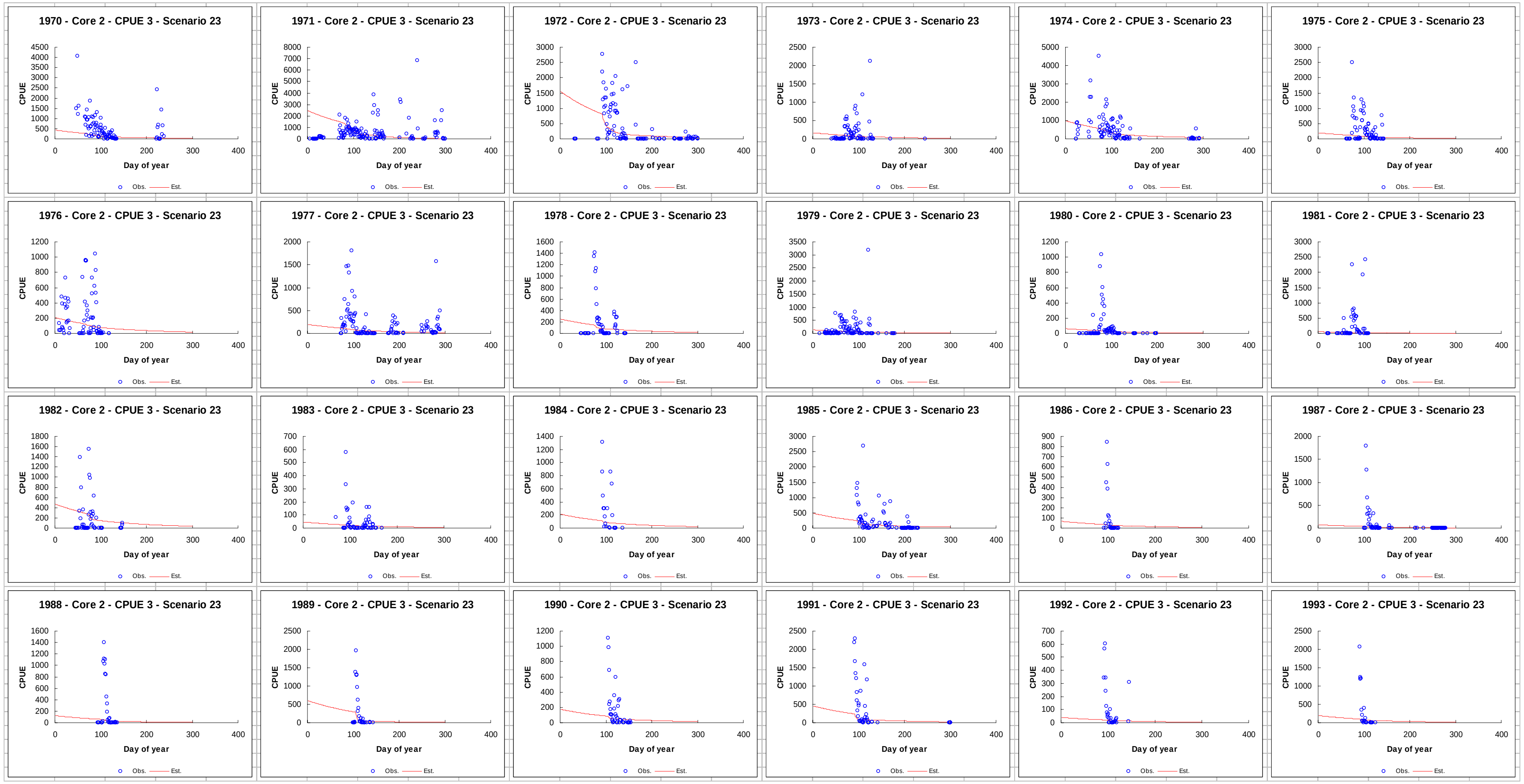


Figure 29: Daily CPUEs for banana prawns from Weipa from 1970 to 1993, calculated from logbook data using the grid cells from core region 2 with the intermediate rather than optimistic or pessimistic assumption regarding CPUEs in non-fished grid cells. The values of CPUE predicted by the model when fitted using Scenario 23 are also presented.

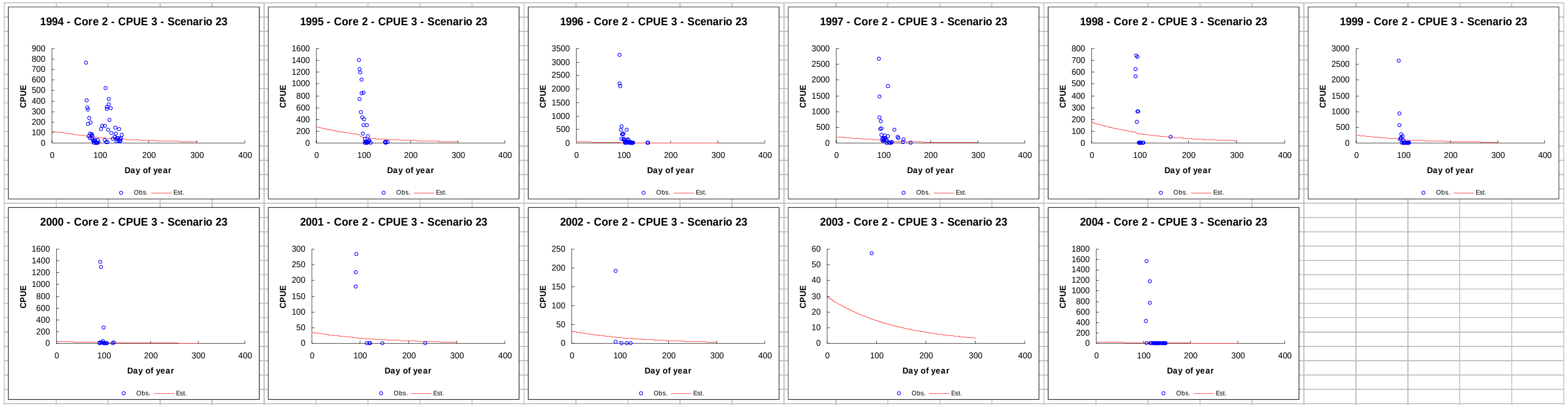


Figure 30: Daily CPUEs for banana prawns from Weipa from 1994 to 2004, calculated from logbook data using the grid cells from core region 2 with the intermediate rather than optimistic or pessimistic assumption regarding CPUEs in non-fished grid cells. The values of CPUE predicted by the model when fitted using Scenario 23 are also presented.

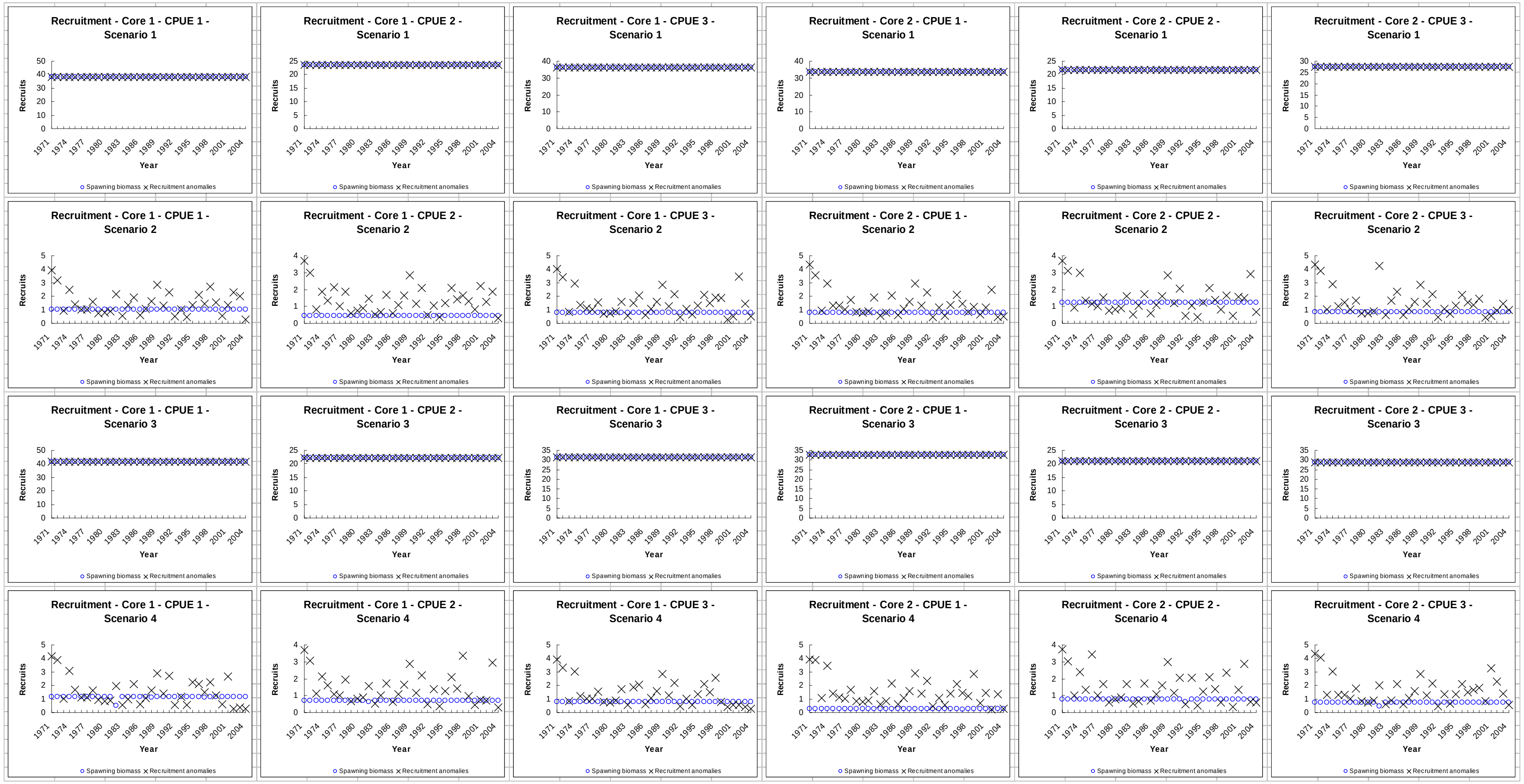


Figure 31: Estimates of annual recruitment of banana prawns from Weipa, obtained using CPUEs derived from logbook data using the grid cells from core regions 1 and 2 with the optimistic (“CPUE 1”), pessimistic (“CPUE 2”) and intermediate (“CPUE 3”) assumptions regarding CPUEs in non-fished grid cells, and calculated using Scenarios 1 to 4.

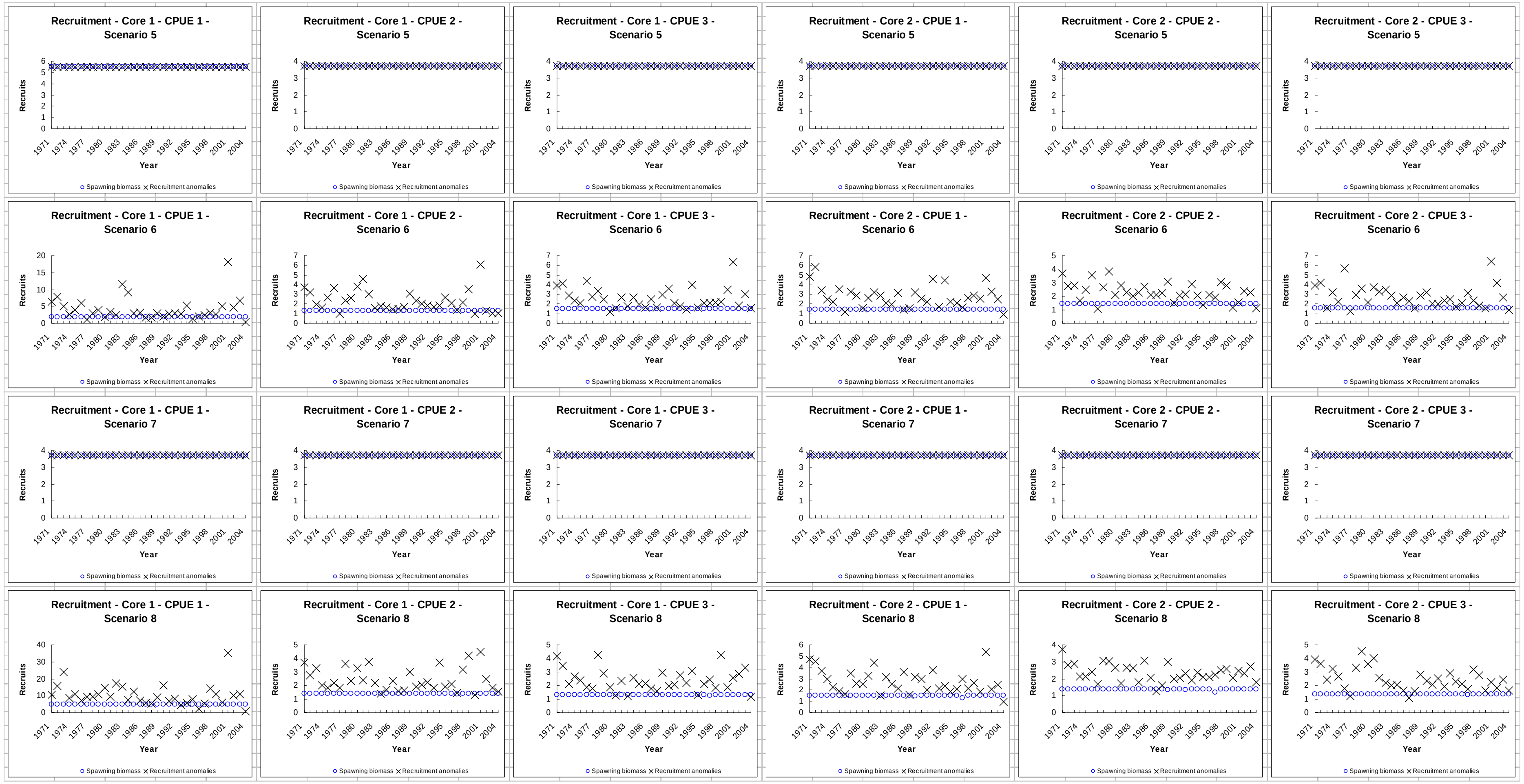


Figure 32: Estimates of annual recruitment of banana prawns from Weipa, obtained using CPUEs derived from logbook data using the grid cells from core regions 1 and 2 with the optimistic ("CPUE 1"), pessimistic ("CPUE 2") and intermediate ("CPUE 3") assumptions regarding CPUEs in non-fished grid cells, and calculated using Scenarios 5 to 8.

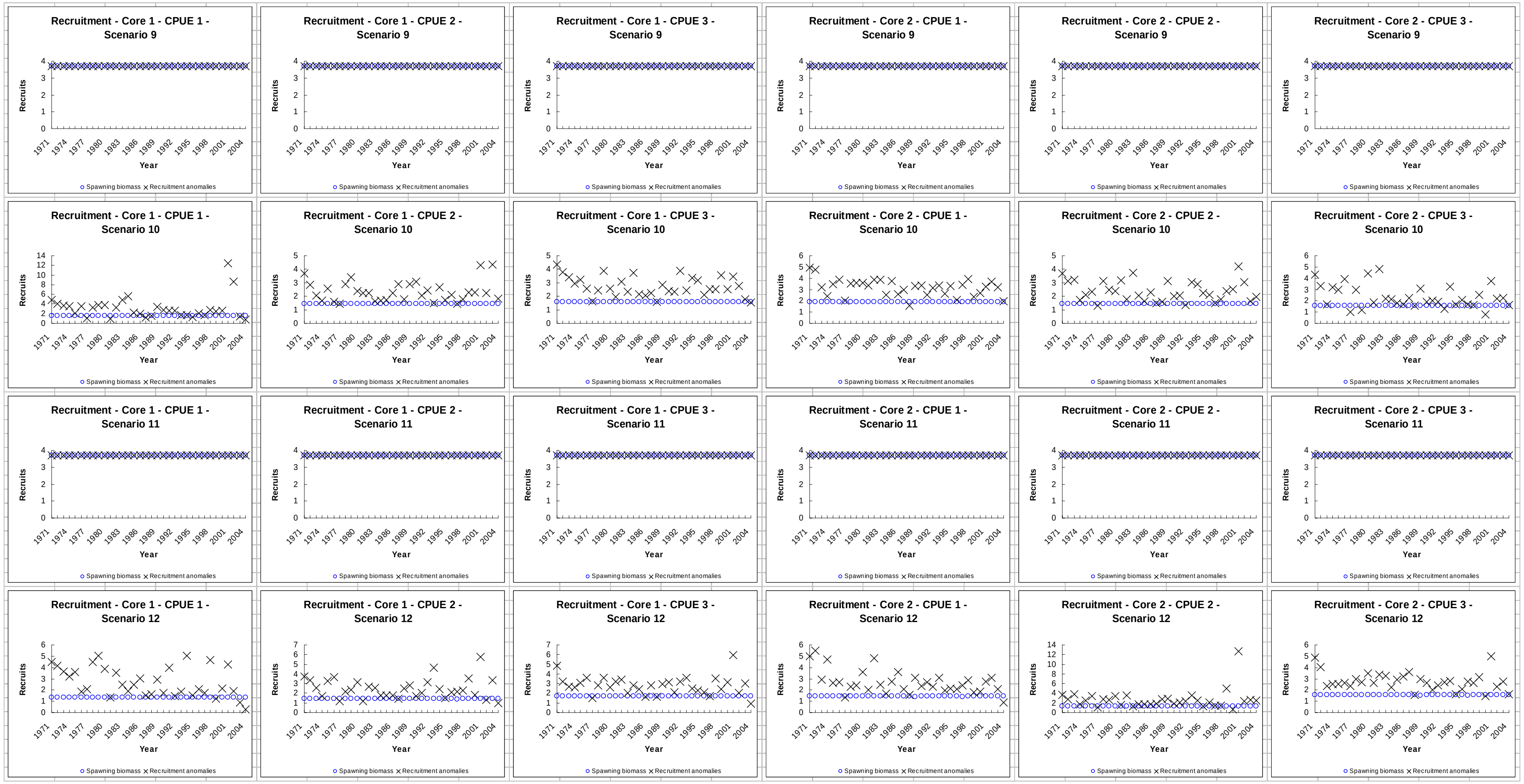


Figure 33: Estimates of annual recruitment of banana prawns from Weipa, obtained using CPUEs derived from logbook data using the grid cells from core regions 1 and 2 with the optimistic (“CPUE 1”), pessimistic (“CPUE 2”) and intermediate (“CPUE 3”) assumptions regarding CPUEs in non-fished grid cells, and calculated using Scenarios 9 to 12.

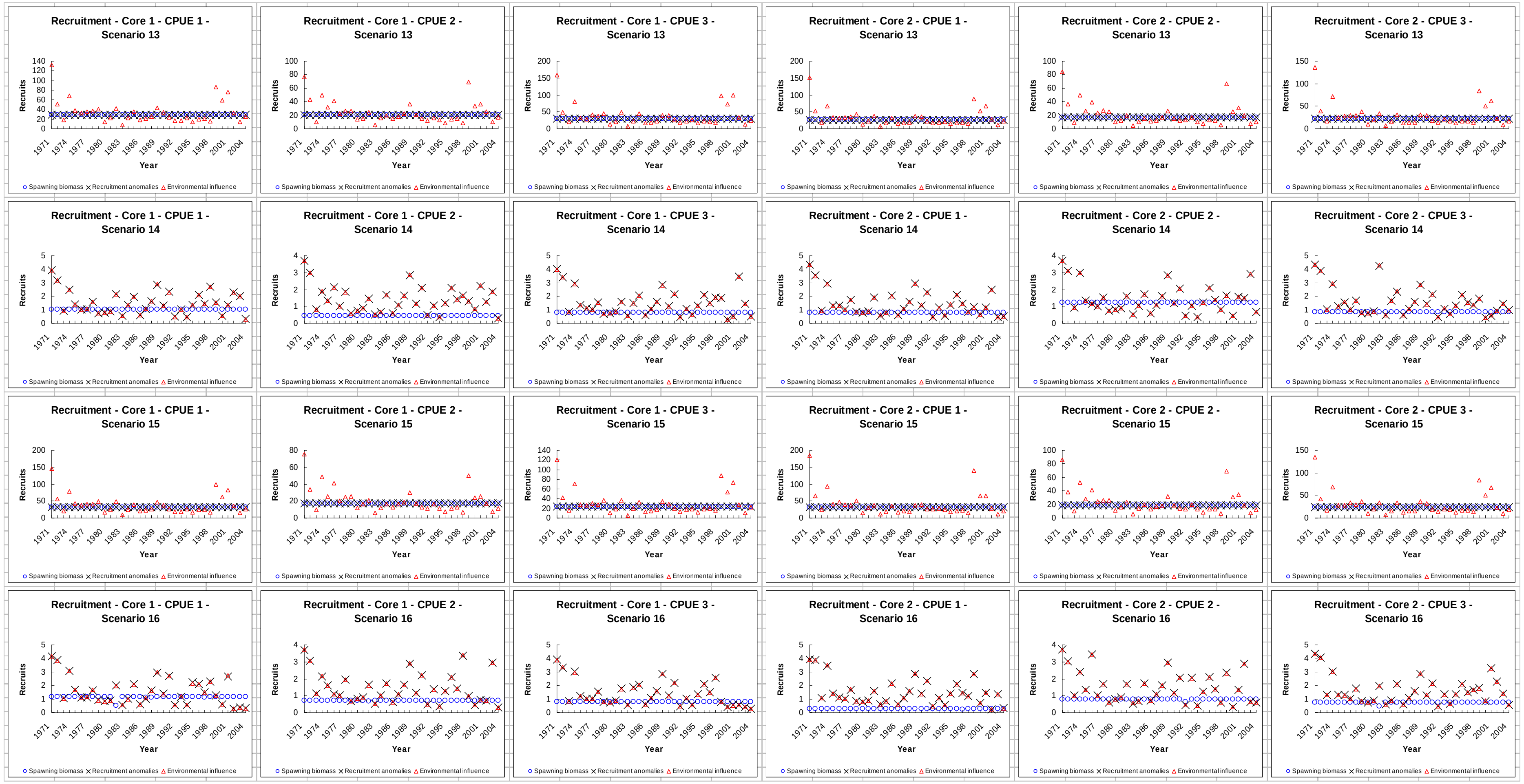

Recruitment - Core 1 - CPUE 1 - Scenario 13
Recruitment - Core 1 - CPUE 2 - Scenario 13
Recruitment - Core 1 - CPUE 3 - Scenario 13
Recruitment - Core 2 - CPUE 1 - Scenario 13
Recruitment - Core 2 - CPUE 2 - Scenario 13
Recruitment - Core 2 - CPUE 3 - Scenario 13
Recruitment - Core 1 - CPUE 1 - Scenario 14
Recruitment - Core 1 - CPUE 2 - Scenario 14
Recruitment - Core 1 - CPUE 3 - Scenario 14
Recruitment - Core 2 - CPUE 1 - Scenario 14
Recruitment - Core 2 - CPUE 2 - Scenario 14
Recruitment - Core 2 - CPUE 3 - Scenario 14
Recruitment - Core 1 - CPUE 1 - Scenario 15
Recruitment - Core 1 - CPUE 2 - Scenario 15
Recruitment - Core 1 - CPUE 3 - Scenario 15
Recruitment - Core 2 - CPUE 1 - Scenario 15
Recruitment - Core 2 - CPUE 2 - Scenario 15
Recruitment - Core 2 - CPUE 3 - Scenario 15
Recruitment - Core 1 - CPUE 1 - Scenario 16
Recruitment - Core 1 - CPUE 2 - Scenario 16
Recruitment - Core 1 - CPUE 3 - Scenario 16
Recruitment - Core 2 - CPUE 1 - Scenario 16
Recruitment - Core 2 - CPUE 2 - Scenario 16
Recruitment - Core 2 - CPUE 3 - Scenario 16

Figure 34: Estimates of annual recruitment of banana prawns from Weipa, obtained using CPUEs derived from logbook data using the grid cells from core regions 1 and 2 with the optimistic (“CPUE 1”), pessimistic (“CPUE 2”) and intermediate (“CPUE 3”) assumptions regarding CPUEs in non-fished grid cells, and calculated using Scenarios 13 to 16.

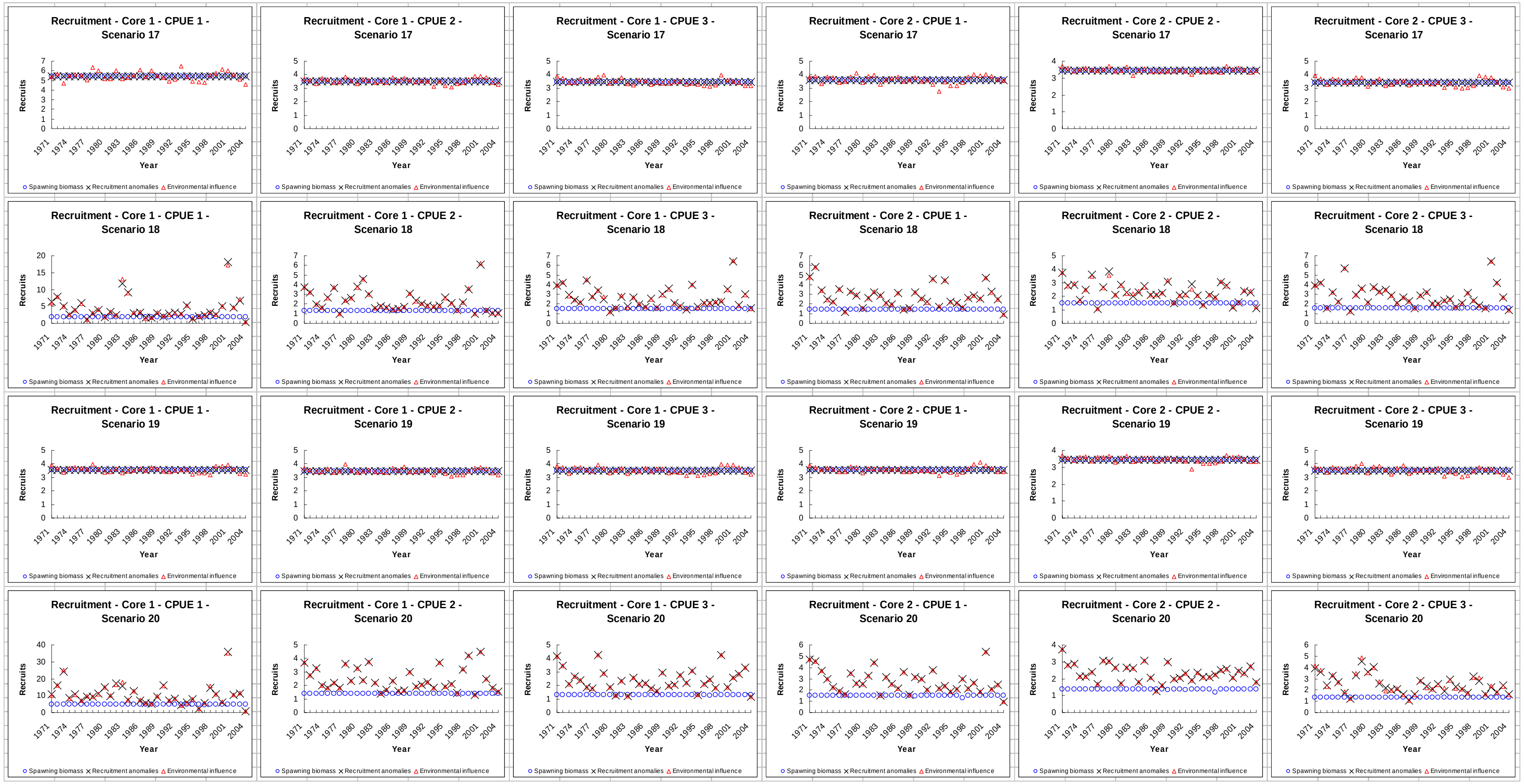


Figure 35: Estimates of annual recruitment of banana prawns from Weipa, obtained using CPUEs derived from logbook data using the grid cells from core regions 1 and 2 with the optimistic (“CPUE 1”), pessimistic (“CPUE 2”) and intermediate (“CPUE 3”) assumptions regarding CPUEs in non-fished grid cells, and calculated using Scenarios 17 to 20.

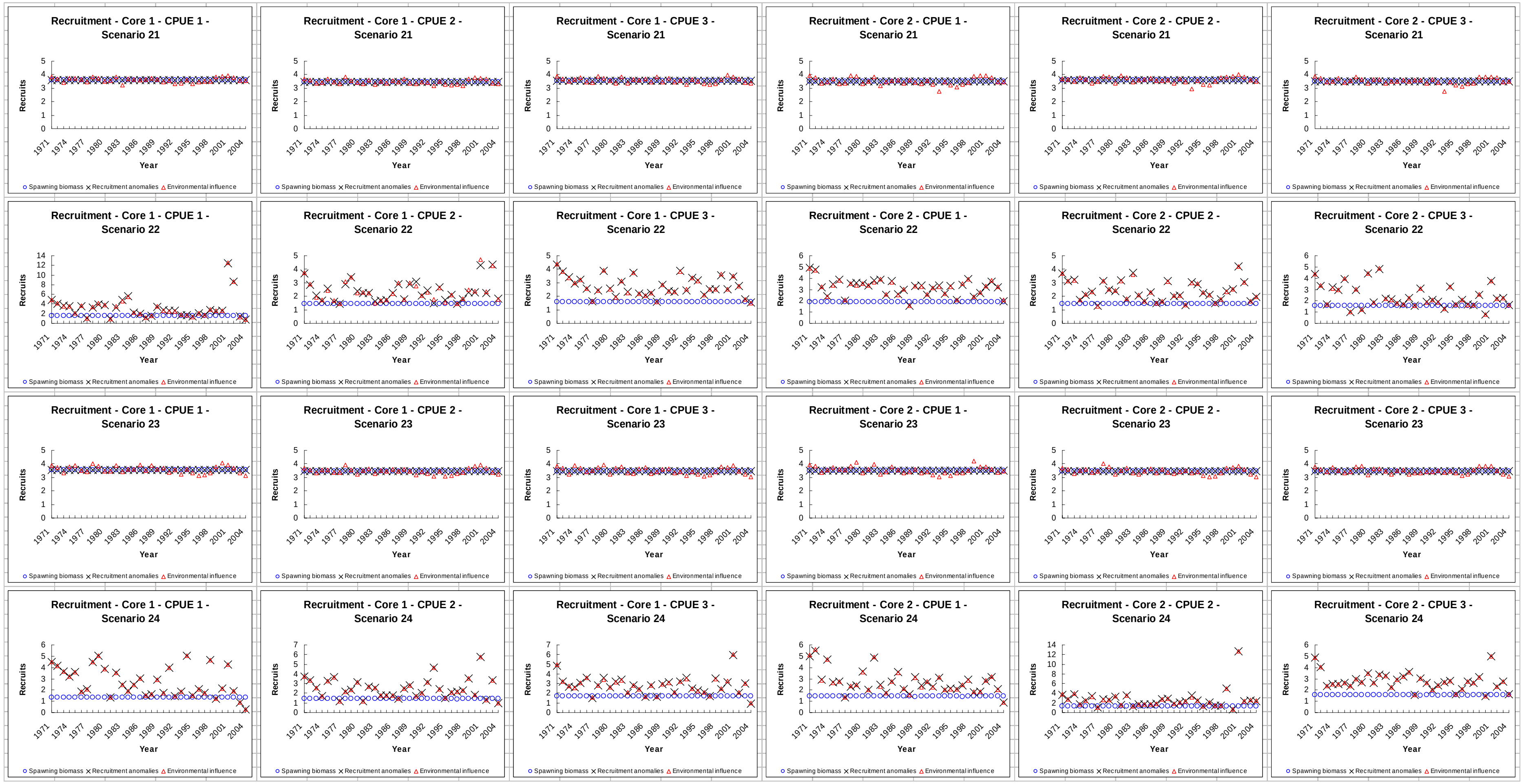


Figure 36: Estimates of annual recruitment of banana prawns from Weipa, obtained using CPUEs derived from logbook data using the grid cells from core regions 1 and 2 with the optimistic (“CPUE 1”), pessimistic (“CPUE 2”) and intermediate (“CPUE 3”) assumptions regarding CPUEs in non-fished grid cells, and calculated using Scenarios 21 to 24.

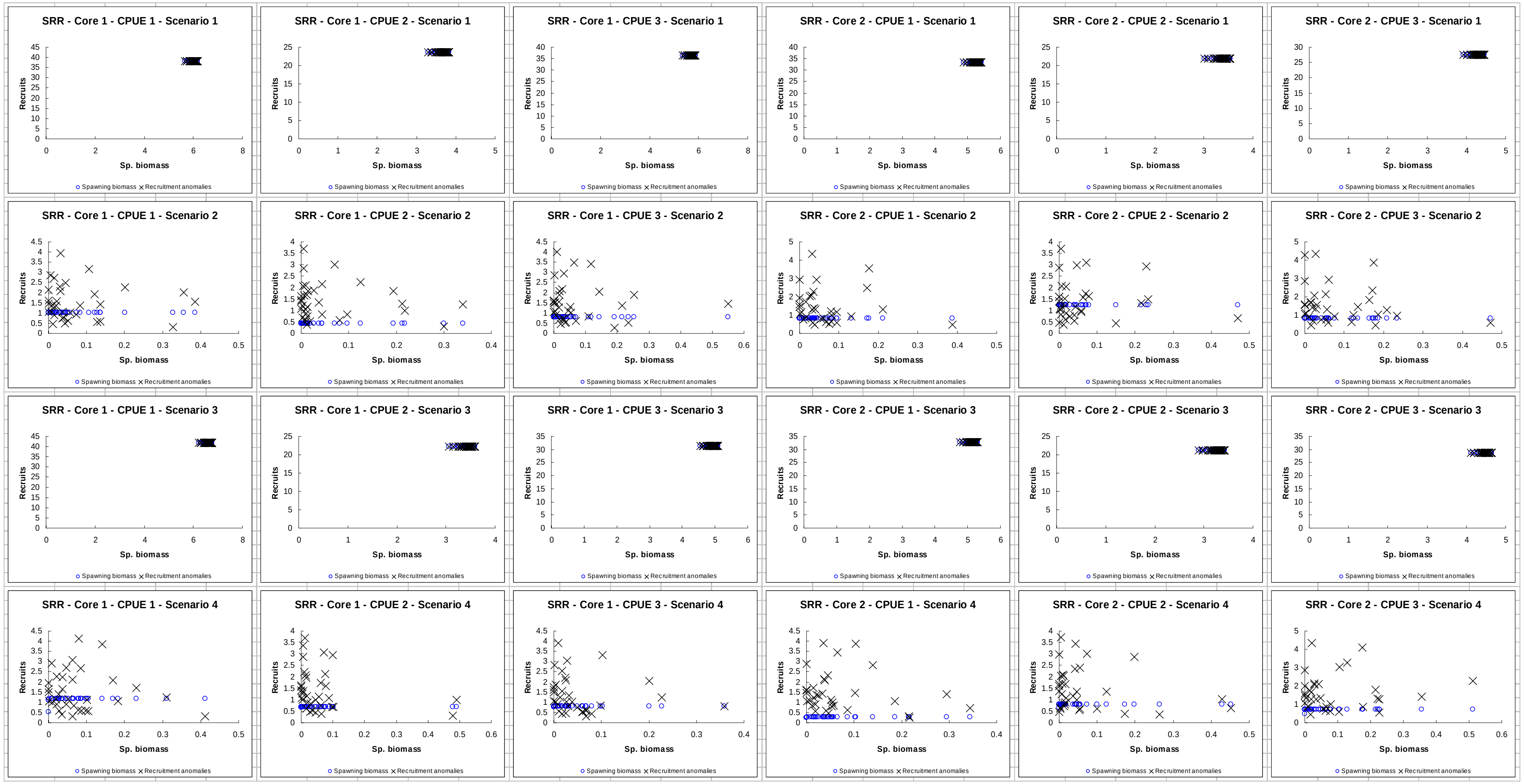


Figure 37: Recruitment of banana prawns from Weipa that would be expected given the estimated spawning stock and that which would be expected to result from stochasticity in annual recruitment and/or the influence of environmental variables. Estimates obtained using CPUEs derived using the grid cells from core regions 1 and 2 with the optimistic (“CPUE 1”), pessimistic (“CPUE 2”) and intermediate (“CPUE 3”) assumptions regarding CPUEs in non-fished grid cells, and calculated using Scenarios 1 to 4.

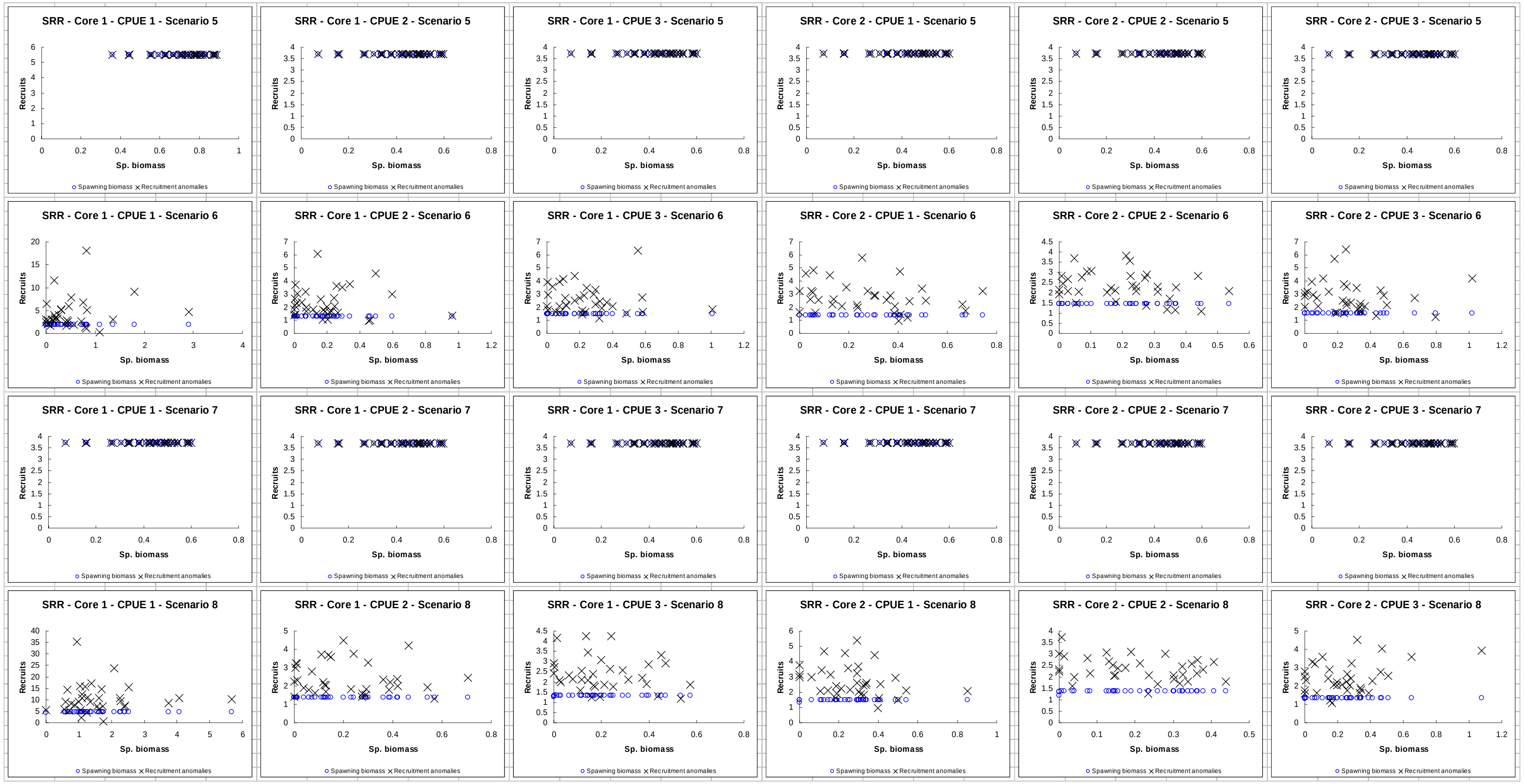
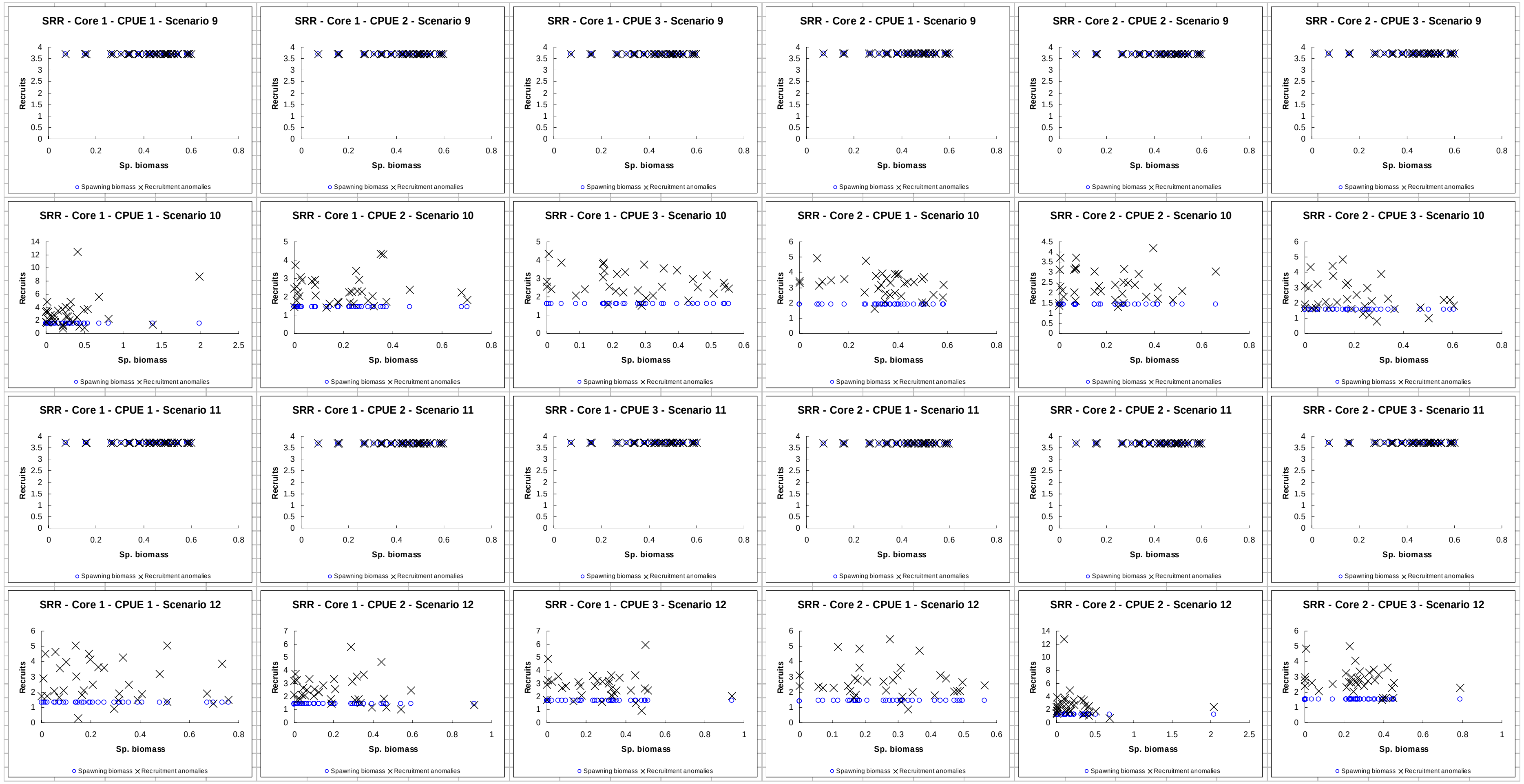


Figure 38: Recruitment of banana prawns from Weipa that would be expected given the estimated spawning stock and that which would be expected to result from stochasticity in annual recruitment and/or the influence of environmental variables. Estimates obtained using CPUEs derived using the grid cells from core regions 1 and 2 with the optimistic ("CPUE 1"), pessimistic ("CPUE 2") and intermediate ("CPUE 3") assumptions regarding CPUEs in non-fished grid cells, and calculated using Scenarios 5 to 8.



SRR - Core 1 - CPUE 1 - Scenario 9

SRR - Core 1 - CPUE 2 - Scenario 9

SRR - Core 1 - CPUE 3 - Scenario 9

SRR - Core 2 - CPUE 1 - Scenario 9

SRR - Core 2 - CPUE 2 - Scenario 9

SRR - Core 2 - CPUE 3 - Scenario 9

SRR - Core 1 - CPUE 1 - Scenario 10

SRR - Core 1 - CPUE 2 - Scenario 10

SRR - Core 1 - CPUE 3 - Scenario 10

SRR - Core 2 - CPUE 1 - Scenario 10

SRR - Core 2 - CPUE 2 - Scenario 10

SRR - Core 2 - CPUE 3 - Scenario 10

SRR - Core 1 - CPUE 1 - Scenario 11

SRR - Core 1 - CPUE 2 - Scenario 11

SRR - Core 1 - CPUE 3 - Scenario 11

SRR - Core 2 - CPUE 1 - Scenario 11

SRR - Core 2 - CPUE 2 - Scenario 11

SRR - Core 2 - CPUE 3 - Scenario 11

SRR - Core 1 - CPUE 1 - Scenario 12

SRR - Core 1 - CPUE 2 - Scenario 12

SRR - Core 1 - CPUE 3 - Scenario 12

SRR - Core 2 - CPUE 1 - Scenario 12

SRR - Core 2 - CPUE 2 - Scenario 12

SRR - Core 2 - CPUE 3 - Scenario 12

Figure 39: Recruitment of banana prawns from Weipa that would be expected given the estimated spawning stock and that which would be expected to result from stochasticity in annual recruitment and/or the influence of environmental variables. Estimates obtained using CPUEs derived using the grid cells from core regions 1 and 2 with the optimistic ("CPUE 1"), pessimistic ("CPUE 2") and intermediate ("CPUE 3") assumptions regarding CPUEs in non-fished grid cells, and calculated using Scenarios 9 to 12.

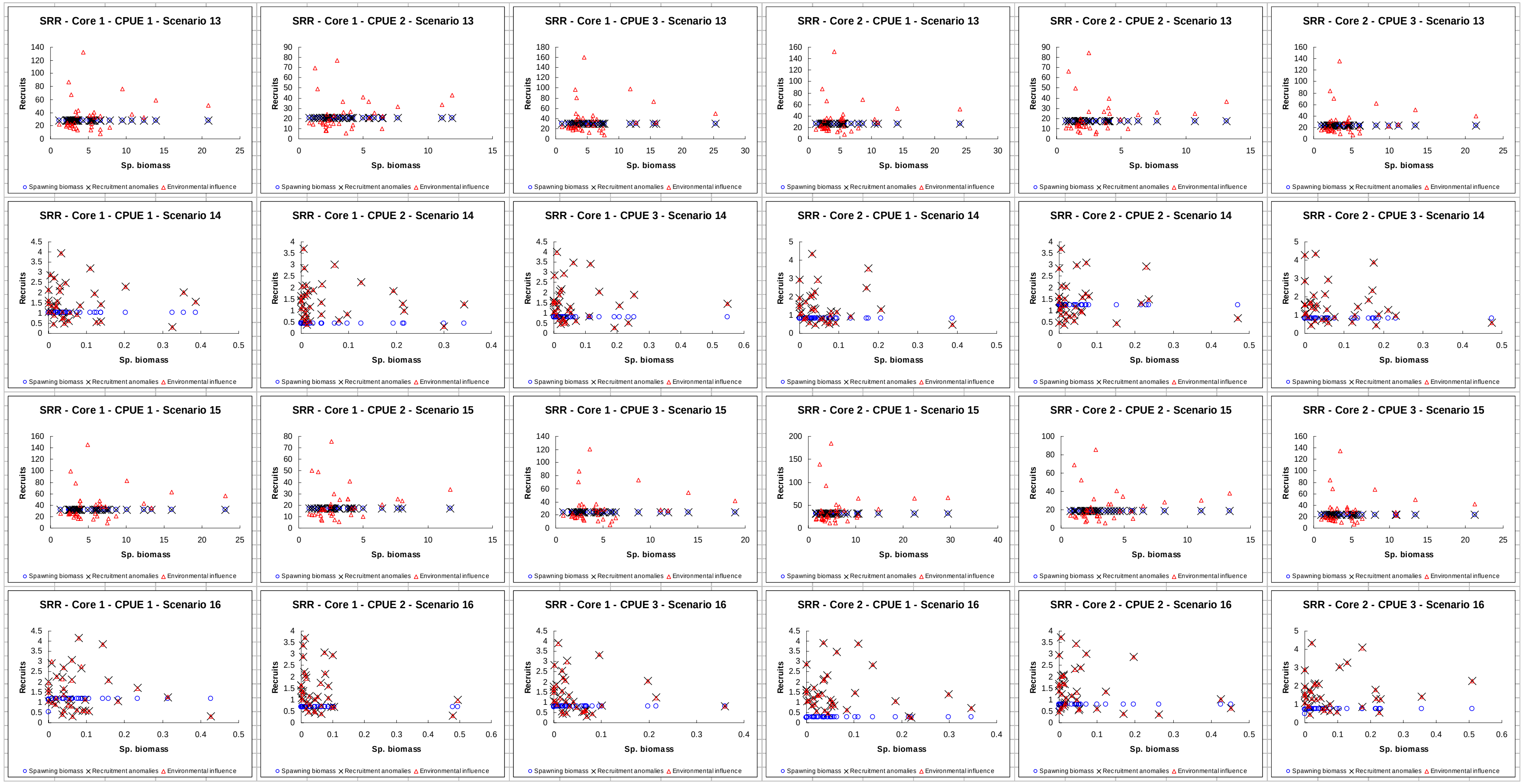


Figure 40: Recruitment of banana prawns from Weipa that would be expected given the estimated spawning stock and that which would be expected to result from stochasticity in annual recruitment and/or the influence of environmental variables. Estimates obtained using CPUEs derived using the grid cells from core regions 1 and 2 with the optimistic (“CPUE 1”), pessimistic (“CPUE 2”) and intermediate (“CPUE 3”) assumptions regarding CPUEs in non-fished grid cells, and calculated using Scenarios 13 to 16.

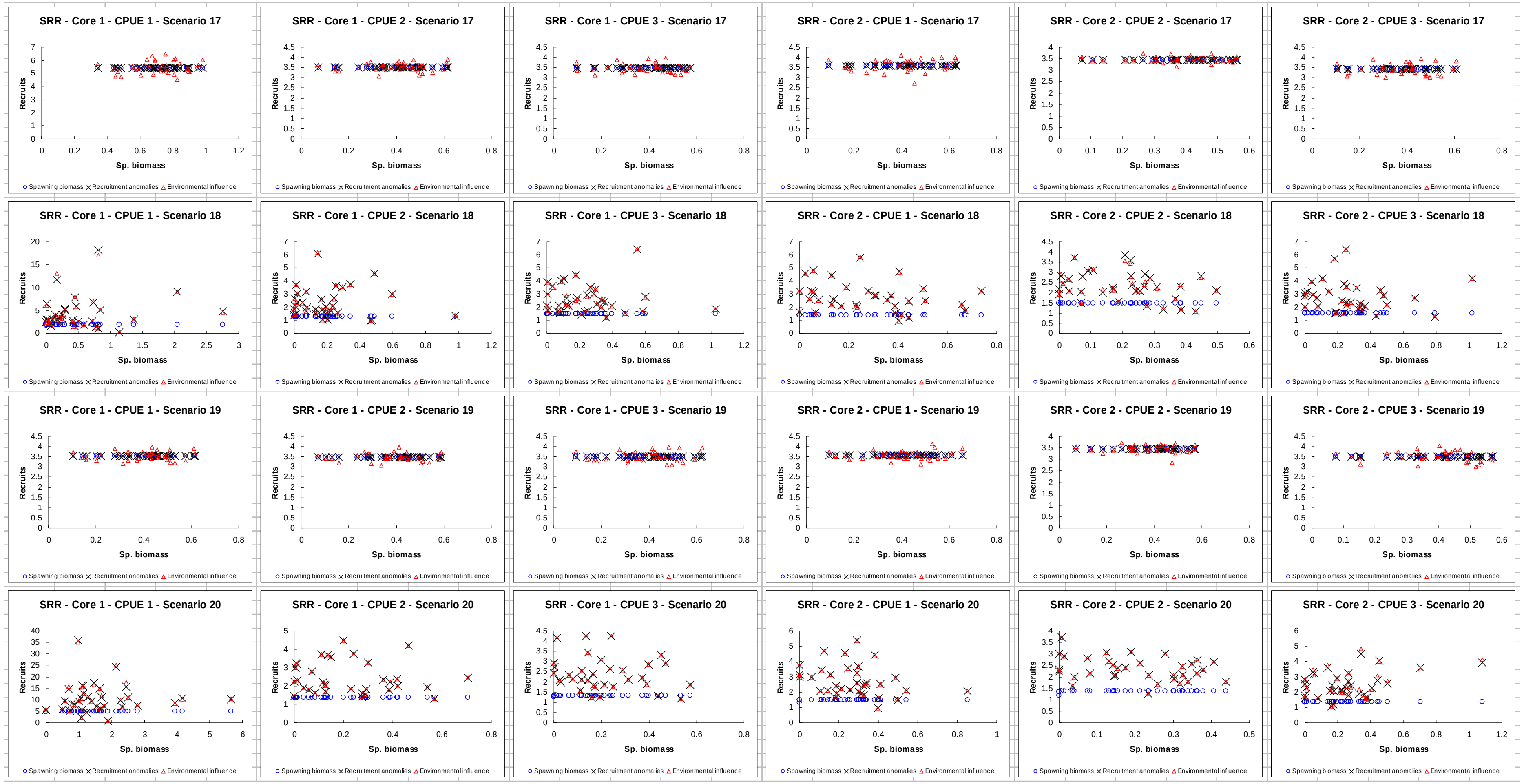


Figure 41: Recruitment of banana prawns from Weipa that would be expected given the estimated spawning stock and that which would be expected to result from stochasticity in annual recruitment and/or the influence of environmental variables. Estimates obtained using CPUEs derived using the grid cells from core regions 1 and 2 with the optimistic ("CPUE 1"), pessimistic ("CPUE 2") and intermediate ("CPUE 3") assumptions regarding CPUEs in non-fished grid cells, and calculated using Scenarios 17 to 20.

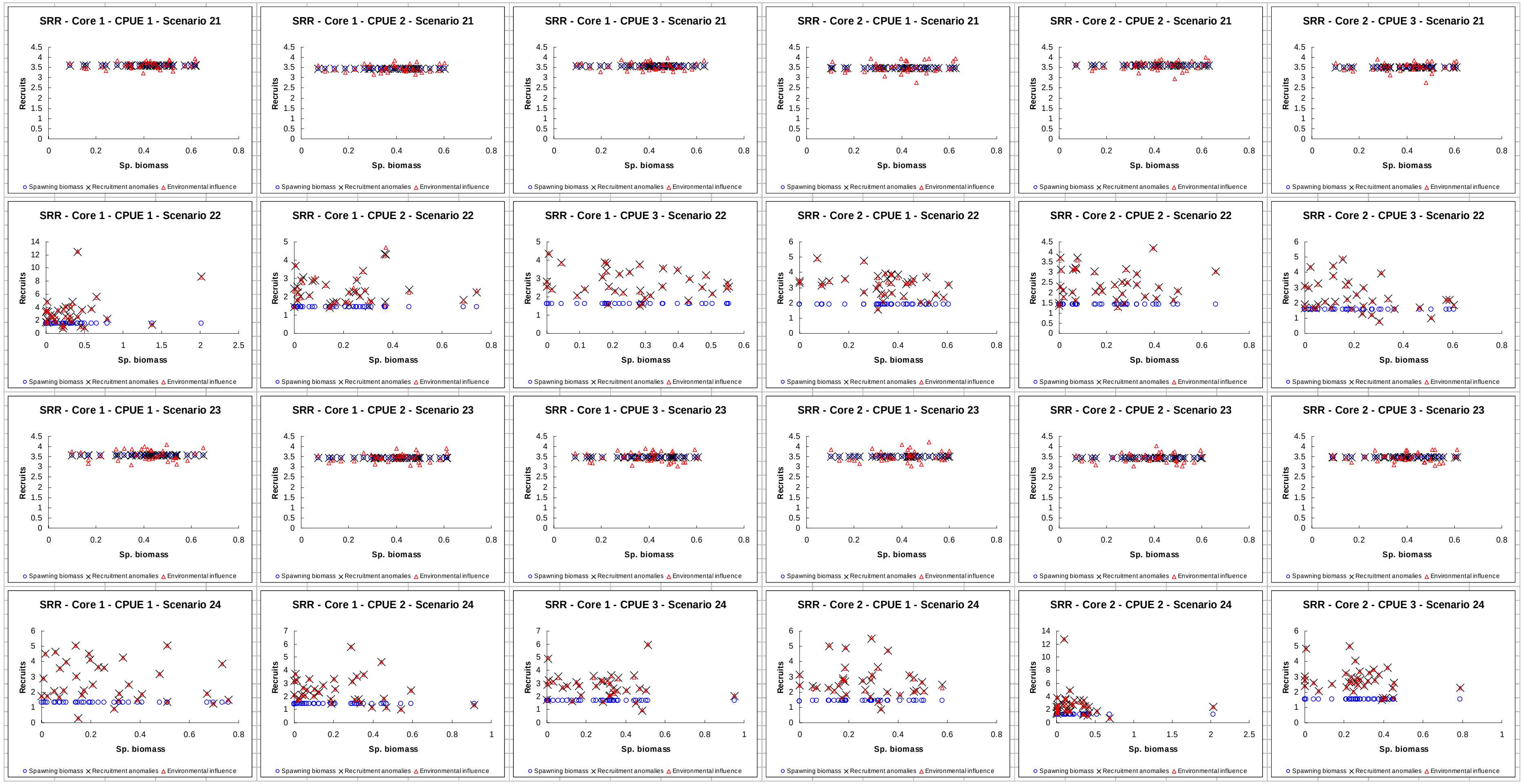


Figure 42: Recruitment of banana prawns from Weipa that would be expected given the estimated spawning stock and that which would be expected to result from stochasticity in annual recruitment and/or the influence of environmental variables. Estimates obtained using CPUEs derived using the grid cells from core regions 1 and 2 with the optimistic ("CPUE 1"), pessimistic ("CPUE 2") and intermediate ("CPUE 3") assumptions regarding CPUEs in non-fished grid cells, and calculated using Scenarios 21 to 24.

Discussion and conclusions

Although there appears to be a relationship between the daily CPUEs recorded for banana prawns at Weipa and the underlying abundance of those prawns, there is considerable variation in the values of CPUE that might be observed for any given population size. The fact that the individuals of this species form large aggregations, and that fishers have the ability to locate and exploit these aggregations, explains much of this variability. The data that are available do not allow the calculation of greatly refined estimates. While pooling of data over vessels, time and space would be typical methods of producing CPUE data with greater precision, the limited duration of the current fishing season at Weipa, coupled with the paucity of daily CPUE observations, allow the application of these approaches in only a very limited way. Although CPUEs have been calculated for two core regions in which fishing has historically occurred, the daily data for each region is often limited to a few vessels within a limited number of fishing grids. Thus, despite the attempt made to accommodate changes in the spatial distribution of the fishing fleet at Weipa, the resulting CPUEs remain imprecise, possibly explaining why the results of the depletion analysis were not markedly affected by the choice of core region employed when calculating CPUEs for the region.

Neither the tuned VPA nor the depletion model provided sufficient evidence to demonstrate a clear relationship between recruitment and the associated spawning biomass. Although the tuned VPA indicated some support by the data for such a relationship, the weight of evidence in favour of a constant recruitment model was approximately three times greater than that favouring a stock-recruitment relationship. While the results obtained from the tuned VPA indicated that recruitment between 2000 and 2003 was low, and that there had been a slight recovery in 2004, similar conclusions could not be drawn from the depletion analysis. The models are, however, essentially identical, differing mainly in the objective functions used in the analysis and the prior probability distributions imposed when fitting the depletion model.

Results from the tuned VPA revealed essentially no support for the hypothesis that recruitment estimates had been affected by environmental variables. The depletion analysis suggested that, if any such impact was present, it would have resulted in higher recruitments in the early 1970s and in 1999. There was no indication that environmental factors might have adversely affected the recruitment during the early 2000s.

Although the results from the tuned VPA provide no evidence of a strong relationship between recruitment and spawning biomass, there remains some support for this hypothesis. Recruitment to the banana prawn stock at Weipa appears highly variable and, although the recruitment for 2000 to 2004 appears markedly lower than earlier recruitment levels, there appears to be no indication of a declining trend in spawning biomass. Could the apparent decline in recent recruitment be attributed to the impact of fishing on spawning stock? It is certainly possible that the reduction of spawning biomass through fishing impacted the stock to produce the decline in recruitment; however this could not be demonstrated with the data that are available for the banana prawn fishery at Weipa. It is also possible that environmental factors, acting either alone or in combination with the effect of fishing on spawning biomass, were implicated in the decline. Again, there is no evidence in the available data that this was the case. The highly variable and imprecise CPUEs provide insufficient information regarding the factors that affected recruitment to demonstrate that either spawning stock or environment affected recruitment. More importantly, however, there was insufficient power in the analysis to conclude, with confidence, that recruitment was not affected by a reduction in spawning biomass resulting from fishing and/or the effect of environmental factors. In the absence of such evidence, it remains appropriate to manage the fishery in accordance with the precautionary principle, *i.e.* under the assumption that recruitment is affected by a reduction in spawning biomass induced by fishing. Thus, appropriate strategies should be implemented such that, should the decline be due to the effects of fishing, recruitment of banana prawns to the Weipa region is allowed to recover to the levels experienced from the mid-1970s to the mid-1990s.

Acknowledgements

This study would not have been possible without the considerable support that was provided by many staff at CSIRO, Cleveland. Particular thanks are expressed to Janet Bishop, David Vance, Cathy Dichmont and Roy Deng.

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IV-4. Contraction of the banana prawn fishery of Albatross Bay in the Gulf of Carpentaria, Australia

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Introduction

Many marine organisms aggregate and school to reproduce, to reduce predation risk, or to take advantage of favourable feeding or environmental conditions. This behaviour and increasing fisher knowledge of aggregation dynamics must be taken into account when assessing the potential impacts of fishing. The catchability of a species (q - the proportion of a stock captured with each unit of effort) is very sensitive to the ability of fisheries to target aggregations as well as to factors that impact the ability of fishers to search for aggregations. Catch rate (CPUE) can be a misleading index of stock abundance in fisheries where aggregations are targeted (Paloheimo and Dickie 1964; Clark & Mangel 1978; Condrey 1984, Hilborn and Walters 1992). Catch rates can represent relative abundance adequately, when searching time is;

- adequately represented in the measure of fishing effort, and
- a stable proportion of the overall fishing effort across a wide range of stock abundances.

The predictability of aggregation behaviour, particularly in the location of the aggregation in time and space, reduces the need to search, which increases catchability and thus the vulnerability of a stock to fishing as the stock size declines (Paloheimo and Dickie 1964; Winters and Wheeler 1985; Crecco & Overholtz 1990; Hilborn and Walters 1992; Prince 1992). Under these conditions the escalation of catchability maintains high catch rates despite declining biomass corrupting catch per unit effort as an index of stock abundance. In these circumstances the raw trend in fishing effort may provide a better index of stock abundance, because it reflects the fishers' evaluation of the extent of stock available to fishing.

In their study of the herring purse-seine fishery in the Canadian northwest Atlantic maritime region, Winters and Wheeler (1985) provided a clear description of how herring stocks contract spatially as abundance declines, leading to an exponential increase in catchability by allowing the fishery to concentrate its searching and fishing on the aggregated stock in a much reduced area. Based on their study and a wide review of the literature, they argued 'that the inverse relationship between q – and stock abundance may be a general feature of marine fish populations and that this relationship is probably mediated through systematic changes in stock area.' They also noted that the spatial extent of the fishing grounds is rarely measured as a co-variate of catchability, and so it is rarely incorporated into the standardization of trends in CPUE.

Some species of prawns or shrimp are known to form aggregations. For example *Penaeus setiferus, P. indicus, P. merguiensis* and *P. chinensis*, are a group of species that prefer muddy sediments and "seldom burrow during the day", "appear to rely upon high turbidity to avoid being detected by predators" and "… occasionally show schooling behaviour" (Dall et al. 1990). In Kuwait, *P. semisulcatus* formed aggregations prior to heavy fishing (Van Zalinge 1984; Mathews & Abdul-Ghaffar 1986). In Exmouth Gulf, Western Australia, a small banana-prawn (*P. merguiensis*) fishery similar to that of the Northern Prawn Fishery (NPF) targeted aggregations with the aid of spotter planes until the end of the 1960s when it changed into a night time fishery for *P. esculentus* and *P. latisulcatus* (Penn 1984).

Catch declines in prawn fisheries apparently related to aggregation behaviour have been recorded for *P. orientalis* [= *P. chinensis*] in the Yellow Sea (Kristjonsson 1969) and for *P. indicus* in Madagascar (Marcelle 1978) and south-western India (Kristjonsson 1969). Although Penn (1984) suggested that aggregation behaviour makes penaeids prone to recruitment overfishing relatively little research has been conducted on this aspect of penaeid behaviour.

P. merguiensis is an aggregating Indo-Pacific species that comprises about 40% of the catch in Australia's Northern Prawn Fishery (NPF) catch some 4,000t per annum. Munro (1975) and Somers (1977) provide basic descriptions of the fishing of *P. merguiensis* aggregations in the eastern Gulf of Carpentaria. Munro (1975) suggests that the aggregations coincide with times of least water movement; particularly neap tides or, the slack water of high and low tides. He postulated that at such times the prawns can maintain near static position relative to a preferred area of bottom, and emerge from buried positions to perform some function such as; ecdysis, cleansing or mating. However, the evidence to show any of these activities drive aggregation is inconclusive. On the basis of samples of 50 to 60 prawns from each of 22 shots in 1964 to 65, which were taken to be indicative of aggregations on the basis of catch size (40 to 770 kg), Munro (1975) found no evidence that a greater rate of ecdysis or mating was occurring inside rather than outside aggregations. While Wassenberg and Hill (1993) examined the gut contents of 232 schooling and 235 non-schooling prawns from 6 differing sites and found only subtle differences in diet. The same range of dietary items occurred in both groups. However, bivalves were eaten by 80% of the schooling prawns, while crustaceans, gastropods, echinoderms and unidentified tissue comprised 60 to 80% of the diet of non-schooling prawns. About 7% of the non-schooling prawns had empty fore-guts, while just 2% of the schooling prawns. Schooling prawns had a higher number of species in their foregut than non-schooling prawns. Wassenberg and Hill (1993) felt "these quantitative differences between schooling and non-schooling prawns do not support the hypothesis that schooling behaviour may be a response to the presence or absence of a particular food type."

Lucas *et al.* (1979) and Somers (1994) summarized the origins of the NPF fishery. It started during 1960s out of Karumba in the south eastern Gulf of Carpentaria after it was discovered that discoloured water, or mud boils, visible from the air indicated the presence of *P.merguiensis* aggregations. The early fishery expanded to include Albatross Bay off Weipa in the north-eastern Gulf of Carpentaria where the mud-boils were rare and aerial spotting played little role. At that time these towns offered the main berthing and unloading facilities for the Gulf until 1970-1 and so the adjacent areas of the fishery were the main focus of early fishing.

By the early 1970s the fishery was searching almost the entire eastern shoreline of the Gulf, and a large proportion of the western Gulf, every season. During the 1970s, the seasonal fishing pattern was to fish down banana prawns in the eastern gulf before targeting the more remote western gulf banana prawn stocks. Based on their 1979 analysis of exploitation rates ($Z = 0.18$ week^{-1} in 1974) and yield per recruits, Lucas *et al.* (1979) concluded that the eastern areas had been exploited fully since 1974. These authors considered that searching time comprised 70 to 90% of the time spent at sea, and thus considered days at sea to be the most useful unit of effort for the *P. merguiensis* fishery. The time taken to catch 90% of the banana prawn catch in the Gulf of Carpentaria has declined from a few months in the 1970s to a few weeks in the 1990s (Somers 1994). In 1992, 90% of the banana prawn catch was taken in only 15 days.

Since the mid 1970s, other species of prawns have also been targeted and the tiger prawn group (*P.semisulcatus, P. esculentus*) comprise about 40% of the annual catch in the NPF. The tiger prawn fishery expanded rapidly, until catches began declining in the mid-1980s. A fishery that targets a different banana prawn species (*P. indicus*) started in the Joseph Bonaparte Gulf, about 1,900 km west of the main fishing ground in the Gulf of Carpentaria (Figure 43), during the early 1980s. As a result, from the 1980s the Northern Prawn Fishery covered the full range of commercial prawn species available in the northern region.

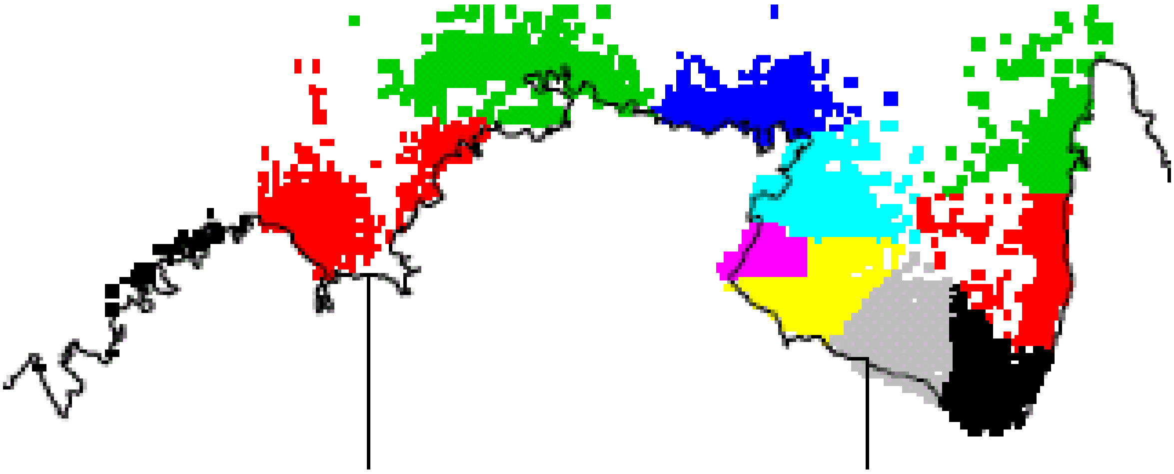

Figure 43: Map of the eleven statistical zones for banana prawns in the Northern Prawn Fishery. The Albatross Bay or Weipa zone is the green 11th zone at the far top right.

Catches of *P. merguiensis* peaked at more than 12,000 t in 1974 and have remained high, although they fluctuate from year to year. These large catches, together with open access to the fishery (which attracted large foreign vessels in the 1960s and 70s) and government boat-building subsidies resulted in the fishing fleet growing to about 280 vessels in the early 1980s. Robbins and Sachse (1994) described the evolution of the fleet and its progressive improvement of fishing efficiency. The early fleet was comprised of small wooden otter trawlers, with a modal length of ~16 m. It had rudimentary electronic equipment, towed four relatively small nets and stored its catch in brine tanks. Today's efficient fleet is comprised of steel trawlers with a modal length of about 22 m, that tow two large nets and are equipped with colour sounders, satellite-based tracking systems and large freezers.

In an attempt to counteract this trend and counteract the decline in tiger prawn catches that occurred during the 1980s a series of management measures have been implemented to limit the intensity of fishing; including reduced fishing seasons, closed areas, boat replacement policies and tradable gear units. By 2004 the number of vessels in the fishery had been reduced to 85 vessels, while the number of fishing days declined from 34,000 per annum in the mid-1980s to the current level of around 12,500 days per annum. Debate continues however as to the extent that actual fishing power of the fleet has been reduced.

Large year-to-year variation in the catch and catch rate of banana prawn stocks have been a characteristic of the fishery and are attributed to environmental variability, particularly rainfall and river flow (Vance et al. 1985; 1998; Loneragan and Bunn 1999). In this context it has generally been assumed that long term banana prawn abundance is primarily environmentally driven and, in contrast to the tiger prawns, that there is little need to control the level of fishing effort on banana prawns (Die & Ellis 1999).

Stock assessments on NPF stocks (tiger and banana prawns) have tended to assume that catchability has been relatively constant and independent of stock size. Die and Ellis (1999) analysed reported within season trends in banana prawn catch rates during the 1977, 1991, and 1992 seasons with the aim of studying the relationship between catchability and stock size. They concluded that fisheries ability to target aggregations of banana prawns was likely to decline with smaller stock sizes, resulting in a linear relationship between stock size and catchability, rather than an inverse relationship. They suggested that as "stock abundance decreases the probability of finding an aggregation decreases". This conclusion, however, was based largely on their assumption that "searching time is the main component of fishing effort," and that the "area to be searched remains constant."

Until the late 1990s, the Weipa and Karumba regions were the two most important areas for banana prawn fishing in the NPF, each with long-term average annual catches of about 800 tonnes, valued at over AUD $12 million. However, since 2000, the annual catch from the Weipa region has declined markedly and has not exceeded 70 tonnes. This has occurred despite continuing good catches from other NPF regions over the same time e.g. catches from Karumba were 2,230 in 2001 and 1,837 tonnes in 2002. A number of alternative hypotheses have been proposed by members of the fishing industry and researchers to explain this decline: the reduction in fleet size and days of fishing has reduced searching power and thus catchability; environmental or ecosystem changes; and recruitment overfishing.

In this paper, we describe the contraction of the fishery at Weipa focusing on the relationship between catchability, stock area and stock size. The purpose of this analysis is to describe and highlight fishery dynamics we believe to be suggestive of recruitment-overfishing. Suggesting that recruitment overfishing has occurred at Weipa does not preclude a range of factors also being involved and it is not the purpose of this paper to discount these other factors, however it is beyond the scope of this paper to exhaustively analyse all the potential mechanisms underlying the observed contraction.

Methods

Eleven banana prawn areas or ‘stocks’ have been defined in the Northern Prawn Fishery for stock assessment and statistical analyses (Figure 43)

Logbook data

We used processed daily logbook data for each vessel that fished in the NPF from 1970 to 2003, held by AFMA. These data included the gear type, location (by 6’ grids), total banana prawn catch (kg) and, for banana prawns, the identity of the banana prawn stock to which the catch had been attributed. The data were filtered to extract the logbook data for banana prawns and for the Albatross Bay (i.e. Weipa) stock. Three simple analyses of these data are presented here, each providing a different view of the same spatial phenomena. The data have been analysed in a Microsoft Access database, and an ArcView Geographic Information System.

Time series trends

The average reported daily vessel catch rate (kg/day) from Weipa 1970 to 2003 was plotted against cumulative catch (kgs) for each year following the Leslie-Delury approach making it possible to estimate some index of catchability (the slope of the curve) and initial biomass available to the fishery from the intercept of the extrapolated line with abscise. Strictly speaking, the rapid growth and mortality rates and the aggregation dynamics of banana prawns invalidate the assumptions of the Leslie-Delury analysis. This is accepted and we do not believe the estimates presented here can be used as accurate measures of biomass or catchability; however we contend the analysis still provides crude indices suggestive how both catchability and available biomass may have changed since 1970. To this end we have left our analyses relatively raw and simple intending for descriptive rather than quantitative purposes.

Normalized rank order curves

An alternative view of these spatial trends can be derived through the use of ‘normalized rank order curves’ (e.g. Walters & Cahoon 1985). These curves have been derived for each year by sorting the grid cells by the magnitude of their catch and then plotting the cumulative catch against their rank order. These plots will tend towards being a diagonal (45°) straight line when the catch is evenly distributed across all cells, and towards a 90° angle as catch becomes increasingly concentrated in a limited number of cells.

The normalized rank order curves were converted into a one dimensional ‘area index’ for each year, which is simply the total area under the ‘normalized rank order curve’ of each year. The area index was calculated for each year in each stock region. The area index has also been plotted against total catch in each year for Weipa.

Results

The relationship between average daily catch per vessel and cumulative catch for the season shows that the number of days (points on each graph) taken to make annual catch has declined over the time series (Figure 44). Catches remained variable until mid-1990s with catches of around 1,000t being recorded in 1991 and 1996. Since 2000 catches have been <100t per annum and there has been minimal recorded effort. The estimated slope from the Lesley-Deluury analysis (Figure 45) increased gradually from between 0.0007 and 0.0041 during the first half of the 1970s to between 0.0060 and 0.0240 during the last half of the 1990s, suggesting that catchability may have increased by five to ten times. The index of biomass from these analyses suggests that initial biomass available to the fishery in the early 1970s was 1,000 to 1,500t and that this declined to 500 to 1,000t through the 1980s and 1990s (Figure 46). In the late 1980s and mid-1990s the estimated initial biomass exceeded 1,000t in three years, but declined to <500t by the late 1990s. Plotting estimates of catchability against estimates of biomass suggests a negative relationship exists with catchability increasing as biomass declines (Figure 47). It should be noted that the values for recent years plotted at the extreme left hand side of this figure are highly imprecise being based on just a few days fishing in each year.

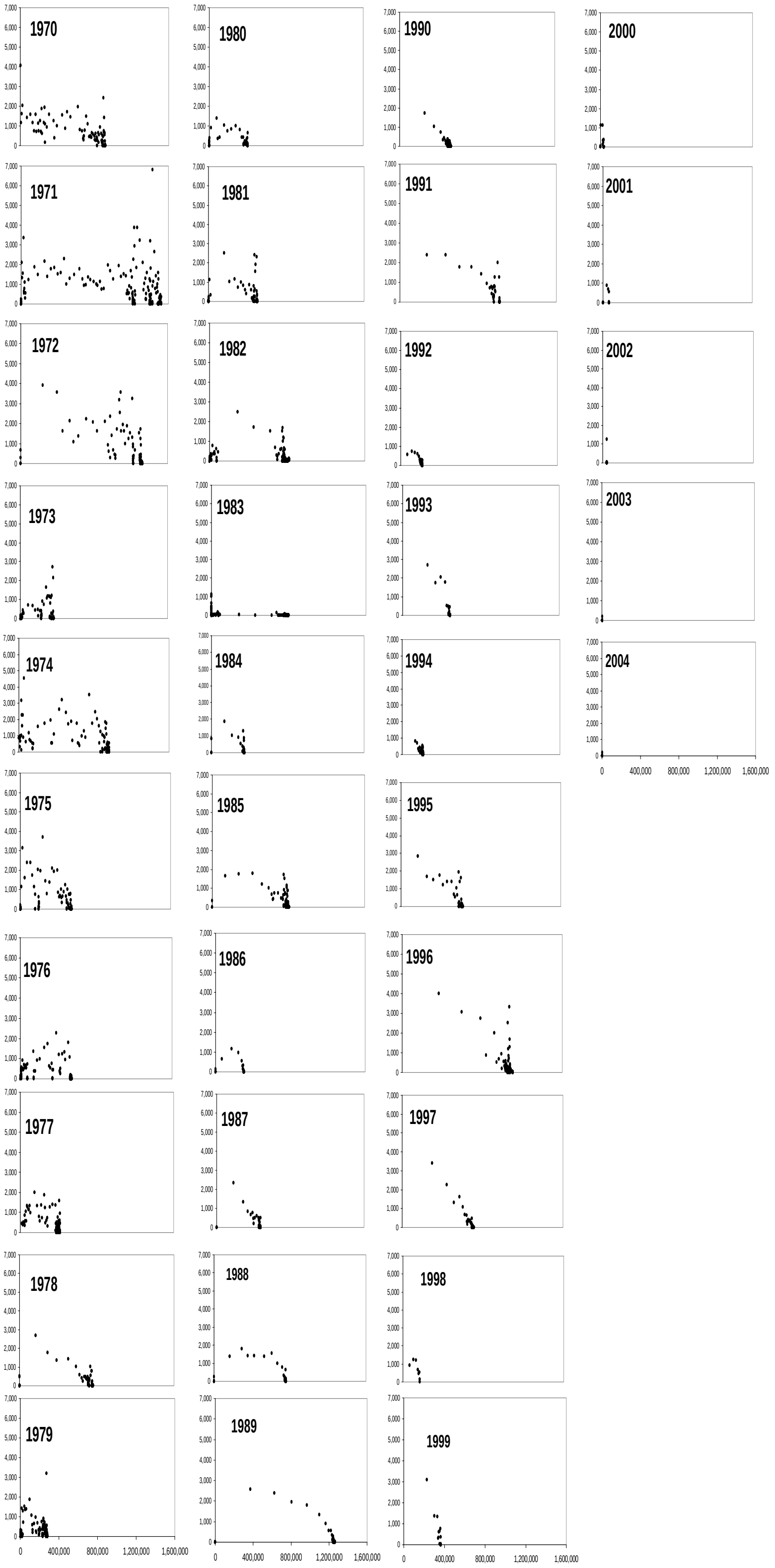

Figure 44: Within season trends in average reported daily catch rates (kg/day) for from Weipa 1970-2003 plotted against cumulative catch (kg).

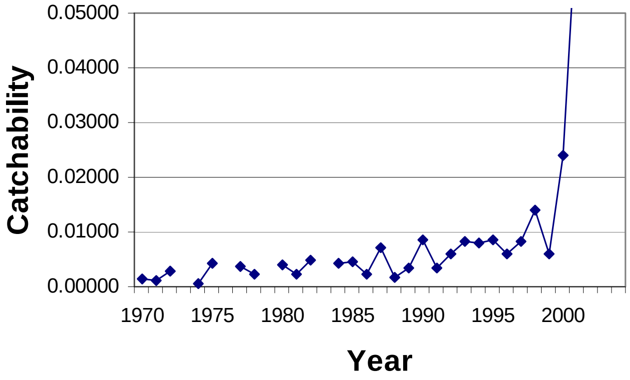

Figure 45: Estimated trend in catchability (q) in Albatross Bay 1970-2004; estimated from the slope of the seasonal trend in average daily catch rate versus cumulative catch through each season.

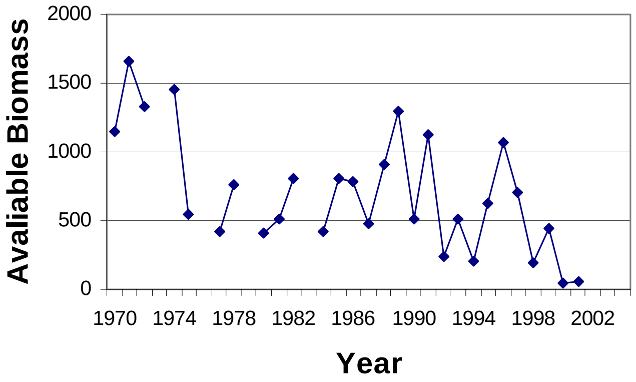

Figure 46: The estimated trend in available banana prawn biomass (t) in Albatross Bay 1970 to 2004; estimated from intercept of the extrapolated seasonal trend line for average daily catch with abscise (cumulative catch).

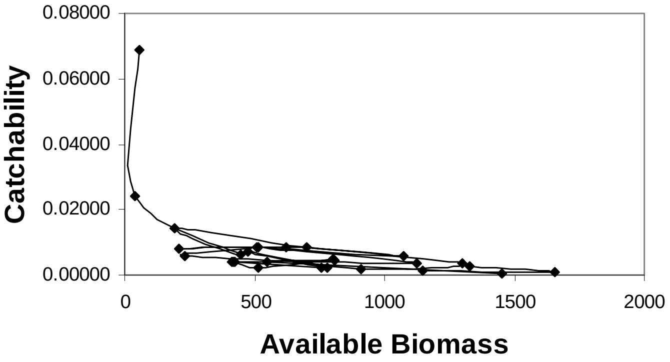

Figure 47: The plotted relationship between estimates of available banana prawn biomass (t) in Albatross Bay 1970 to 2004 plotted against estimates of catchability (q) in each year.

Figure 48 shows that catches have remained localized within the same area of Albatross Bay since 1970 and that catches have contracted towards the centre of that area. Since 1970 greater than 90% of the reported catch and effort has been attributed to some 56 6' statistical cells bounded by latitudes 12.25°S to 12.95°S and longitudes 141.25°E to 141.85°E. A smaller central subset of 25 statistical cells have comprised >75% of the historic catch. At the core of this area are two cells for which catch and effort data have been reported for all 34 years of the time series. Surrounding the core of the fishery are a further 10 cells for which data has been reported for ≥ 30 years and around that area are a further 16 cells for which data have been reported in ≥ 20 years.

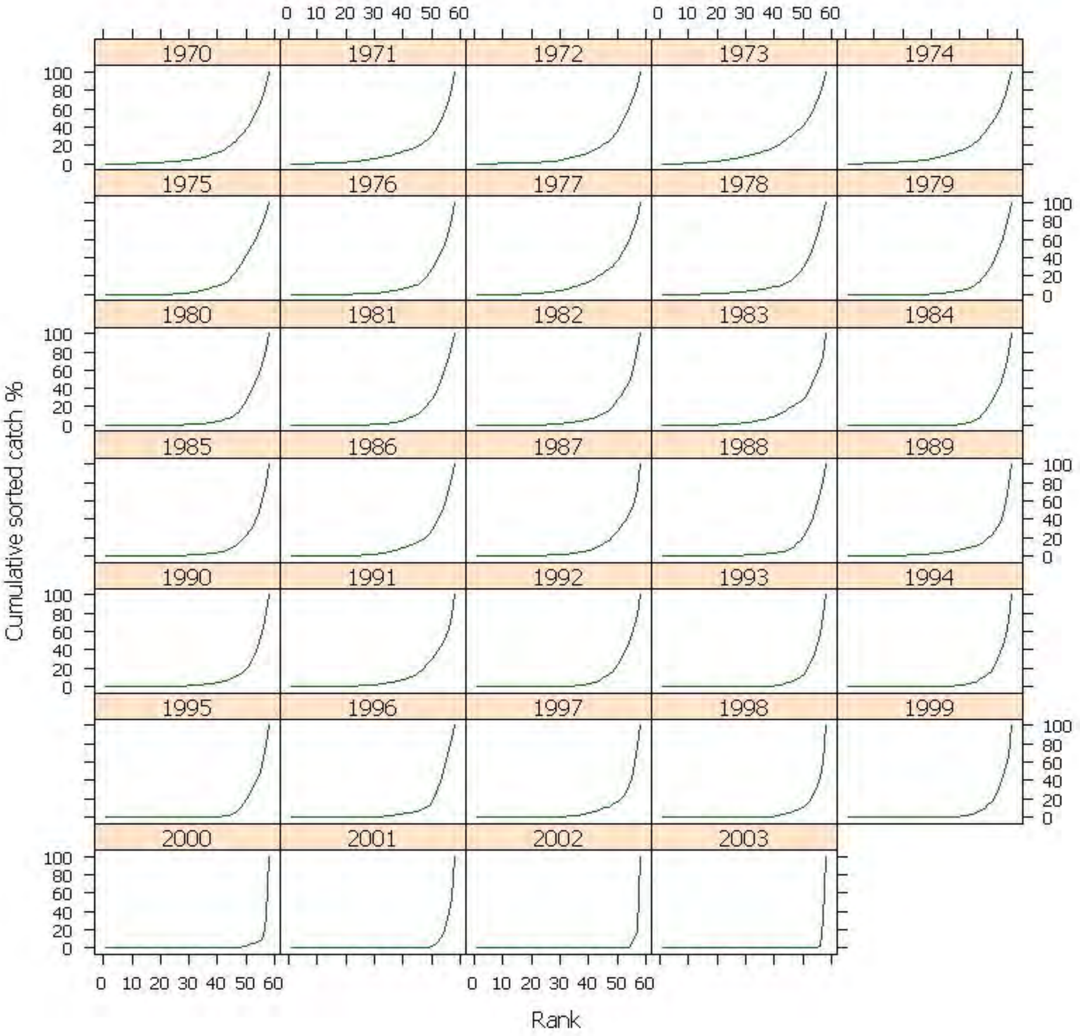

Figure 48: Normalized rank order curves for Weipa 1970 – 2003.

The normalized rank order curves presented in Figure 49 formalize the trend mapped in Figure 48. The rank order curves for earlier years being closest to a diagonal line (45°) indicating a dispersed catch while those in later years begin to resemble a 90° angle indicating the catch is increasingly concentrated in a small area of the fishery. By reducing the 34 normalized rank order curves to a single trend line through time the Area Index depicts the same trend more clearly (Figure 50). Noting that this is a trend in the distribution of catches across the fishery rather than the magnitude of catches this figure shows both the inter-annual variability and, despite the variability, a long term decline that commenced during the 1970s and accelerated through each successive decade. Plotting the Area Index against the annual catch (Figure 51) provides an alternate view of the same dispersion but this time with reference to the magnitude of the annual catches. Again the inter-annual variability is striking, with the variation in catch around similar levels of ‘Area Index’ being particularly marked. While larger catches in a year show a slight tendency to be associated with fishing over a broader area, it appears that over 5 to 6 year periods the variation in catch is more marked than variation in the area index. Through the variability the progression over time towards the origin is conspicuous. Years of widespread fishing became increasingly intermittent through the decades until recently when low catches are consistently taken from a very small area at the centre of the original fishing grounds.

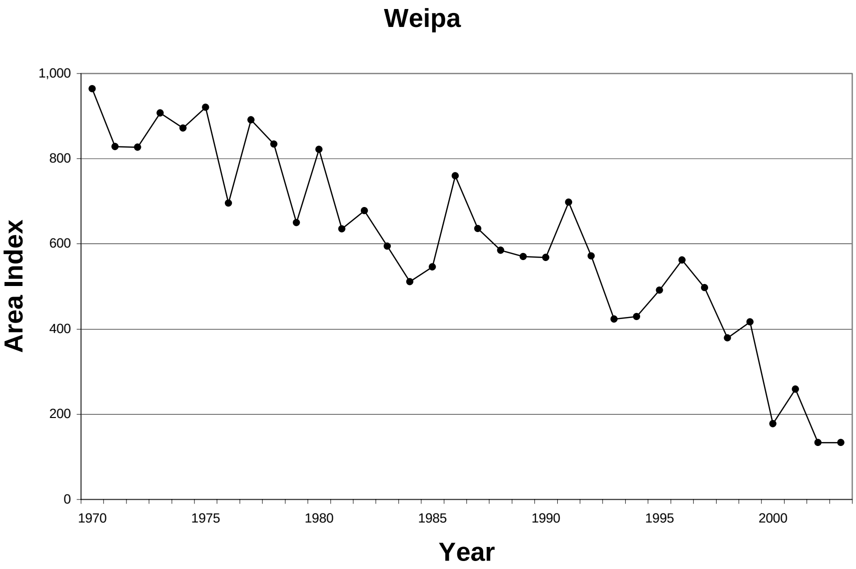

Figure 49: The trend in ‘area index’ for Weipa 1970 -2003. The ‘area index’ has been calculated from the total area under the ‘normalized rank order curve’ for each year.

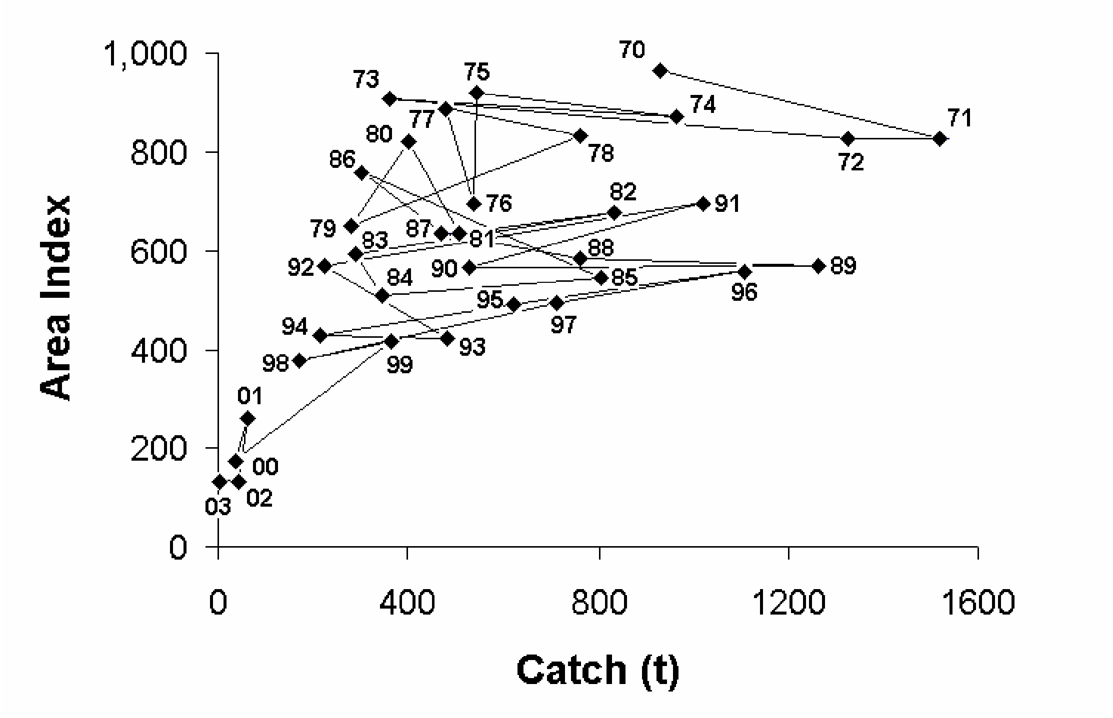

Figure 50: A plot of the ‘area index’ against total catch for Weipa 1970-2003.

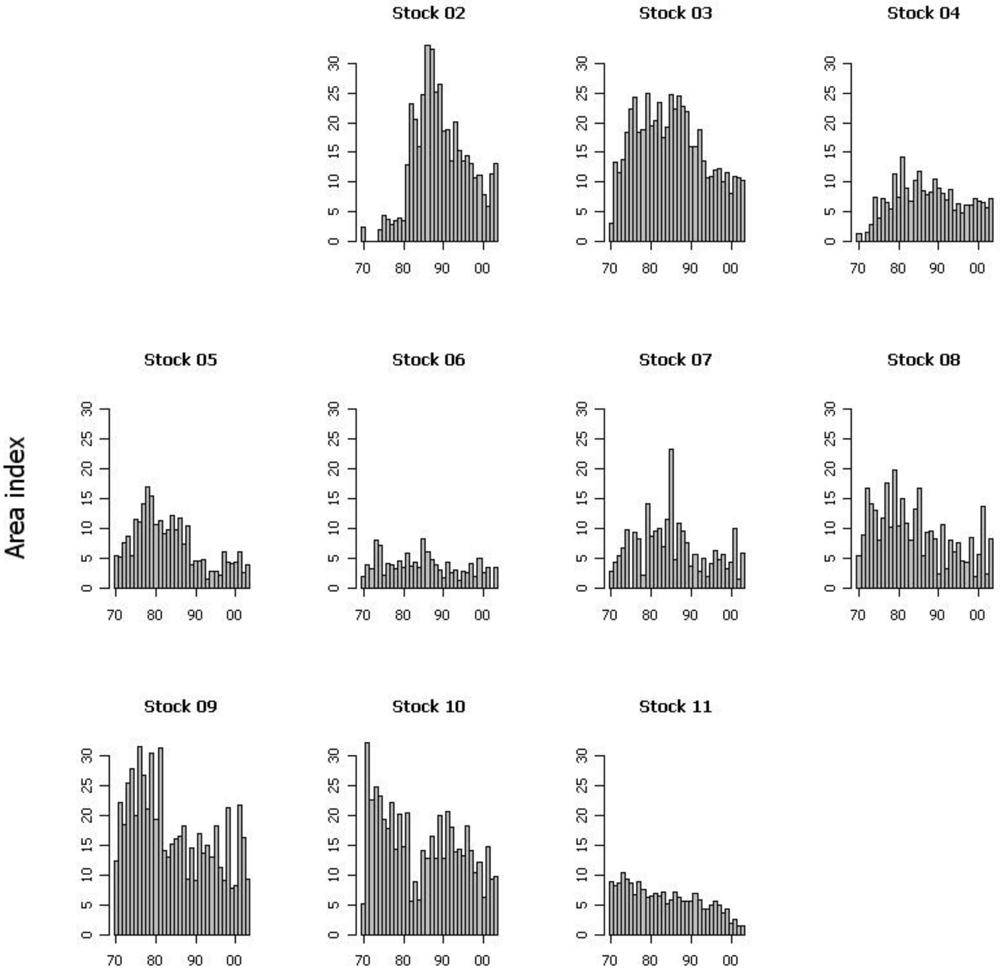

Figure 51: Trends in ‘area index’ for statistical zones 1-11 of the Northern Prawn Fishery 1970 -2004. The ‘area index’ has been calculated from the total area under the ‘normalized rank order curve’ for each year.

Our Rank Order Curve analysis of the other statistical zones of the banana prawn fishery suggest that similar, although less advanced, trends are also underway in other regions of the NPF (Figure 51).

Discussion

The results of our Lesley-Deluury analysis can be regarded as indicative only, because as noted in the methods section, the assumptions underlying the Leslie-Delury concerning closed populations unaffected by processes of mortality and growth are violated by the short life-cycle of prawns in comparison to the length of the fishing season. Furthermore aggregation dynamics can cause estimated daily catch rates to decline biasing estimates of depletion rates. Even within this context the estimates produced for the years after 1999 must be considered particularly imprecise because very few days of fishing occurred on which to base these analyses. However, we believe these rudely analysed trends are instructive and highly suggestive of the fishery dynamics being observed in the Albatross Bay region.

The quality of the spatial data used here has improved over time; basically being recorded as bearings on landmarks during the 1970s, radar determined positions on a grid during much of the 1980s and early 1990s, and GPS bearings since the mid-1990s. Compliance with position reporting requirements also appears to have improved as position fixing technology has improved, and as the industry has matured. Some of the broader spread of catches in the earlier years may be attributable to errors in position fixing and data recording. However the long term decline in area index displayed in Figure 50 continues through each of these epochs suggesting that a real spatial contraction has also occurred within Albatross Bay. Moreover, these analysed trends are also consistent with the anecdotal accounts received from experienced fishers and which originally gave us cause to look at these data in this way.

In our opinion, three broad features of the data are apparent, through these analyses;

1. The central area of catches, or hotspot, remains stationary and predictable through time.
2. There is considerable inter-annual variability with years of fishing over a broader area (i.e. 1971, 1974, 1978, 1982, 1985, 1988, 1989, 1991, 1996, 1997) being interspersed with years of fishing within a smaller area (i.e.1973, 1976, 1979, 1983, 1984, 1986, 1992, 1994, 1998).
3. The area of the Albatross Bay fishery has contracted towards the stable centre of the fishing area over the 1970-2004 time series.

In our view the contraction of fishing over time towards a stable and predictable hotspot indicates that the stock has steadily contracted making it likely that the catchability of banana prawns in Albatross Bay will have increased considerably over this time. While not proven by our data it is reasonable to assume that the industry will have tracked the spatial dynamics of the prawns and progressively refocused their searching power on the ‘hotspot’ as it contracted. At low stock sizes, each steaming hour searches an increased proportion of the area most likely to produce aggregations each year. Each shot of the net through an aggregation represents a larger proportion of the remaining biomass. The catchability of banana prawns will thus have increased as stock size has declined, probably exponentially.

This interpretation of the data is also consistent with the basic Leslie-Deluury analysis presented in Figure 44 and Figure 45, suggesting a steadily increasing rate of seasonal depletion through the time series, and escalating catchability at low stock sizes.

Die and Ellis’ (1999) concluded that catchability of banana prawns in the NPF was likely to decline with decreasing stock size, rather than increase as indicated here. Their conclusion was based on the assumption that the area of the fishery has remained relatively constant over time, but it is not clear whether they formally analysed this assumption. In parallel to their conclusions, others have proposed that a loss of searching power following industry rationalization over the last decade has driven the recent banana prawn catch declines in the Weipa area.

Our analysis supports the contrary hypothesis; that the fishery has increased searching power by reducing the area to be searched and concentrating on the known central hotspot. In particular the relatively steady contraction of the fishing grounds observed over several decades at Albatross Bay, and which is apparently also occurring more generally across the NPF is consistent with a long term progressive impact like fishing rather than more recent attempts to rationalize the fishery. In fisheries where catches collapse towards a stable and predictable geographic location within the fishing grounds, catchability is most likely to have increased with declining stock size, thus offsetting reductions in fishing effort measured in boat days and maintaining, or increasing, fishing pressure.

Gulland (1984) observed that stock-recruitment relationships had “received remarkably little attention” in penaeid prawn fisheries assessments. The possibility that penaeid prawns can be recruitment-overfished has been gaining credibility since that time (Bowen & Hancock 1985; Penn and Caputi 1986; Penn *et al.* 1989; Garcia 1996; Wang and Die 1996; Ye 2000). Penn *et al.* (1989) noted various aspects of penaeid stocks that they believed made particular stocks vulnerable to recruitment-overfishing:

- Confinement to geographically discrete areas;
- High catchability, particularly for species that aggregate;

- Overlapping ranges of stocks such that multi-species fisheries over-exploit vulnerable stocks by adjusting effort to less vulnerable stocks;
- Limited entry arrangements that contributed to maintaining excessive levels of effort when stock levels declined.

The banana prawns from the Weipa area meet all the criteria specified by Penn *et al.* (1989) for a penaeid stock to be vulnerable to recruitment-overfishing. The fishery dynamics described here are highly suggestive of recruitment overfishing having driven the long term decline in catch and the contraction in the area of the fishery.

Stock assessments which are not conditioned with the assumption that catchability increases as biomass declines, but assume a declining or trendless catchability, may well fail to detect recruitment overfishing. With the current low level of effort stock assessments containing these alternative assumptions will estimate that fishing pressure has been low in recent years and predict stock size to be rebuilding but has yet to be found by the fleet. A range of environmentally and management linked hypotheses have been proposed to explain the decline of the Weipa catch some of which suggest just this; that the stock has rebuilt but has not been found, while others propose environmental or ecosystem effects have indeed caused the stock’s decline. In particular it should be noted that a recent series of CSIRO surveys suggests the Weipa banana prawn biomass is actually around 1980s levels which if correct could strongly support several alternative explanations of the observed contraction of fishing at Weipa, and suggest that if recruitment-overfishing has occurred it has already been reversed.

Our interpretation of these data can in no way disprove these alternative interpretations. The purpose of this analysis has been to describe and highlight the spatial dynamics of the Weipa banana prawn fishery which are highly suggestive of the type of dynamics observed in other cases of recruitment-overfishing. Suggesting that recruitment overfishing may have occurred in Albatross Bay does not exclude a range of factors from also being involved. It is beyond the scope of this paper to exhaustively analyse all the potential mechanisms underlying the contraction of the Weipa banana prawn fishery.

Conclusions

The core characteristic of the trend described here is the contraction of the Weipa fishery towards its stable geographic centre or hotspot. Our analyses suggest that the most recent decline of banana prawn catches at Weipa is an extension of a trend that began in the early 1970s. This trend is consistent with a pattern being observed for banana prawns throughout the NPF’s banana prawn stocks, although the trend is generally less advanced in other regions of the fishery. It is also consistent with the fact that Weipa was one of the original home ports for the NPF fleet, and because of this Albatross Bay has one of the longest and, it might be assumed, intense fishing histories in the NPF.

The banana prawn stock of Albatross Bay meets all the criteria specified by Penn *et al.* (1989) for a penaeid stock to be vulnerable to recruitment-overfishing. While other factors will undoubtedly be shown to help explain the decline in the banana prawn catch at Weipa, the spatial trends in catch for this region are consistent with the notion that banana prawns have been recruitment-overfished in the Albatross Bay area. The evidence of similar spatial contractions in other NPF banana prawn stocks suggests that recruitment overfishing may also be occurring in other regions of the Northern Prawn Fishery.

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IV-5. Documentation of Ecopath/Ecosim Parameterisation

Parameter derivations for the preliminary Ecopath model of Albatross Bay, Gulf of Carpentaria, Australia, for the period 1986-1992

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Defining the Albatross Bay Ecosystem

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For the purposes of the present Ecopath model, the Albatross Bay marine ecosystem extends from Mean Higher High Water (including estuarine areas) to the 40 m isobath offshore of Albatross Bay proper. The northern and southern boundaries are 12º10’30” S and 13º S latitudes, respectively. This area covers 5,788 km2 of the eastern Gulf of Carpentaria and it encompasses the entire ‘Weipa area’ commercial fishing zone that that the Australian Fisheries Management Authority (AFMA) reports on.

Defining the ecosystem

The area represented by the Ecopath model of the Albatross Bay marine ecosystem (Figure 52). This area extends from Mean Higher High Water (including estuarine areas) to the 40 m isobath. It includes offshore slope areas adjacent to Albatross Bay proper as well as areas just to the north and south. The northern and southern boundaries of the modelled areas are the edges of the figure (latitudes 12º10’30” S and 13º S, respectively). Thus, the model characterizes all of the shaded areas in Figure 52.

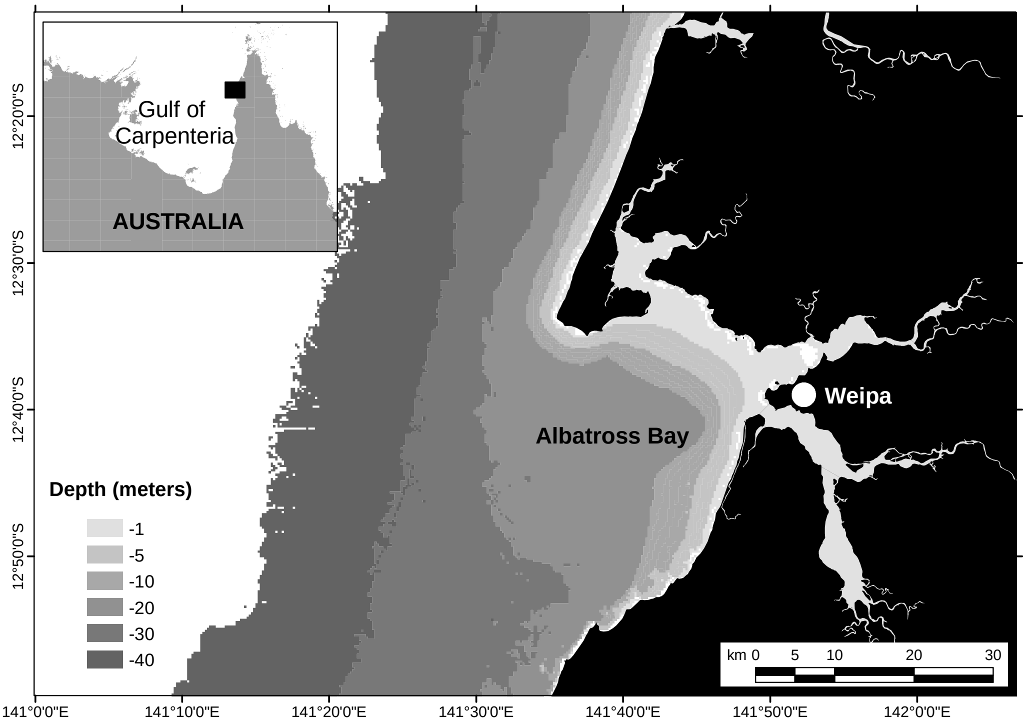

Figure 52: Bathymetric map of the Albatross Bay marine ecosystem including adjacent estuaries (produced by Ian McLeod, CSIRO Marine Research, Cleveland). This map provides the spatial delineation of the area that is represented by the Ecopath model of Albatross Bay.

This areal configuration was chosen based on two criteria: (1) the area corresponds to the spatial distribution of monthly faunal sampling stations that were used during intensive studies of the area from 1986-1992, and (2) it encompasses the distribution of banana prawns (Penaeus merguiensis) of this region and their associated fishery as well as much of the distribution of this region’s tiger prawns (P. esculentus and P. semisulcatus). The resulting model thus represents the state of the ‘Weipa prawn fishery ecosystem’ during the late 1980s and early 1990s (i.e., 1986-1992), about 10 years before the most recent declines in banana prawn catches starting in 2000. See Crocos and van der Velde (1995) for information on sampling stations and prawn distributions.

Table 4: Estimates of the areas of depth zones in the Albatross Bay ecosystem

Depth (m)	*Area (km^2)*	*Proportion*
0-1	350	0.061
1-5	249	0.043
5-10	1031	0.178
10-20	1049	0.181
20-30	1246	0.215
30-40	1863	0.322
Total	5788	1.000

Surface areas of the Albatross Bay depth zones

The total area of the Albatross Bay marine ecosystem and adjacent estuaries, as defined here, is 5,788 km2 (Table 4). Seven depth zones within that area have been delineated. These zones were delineated, and their areas calculated (Table 4) to aid contributors (who have expertise on the biological components of the system) in the estimation of the biomasses and flow characteristics of input parameters associated with their assigned functional groups. For example, the biomass of banana prawns must represent the area as a whole, and if density of banana prawns changes predictably with depth, biomass for a given time period might be estimated as a weighted average of estimated biomasses in each depth zone.

Functional groups

Ecopath models are focal points for ecosystem synthesis, as large amounts of disparate information is standardized, explored for continuity, and rendered mutually compatible. They must account for the biomasses and flows of all biotic components of the system (either explicitly or implicitly). A prerequisite to Ecopath model construction, therefore, is the definition of a finite number of functional groups. A list of Albatross Bay functional groups (Table 5) was compiled by a working group of experts on the Albatross Bay Ecosystem during a project workshop in November of 2004 (See Appendix A for a list of contributors to the Ecopath model), and this list was subsequently refined through consultation with additional experts. Contributing authors adapted diet composition information for their group(s) of interest (proportions of total annual mass consumed) to this list of functional (prey) groups. Prawns have been broken into different ontogenetic stages (See Section 6-8) for three reasons: (1) This enables much better elucidation of prawn dynamics and interactions with other system components, (2) Prawns are the focus of the fishery, and (3) different life-history stages are found in different habitats. The groups in Table 5 are intended as functional groups rather than taxonomic groups, but they are arranged taxonomically to some extent.

Table 5: Functional groups of the Ecopath model of Albatross Bay and adjacent slope and estuarine areas developed by the broad group of experts listed in Appendix A.

Mammals
- 1 Dolphins
- 2 Dugongs

Reptiles
- 3 Crocodiles
- 4 Turtles
- 5 Sea snakes

Seabirds
- 6 Lesser frigates
- 7 Brown boobies
- 8 Crested terns
- 9 Common terns

Mega-invertebrates
- 41 Octopus
- 42 Squid and cuttlefishes
- 43 Stomatopods
- 44 Banana prawn juvenile
- 45 Banana prawn subadult
- 46 Banana prawn adult
- 47 Tiger prawn juvenile
- 48 Tiger prawn subadult
- 49 Tiger prawn adult
- 50 All other commercial prawns
- 51 Thallasinid prawns (Callianassa)

Offshore fishes

10	Large pelagic piscivores
11	Medium pelagic piscivores
12	Small pelagic piscivores
13	Sawfishes
14	Large teleost benthic piscivores
15	Small benthic piscivores
16	Large elasmo benthopelagic piscivores
17	Large teleost benthopelagic piscivores
18	Small benthopelagic piscivores
19	Large benthopelagic invert feeders
20	Small benthopelagic invert feeders
21	Large elasmo benthic invert feeders
22	Large teleost benthic invert feeders
23	Small benthic invert feeders
24	Polychaete feeders
25	Large pelagic planktivores
26	Small pelagic planktivores
27	Benthic herbivore
28	Scavengers

Estuarine fishes

29	Estuary large elasmo benthopelagic pisc/prawn feeders
30	Estuary large teleost benthopelagic pisc/prawn feeders
31	Estuary large benthic pisc/prawn feeders
32	Estuary large benthopelagic invert feeders
33	Estuary large benthic invert feeders (Rays)
34	Estuary Polychaete feeders
35	Estuary small benthic invert feeders
36	Estuary planktivores
37	Estuary detritivores
38	Estuary benthic herbivores
39	Estuary insectivores
40	Estuary pelagic herbivores
82	Estuarine ichthyoplankton
83	Insects

Microbes

84	Marine microbial heterotrophs
85	Estuarine microbial heterotrophs

Primary production

86	Marine phytoplankton
87	Estuarine phytoplankton
88	Microphytobenthos
89	Seagrass
90	Estuarine macroalgae

52	All other non-commercial prawns
53	Crayfish
54	The mud crab
55	Red mud crab
56	Sand crab
57	Other large crabs
58	Large gastropods
59	Holothurians
60	Spatangoids
61	Echinoids
62	Ophiuroids
63	Asteroids
64	Sessile epibenthos

Macro-invertebrates

65	Marine bivalves
66	Estuarine bivalves
67	Marine small gastropods
68	Estuarine small crustaceans
69	Marine worms
70	Estuarine worms
71	Marine small gastropods
72	Estuarine small gastropods

Meiofauna

73	Marine meiofauna
74	Estuarine meiofauna
75	Marine forams
76	Estuarine forams

Plankton

77	Large jellies
78	Small jellies
79	Marine zooplankton
80	Estuarine zooplankton
81	Marine ichthyoplankton
91	Marine macroalgae
92	Mangroves

Detritus

93	Discards
94	Detached marine macrophytes
95	Detached estuarine macrophytes
96	Estuarine water-column detritus
97	Estuarine sediment detritus
98	Marine water-column detritus
99	Marine sediment detritus

References

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The derivations and sources of biological and fisheries parameters are documented in this section. The basic input parameters of the balanced model are listed in Table 6-1 (unbolded values), along with output estimations for each functional group (bolded values). The bolded biomass estimates, for example, were calculated by the Ecopath modelling routine by entering a reasonable ecotrophic efficiency value in cases where good biomass estimates were not available. Input parameters differ from parameters contributed by experts in cases where adjustments to input values were necessary to balance the model trophodynamically. The diet composition matrix is presented in Appendix B, and Fisheries parameter inputs are summarized in Section 7.

Table 6: Basic biological parameters used in the Albatross Bay model. Values in bold are calculated (outputs) by the Ecopath routine.

Group name	Trophic level	Biomass $(t\cdot km^{-2})$	P/B (/year)	Q/B (/year)	EE
Sea snakes	**4.97**	0.003	0.700	6.100	**0.811**
Lesser frigates	**4.82**	5.000E-05	0.080	36.700	**0.075**
Crested terns	**4.72**	3.400E-04	0.204	47.500	**0.000**
Sawfishes	**4.72**	0.040	0.123	2.575	**0.990**
Dolphins	**4.71**	0.003	0.100	41.070	**0.001**
Brown boobies	**4.71**	0.002	0.080	33.800	**0.000**
Large elasmo benthopelagic piscivores	**4.53**	0.060	0.500	7.856	**0.992**
Large benthopelagic invert feeders	**4.47**	0.002	0.547	7.792	**0.997**
Small benthic piscivores	**4.43**	**0.339**	1.042	5.168	0.950
Large teleost benthopelagic piscivores	**4.42**	0.523	0.451	3.421	**0.520**
Small pelagic piscivores	**4.30**	0.053	0.831	14.400	**0.837**
Large pelagic piscivores	**4.28**	5.650E-05	0.500	7.767	**0.014**
Common terns	**4.23**	3.600E-04	0.160	65.100	**0.000**
Large teleost benthic invert feeders	**4.21**	0.074	0.577	4.714	**0.977**
Medium pelagic piscivores	**4.19**	0.013	0.577	12.307	**0.930**
Small benthopelagic piscivores	**4.16**	**0.183**	0.868	8.172	0.950
Large elasmo benthic invert feeders	**4.13**	0.075	0.320	9.932	**0.530**
Large pelagic planktivores	**4.12**	**0.018**	2.188	16.150	0.960
Large teleost benthic piscivores	**4.11**	**0.089**	0.566	6.460	0.850
Crocodiles	**4.05**	**6.890E-05**	0.318	2.080	0.800
Small benthopelagic invert feeders	**3.91**	**1.687**	2.000	4.800	0.950
Estuary lg elasmo benthopelagic pisc/prawn feeders	**3.89**	0.317	0.354	4.456	**0.149**
Octopus	**3.82**	**0.084**	2.370	7.900	0.900
Estuary lg teleost benthopelagic pisc/prawn feeder	**3.80**	0.317	0.439	8.392	**0.998**
Scavengers	**3.73**	0.001	0.450	6.100	**0.994**
Estuary large benthic pisc/prawn feeders	**3.69**	0.496	0.370	4.067	**0.574**
Small benthic invert feeders	**3.67**	0.493	1.500	5.026	**0.982**
Estuary large benthopelagic invert feeders	**3.64**	0.074	0.506	5.375	**0.079**

Group name	Trophic level	Biomass (t·km^{-2})	P/B (/year)	Q/B (/year)	EE
Squid and cuttlefishes	**3.62**	**0.864**	2.370	7.900	0.950
Estuary small benthic invert feeders	**3.58**	**0.298**	1.280	11.100	0.980
Estuary large benthic invert feeders (Rays)	**3.50**	2.444	0.273	6.871	**0.000**
Polychaete feeders	**3.44**	**0.527**	1.450	7.554	0.950
Banana prawn subadults	**3.44**	0.020	3.120	27.181	**0.922**
Tiger prawn juvenile	**3.43**	0.012	3.400	45.234	**0.131**
Estuary planktivores	**3.42**	**0.315**	2.326	16.420	0.980
Estuary insectivores	**3.42**	**0.043**	0.690	9.500	0.980
Stomatopods	**3.41**	**0.345**	3.500	7.432	0.950
Banana prawn adult	**3.34**	0.079	3.200	19.200	**0.957**
Tiger prawn subadults	**3.32**	0.021	3.200	28.160	**0.937**
Tiger prawn adult	**3.32**	0.121	2.340	19.200	**0.663**
Estuary polychaete feeders	**3.30**	0.286	1.043	9.433	**0.325**
All other commercial prawns	**3.30**	**0.101**	3.000	25.000	0.900
Large gastropods	**3.28**	0.023	2.800	14.000	**0.389**
Turtles	**3.24**	0.035	0.192	3.500	**0.812**
Small pelagic planktivores	**3.20**	**2.770**	2.189	16.830	0.980
Thallasinid prawns (Callianassa)	**3.17**	**0.812**	3.000	25.000	0.950
All other non-commercial prawns	**3.17**	**8.830**	3.000	25.000	0.950
Sand crab	**3.12**	**0.063**	2.800	8.500	0.900
Marine forams	**3.09**	**3.717**	12.500	25.000	0.950
Estuarine forams	**3.09**	**0.029**	12.500	25.000	0.950
The mud crab	**3.07**	**0.060**	2.800	8.500	0.900
Red mud crab	**3.07**	**0.050**	2.800	8.500	0.900
Banana prawn juvenile	**3.03**	0.011	3.720	43.888	**0.123**
Other large crabs	**2.98**	**4.657**	2.800	8.500	0.900
Spatangoids	**2.93**	2.142	1.400	2.810	**0.142**
Crayfish	**2.87**	**0.011**	3.000	25.000	0.950
Asteroids	**2.77**	0.051	0.490	3.240	**0.132**
Large jellies	**2.73**	**0.015**	40.000	80.000	0.500
Marine ichthyoplankton	**2.62**	**0.002**	50.448	132.130	0.990
Marine small gastropods	**2.55**	**25.931**	2.500	14.000	0.980
Estuarine small gastropods	**2.55**	**0.209**	2.500	14.000	0.980
Small jellies	**2.44**	**0.027**	40.000	80.000	0.500
Estuarine ichthyoplankton	**2.41**	**5.700E-05**	50.448	132.130	0.990
Sessile epibenthos	**2.40**	4.985	0.800	9.000	**0.614**
estuarine small crustaceans	**2.40**	**0.250**	7.010	27.140	0.980
Marine meiofauna	**2.36**	**8.342**	12.500	25.000	0.950
Estuarine meiofauna	**2.36**	**0.506**	12.500	25.000	0.950
Marine small crustaceans	**2.35**	**8.656**	7.010	27.140	0.980
Marine worms	**2.31**	**10.407**	6.850	27.400	0.980
Estuarine worms	**2.31**	**0.793**	4.600	15.900	0.980
Holothurians	**2.16**	0.065	0.610	3.360	**0.959**
Ophiuroids	**2.13**	**10.211**	1.400	2.810	0.950
Marine zooplankton	**2.12**	11.744	52.000	173.333	**0.201**
Estuarine zooplankton	**2.12**	0.757	104.000	347.667	**0.135**
Marine bivalves	**2.11**	**41.222**	1.209	23.000	0.900
Estuarine bivalves	**2.11**	**11.902**	1.209	23.000	0.900
Estuary pelagic herbivores	**2.10**	**0.261**	1.083	36.833	0.900
Echinoids	**2.01**	0.085	1.650	2.810	**0.691**

Group name	**Trophic level**	**Biomass ($t \cdot km^{-2}$)**	**P/B (/year)**	**Q/B (/year)**	**EE**
Dugongs	**2.00**	0.050	0.080	36.500	**0.747**
Benthic herbivores	**2.00**	0.024	1.510	35.167	**0.983**
Estuary detritivores	**2.00**	**1.991**	1.175	19.300	0.800
Estuary benthic herbivores	**2.00**	**0.006**	1.880	45.750	0.980
Insects	**2.00**	**0.015**	12.600	51.930	0.980
Marine microbial heterotrophs	**2.00**	**5.416**	100.000	215.000	0.950
Estuarine microbial heterotrophs	**2.00**	**0.494**	100.000	215.000	0.950
Marine phytoplankton	**1.00**	3.905	933.083	-	**0.345**
Estuarine phytoplankton	**1.00**	0.389	933.083	-	**0.318**
Microphytobenthos	**1.00**	**0.667**	706.496	-	0.950
Seagrass	**1.00**	**1.938**	2.145	-	0.600
Estuarine macroalgae	**1.00**	**0.852**	12.000	-	0.500
Marine macroalgae	**1.00**	**19.593**	12.000	-	0.500
Mangroves	**1.00**	**0.178**	3.300	-	0.400
Discards	**1.00**	0.700	-	-	**0.328**
Detached Marine macrophytes	**1.00**	5.000	-	-	**0.546**
Detached Estuarine macrophytes (estuarine)	**1.00**	5.000	-	-	**0.056**
Estuarine Water-column detritus	**1.00**	0.322	-	-	**0.214**
Estuarine Sediment detritus	**1.00**	250.000	-	-	**0.177**
Marine Water-column detritus	**1.00**	33.351	-	-	**0.306**
Marine Sediment detritus	**1.00**	250.000	-	-	**0.229**

Notes: Values in bold have been calculated with the Ecopath software; Biomass is in wet weight; P/B and Q/B are the ratios of production and consumption to biomass, respectively; ecotrophic efficiency (EE) is the proportion of production consumed within the system.

Primary producers

Phytoplankton

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The net phytoplankton of the coastal region near Weipa is dominated by the nitrogen-fixing cyanobacterium *Trichodesmium*, a range of tropical diatom species, including a number of symbiotic species and dinoflagellates (Burford et al. 1995). There is also a substantial biomass of nanoflagellates and unicellular cyanobacteria but they are less well understood (Hallegraeff and Jeffrey 1984, Hallegraeff and Burford, 1996). The biomass of phytoplankton, as measured by chlorophyll-*a* concentration, is comparable with that found in other tropical coastal regions where eutrophication has not occurred (Burford et al. 1995,Table 7). Satellite ocean colour estimates of chlorophyll-*a* from a later period (1997-2003) yield significantly higher values (Figure 53, Table 7), although suspended sediment loads may have biased this signal. The seasonality of chlorophyll-*a* concentration, with higher concentrations during the wet summer months, is more marked closer to the coast than in the deeper waters offshore. However, monthly sampling over six years did not demonstrate a seasonal successional pattern of net phytoplankton, possibly because summer/winter differences in physico-chemical factors were not sufficiently large. Typically the proportion of diatoms was higher nearer the coast.

Table 7: Estimates of phytoplankton biomass in Weipa region.

Value	**Provided unit**	**Source**	**Habitat**	**Biomass in habitat (t ww·km^{-2})**	**Biomass as proportion of total area (t ww km^{-2})***
10	mg chl-*a* /m2	Burford et al. (1995) 1986-92	Albatross Bay	4.16	3.90
15	mg chl-*a* /m2	Burford, unpubl. Data 2005	Weipa estuary	6.43	0.39
22.5	mg chl-*a* /m2	SeaWiFS ocean colour 1998-02	Weipa region (0 – 20 m)		3.15
16.3	mg chl-*a* /m2	SeaWiFS ocean colour 1998-02	Weipa region (20 – 40 m)		4.85
18.3	mg chl-*a* /m2	SeaWiFS ocean colour 1998-02	Weipa region (0 – 40 m)		8.00

*Weighted by proportion of model area covered by the habitat

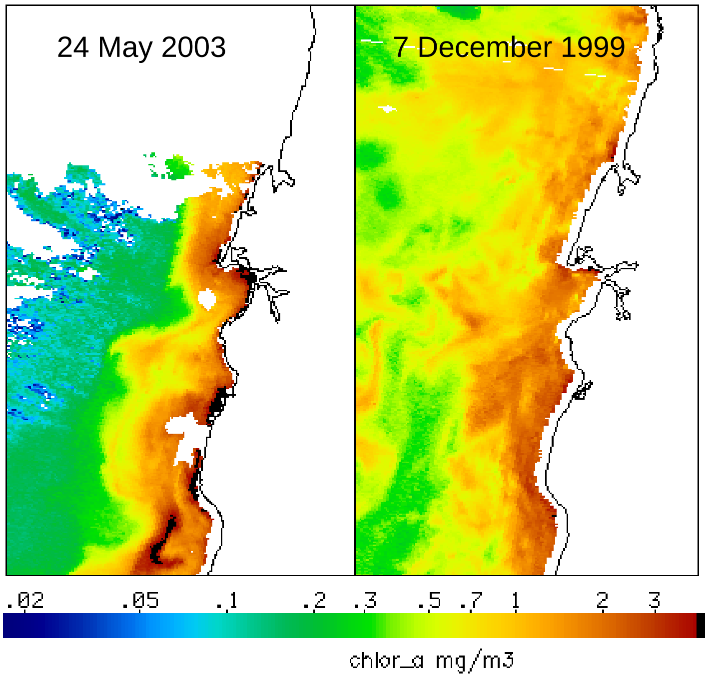

Figure 53. Estimates of chlorophyll-*a* concentration (mg m^{-3}) in the northeast of the Gulf of Carpentaria from SeaWiFS ocean colour data. White areas indicate unreliable data, mostly associated with cloud cover.

Primary productivity in Albatross Bay is comparable with those of other shallow tropical systems not impacted by eutrophication (Burford & Rothlisberg 1999,Table 8). Satellite estimates are significantly higher (Table 8), but are likely to be confounded in shallow coastal waters by high suspended sediment loads. Summer productivities were higher than those in winter. Primary productivity has not been measured in the estuary.

Table 8: Estimates of phytoplankton production in Weipa region

Value	Provided unit	Source	Region	Production in habitat (t ww·km^{-2})	Production as proportion of total area (t ww·km^{-2})*
310	g C·m^{-2}·year^{-1}	Burford & Rothlisberg (1999) 1986-92	Albatross Bay	3878	3643
1203	g C·m^{-2}·year^{-1}	SeaWiFS ocean colour 1998-02	Weipa region (0 – 20 m)		15032
625	g C·m^{-2}·year^{-1}	SeaWiFS ocean colour 1998-02	Weipa region (20 – 40 m)		7811
810	g C·m^{-2}·year^{-1}	SeaWiFS ocean colour 1998-02	Weipa region (0 – 40 m)		10121

*Weighted by proportion of model area covered by the habitat

Phytoplankton not only plays an important role in fuelling the food web in Albatross Bay but also provide a direct food source for prawns during the first week of larval life (Dall et al. 1990, Preston et al. 1992). In the next few weeks of larval life, phytoplankton provides an indirect food source, via zooplankton.

Table 9: Derivation of production/biomass values from assimilation value estimates.

Assimilation value (mg C·mg chl a^{-1}·hr^{-1})	Source	Region	P/B (·year^{-1})
5.5	Burford et al. (1995), Burford & Rothlisberg (1999)	Albatross Bay	933
	SeaWiFS ocean colour	Weipa region (0 – 20 m)	4772
	SeaWiFS ocean colour	Weipa region (20 – 40 m)	1610
	SeaWiFS ocean colour	Weipa region (0 – 40 m)	1265

The measured biomass and productivity data for Weipa is only available from 1986 to 1992. Conversely the SeaWiFS ocean colour data is only available from 1998 to 2002. The biomass and productivity values derived from the SeaWiFS data are higher than those for the measured biomass and productivity data. However it is not possible to conclude that this is due to an increase in biomass and productivity between 1992 and 1998. One of the confounding problems with SeaWiFS data applied to coastal regions is the effect of turbidity, which is likely to inflate biomass and productivity estimates. This is also true in the Weipa region where during the wet season, land runoff results in high turbidity in estuarine and coastal regions.

Conversions used to derive the estimates in Table 8 and Table 9 are shown below (Table 10).

Table 10: Conversions used for conversions to wet weights.

Conversion	Ratio	Source
Chlorophyll a to Carbon	1 to 25	Parsons et al. 1977 in Browder 1993
Chlorophyll a to Carbon (Phytoplankton)	1 to 44.9	Durbin & Durbin 1998
Carbon to dry organic matter	1 to 2.5	Parsons et al. 1977 in Browder 1993
Carbon to dry organic matter (Phytoplankton)	1 to 5.4	Durbin & Durbin 1998
Carbon to dry organic matter (Meiobenthos)	1 to 2.5	Warwick (Plymouth marine laboratory; pers. comm. 12 June 2000)
Carbon to dry organic matter (Benthic macrofauna)	1 to 10	Rowe and Menzel (1971) ("5 to 15 times")
Dry to wet organic matter	1 to 5	Parsons et al. 1977 in Browder 1993

Conversion	Ratio	Source
Dry to wet weight (Benthic primary producers)	1 to 7.7	Arreguín-Sánchez et al. 1993
Dry to wet weight (Benthic macrofauna)	1 to 7.5	Rowe and Menzel (1971) ("5 to 10 times")
Dry to wet weight (Shrimp)	1 to 7.7	Bougis 1979 in Cushing 1984
Carbon to dry organic matter (Crustaceans)	1 to 2.5	Bougis 1979 in Cushing 1984
Carbon to wet weight (Shrimp)	1 to 19.2	Cushing 1984

Conversion References (Table 10)

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Microphytobenthos

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Microphytobenthos are microscopic primary producers that are likely to be important contributors to food web in tropical coastal areas with extensive mudflats, such as the Weipa estuary. However there has been little work done quantifying the biomass, productivity and species composition of microphytobenthos in northern Australia. I measured microphytobenthos biomass to average 150 mg chl *a* m^{-2} in the top 5 cm of sediment in the Weipa estuary. This converts to 64.81 $t{\cdot}km^{-2}$ in the estuary and then 3.93 $t{\cdot}km^{-2}$ when expressed in the whole 5,788 km^2 Albatross Bay area, based on conversions shown in Table 11. A P/B value of 706.496 year-1 was derived from Okey (2002).

Table 11: Conversions used for microphytobenthos biomass estimation

Conversion	***Ratio***	***Source***
Chlorophyll *a* to Carbon (Phytoplankton)	1 to 44.9	Durbin & Durbin 1998
Chlorophyll *a* to Carbon	1 to 25	Parsons et al. 1977 in Browder 1993
Carbon to dry organic matter (Phytoplankton)	1 to 5.4	Durbin & Durbin 1998
Carbon to dry organic matter	1 to 2.5	Parsons et al. 1977 in Browder 1993
Dry to wet organic matter (benthic producers)	1 to 7.7	Arrenguin-Sanchez et al. 1993 in Alahandro's paper
Dry to wet organic matter	1 to 5	Parsons et al. 1977 in Browder 1993
Cubic meters to liters	1 to 1000	

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Mangroves

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There are 197 km2 of mangroves in the Albatross Bay region. The most common mangrove species in this region are *Rhizophora stylosa*, *Avicennia marina* and *Ceriops* sp. These are found in distinct zones parallel to the river, with Rhizophora at the seaward edge and Avicennia to landward (Long et al. 1992, Conacher et al. 1996). The width of the forest ranges from about 50 m to over 1000 m (Manson et al. 2001).

Data on the mangroves of Albatross Bay were obtained from the QDPI&F Assessment and Monitoring Unit. The data were derived by classification of Landsat Thematic Mapper (TM) images taken between 1986 and 1997, using aerial photographs for ancillary information, at a scale of 1:100,000 with associated ground-truthing (Bruinsma 2001). During ground-truthing, data were recorded on mangrove community floristics and structure, including species composition of mangroves, dominant genus, estimated density, composition and hardness of substrate and presence/absence of seedlings. Positional information was collected by Global Positioning System (GPS), which was, on average, accurate to within 15-20 m. An accuracy assessment indicated an overall accuracy of the wetland classification of 90% (Bruinsma 2001).

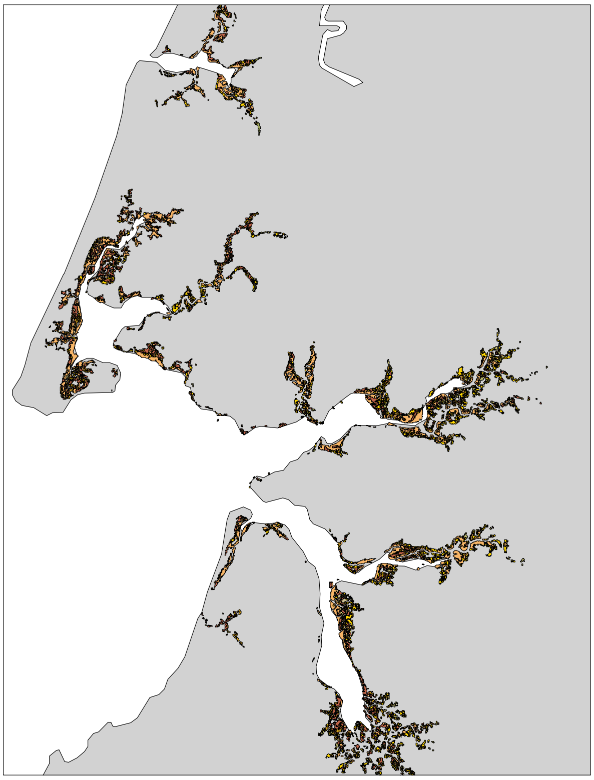

Figure 54: The area of mangroves in km^2 was calculated in ArcView for each community type. Areas defined as mixed species were divided equally between the contributing species.

Estimates of tree height and density, total litter fall and litter standing stock for each species were taken from Conacher et al. 1996. Litter fall was collected in 1 m^2 traps and included leaves, stipules, twigs, wood, flowers, fruit and seedlings. Leaves were the main component of the litter fall. Litter standing stock was measured from accumulated litter collected on the ground in 1 m^2 quadrats (Table 12). This was higher in the Avicennia and Ceriops forests as they are flushed less often by the tide than Rhizophora.

Table 12: Biomass estimates of mangrove litter

Class	**Area (km2)**	**Ave height (m)**	**Tree density (trees/km^2)**	**Total litter fall (t/km^2/yr)**	**Litter standing stock (g/m^3)**
Avicennia	60.781	6	50000	628	579
Ceriops	54.899	11	370000	539	400
Rhizophora	82.136	17	85000	1105	73
Total	197.816				

Ong et al. (1995) identified the partitioning of biomass and net primary productivity (annual biomass increment and turnover) of an average 20-year old *Rhizophora apiculata* tree in Malaysia (Table 13).

Table 13: Estimates of mangrove biomass and productivity.

Plant tissue	*Biomass* t C ha^{-1}	*Biomass %*	*Productivity* t C ha^{-1} yr^{-1}
Leaves	3.0	2.6	0.08
Branches + fruit	9.2	8.0	0.44
Trunk	84.5	74.0	5.56
Stilt roots	11.5	10.0	0.64
Roots	5.8	5.1	0.42

Sherman et al. (2003) estimated % of dry weight allocated to biomass components of three species of mangrove in the Dominican Republic (Table 14).

Table 14: Percentages of dry weight allocated to plant tissues for three mangrove species (from Sherman et al. 2003).

Plant tissue	**Rhizophora mangle**	**Laguncularia racemosa**	**Avicennia germinans**
Trunk	63	81	83
Branches	10	12	11
Twigs	6	5	3
Leaf	3	2	3
Prop roots	17		

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Seagrasses and macroalgae

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Seagrass

I estimated the biomass of seagrass from the enclosure study of Loneragan et al. (2001). I took a mean for the November and April biomass for both seagrass types (*Enhalus* and *Halodule*) (state the mean value), which is equivalent to 41.6775 t·km^{-2} in the study sites. These seagrass species are distributed in the 0-1 and 1-5 m depth range in the Albatross Bay area, which cover 350 and 249 km^2, respectively, or 6.0523 and 4.2937% of the 5,788 km^2 modeled area. However, seagrasses do not cover the whole of the substrate within these zones. Queensland Department of Primary Industries has undertaken a study of the seagrasses of Weipa Port for the Ports Corporation Queensland. They estimate that the area of seagrass in Weipa Port has varied between 3795 ± 403 to 4969 ± 436 ha from September 2000 and September 2002 (Roelofs *et al*., 2003). Furthermore, they estimate that the area of seagrass in their ‘Intensive Monitoring Area’ (the Embley, Hey and Mission Rivers) varied between 1367 ± 134 to 2127 ± 155 ha from April 2000 and September 2002.

I will use an estimate of **40** km^2 (4000 ha) for the area of seagrass in the modeled area. This area is **0.691085**% of the modeled area. Therefore, the biomass of seagrasses in the modeled area can be estimated as **0.2880269** $t \cdot km^{-2}$.

Loneragan et al., 1996 estimated the growth of *Enhalus acoroides* to be vary between 100 and 2000 $mm \cdot m^{-2} \cdot d^{-1}$, depending on site and season. I will use a conservative estimate of 500 $mm \cdot m^{-2} \cdot d^{-1}$, as growth at most sites was equal to this rate. Using this figure, I estimated the annual production of *Enhalus* to be (159.077 $t.km^{-2}y^{-1}$) from an area with a standing biomass of 74.15 $t \cdot km^{-2}$, thus yielding an estimated P/B of **2.145** $year^{-1}$. I used a calculation from Kenyon et al. (1997) to estimate the dry weight of an *Enhalus* leaf at 0.87 $g \cdot m^{-1}$. The estimate agreed with a rough calculation 0.97 $g \cdot m^{-1}$ from the Weipa seagrass data. This estimate is about a quarter with the P/B ratio of 9.014 that used by Okey (2002) in an ECOPATH model of the Florida Shelf.

Algae

I estimated the biomass of estuarine algae from Haywood et al., 1995 (2.2 $g \cdot m^{-2}$ to 10.5 $g \cdot m^{-2}$).

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Detritus

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Fishery discards

Fishery discards are living groups captured by the fishery and discarded. This biomass flows to the 'discards' detritus functional group, which is consumed by detritivores in the system. The flow of fishery discards into the system is estimated to be 2.098 $t \cdot km^{-2} \cdot year^{-1}$ based on the discard information entered into the Ecopath model (see Section 7 of this report). If we assume a discard residence time of one month, this leads to a standing biomass estimate of 0.175 $t \cdot km^{-2} \cdot year^{-1}$.

Detached macrophyte groups

Manson (Section 6.1.3) estimated standing biomass of detached mangrove detritus to be 10.91 in the estuarine area, after Conacher et al. (1996). Values derived from this estuarine estimate (expressed properly for the whole modelled area) would underestimate detached macrophytes in the modelled area, as mangroves are but one component of detached macrophytes on this nearshore sea floor. Place-holder values were used for detached marine macrophytes in the present model. Research is needed on drifting microphyte sources and sinks and rates of production, flow, utilisation, and decomposition.

Water-column detritus groups

Biomass estimates of 0.322 t/kg^2 and 33.351 t/kg^2 for estuarine and marine water-column detritus groups, respectively, were derived by M. Burford, (Griffith University; unpublished data).

Sediment detritus groups

A placeholder biomass value of 250 $t \cdot km^{-2}$ was based roughly on a value of 390 derived by Okey (2002) for the West Florida Shelf Ecopath model.

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Microbial heterotrophs

A P/B ratio value of 100.0 year^{-1} was derived from the West Florida Shelf model (Okey & Mahmoudi, 2002; Okey et al. 2004). A Q/B ratio value of 215 year^{-1} was derived from the West Florida Shelf model (Okey & Mahmoudi, 2002; Okey et al. 2004). Diet composition for this group was adapted from published values in Okey (2004).

Table 15: Basic parameters of the Ecopath model of Albatross Bay for microbes. Values in bold have been calculated with the Ecopath software; other values are empirically based inputs.

Group name	Trophic level	Biomass (t·km^{-2})	P/B (year^{-1})	Q/B (year^{-1})	EE
Marine microbial heterotrophs	**2.00**	**10.336**	100	215	0.950
Estuarine microbial heterotrophs	**2.00**	**0.434**	100	215	0.950

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Zooplankton

Zooplankton of the Albatross Bay Ecopath model consists of zooplankton (both holo- and merozooplankton), ichthyoplankton, and jellies (gelatinous zooplankton). The first two of these are delineated by marine and estuarine habitats, whereas jellies are delineated by size. Six functional groups thus comprise zooplankton for the Albatross Bay model. The basic parameters for these groups and the sources of information for deriving these parameters are summarized in Table 16 and Table 17, respectively.

Table 16: Basic zooplankton parameters of the Ecopath model of Albatross Bay. Groups are ordered by decreasing trophic level. Bolded values were calculated according to Ecopath's mass continuity master equation; other values are empirically based inputs.

Group name	Trophic level	OI	Biomass (t·km^{-2})	P/B (year^{-1})	Q/B (year^{-1})	EE
Large jellies	**2.73**	**0.377**	**0.015**	40	80	0.500
Marine ichthyoplankton	**2.62**	**0.304**	**0.002**	50	132	0.990
Small jellies	**2.44**	**0.300**	**0.027**	40	80	0.500
Estuarine ichthyoplankton	**2.41**	**0.243**	**0.000**	50	132	0.990
Marine H&M zooplankton	**2.12**	**0.110**	11.743	52	173	**0.201**
Estuarine H&M zooplankton	**2.12**	**0.110**	0.757	104	347	**0.135**

Table 17: Sources of basic parameter estimates for zooplankton. These derivations are described further in the following sections.

Group name	**Biomass (t·km^{-2})**	**P/B (year^{-1})**	**Q/B (year^{-1})**	**Diet composition**
H&M zooplankton	Rothlisberg, Section 6.4.1	Rothlisberg, Section 6.4.1	Rothlisberg, Section 6.4.1	Rothlisberg, Section 6.4.1
Jellies		Graham 2002, Okey et al. 1999	Graham 2002, Okey et al. 1999	Graham 2002, Okey et al. 1999
Ichthyoplankton		Okey 2002; Okey et al. 2004	Okey 2002; Okey et al. 2004	Okey 2002

Marine and estuarine holo- and merozooplankton

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Table 18 presents the basic zooplankton parameters derived for the Albatross Bay Ecopath model. Biomass was estimated from zooplankton biomass was estimated from 142 and 250 µm mesh plankton samples from selected inshore stations (1055 samples from 66 cruises between March 1986 and March 1992, see Table 1 in Jackson *et al.* 2001). To determine the biomass of samples they were quantitatively split with a Folsom plankton splitter (McEwan *et al.* 1954) and one half was subjected to a dry weight analysis. To determine the dry weight the samples were oven dried to 70ºC in a forced-draft oven for 1 to 2 d, then weighed on a top loading balance to the nearest 0.01 g. Biomass values were standardized (g/m^3) by calculating the volume of water filtered from calibrated flowmeter readings (see Rothlisberg & Jackson 1982 for details). The samples from the two mesh sizes were compared and standardized to the 142 µm for comparisons with previous studies (Rothlisberg & Jackson 1982). Copepod generation times (P/B estimates in the Ecopath model) were derived from laboratory and field incubations of a number of coastal tropical and subtropical calanoid copepods (McKinnon 1996, McKinnon *e al.* 2003).

These biomass estimates were then expressed for the whole 5,822 km^2 area by multiplying each estimate by the proportion of each habitat (Marine: 0.939477; Estuarine: 0.060523). Production rates (P/B) were estimated by assuming a generation time of 3 weeks for marine zooplankton and 2 weeks for estuarine zooplankton. Consumption rates (Q/B) were then estimated by multiplying each P/B estimate by 3.33. The diet composition assigned to both marine and estuarine zooplankton groups for the Albatross Bay model is 20% carnivores, 60% herbivores, and 20% detritivores in each of the respective habitats.

Table 18: Parameters for marine and estuarine holo- and merozooplankton groups.

Habitat	***Biomass in each habitat (t·km^{-2})***	***Biomass in whole area (t·km^{-2})***	***P/B (year^{-1})***	***Q/B (year^{-1})***
Offshore	12.50	11.743	52	173
Estuarine	12.50	0.757	104	347

<u>*References*</u>

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Large and small jellies

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A P/B ratio of 40.00 year^{-1} and a Q/B ratio of 80.00 year-1 for large jellies was derived from Graham (2002) and values were published in Okey et al. (2004). The diet composition consisting of zooplankton, phytoplankton, and microbial heterotrophs, and detritus was estimated using information in Graham (2002), Okey et al. (1999), and the present author's best judgement.

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Ichthyoplankton groups

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A P/B ratio value of 50.448 year^{-1} was derived from the West Florida Shelf model (Okey & Mahmoudi, 2002; Okey et al. 2004). A Q/B ratio value of 132.130 year^{-1} was derived from the West Florida Shelf model (Okey & Mahmoudi, 2002; Okey et al. 2004). Diet composition for this group was assumed to consist of zooplankton, phytoplankton, microbial heterotrophs, detritus, and microphytobenthos. Diet composition values are published in Okey (2004).

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Insects

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A P/B ratio of 12.60 year^{-1} was derived from Johnson et al. (2000). A Q/B ratio of 51.930 year^{-1} was derived from Vega-Cendejas (2003). The diet composition for insects used in this model was derived from Johnson et al. (2000)

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Meiofauna

Table 19: Basic parameters of the Ecopath model of Albatross Bay for meiofauna. Values in bold have been calculated with the Ecopath software; other values are empirically based inputs

Group name	***Trophic level***	***OI***	***Biomass ($t·km^{-2}$)***	***P/B ($year^{-1}$)***	***Q/B ($year^{-1}$)***	***EE***
Marine forams	**3.09**	**0.003**	**9.166**	12.500	25.000	0.950
Estuarine forams	**3.09**	**0.003**	**0.014**	12.500	25.000	0.950
Marine meiofauna	**2.36**	**0.236**	**18.853**	12.500	25.000	0.950
Estuarine meiofauna	**2.36**	**0.236**	**0.472**	12.500	25.000	0.950

Meiofauna

A P/B ratio value of 12.50 year^{-1} was derived from the West Florida Shelf model (Okey & Mahmoudi, 2002; Okey et al. 2004). A Q/B ratio value of 25.00 year^{-1} was derived from the West Florida Shelf model (Okey & Mahmoudi, 2002; Okey et al. 2004). Diet composition for this group was adapted from published values in Okey (2004).

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Foraminifera

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Benthic foraminifera are a significant component of the meiofauna. Measurements in an intertidal estuary indicate that they make up 37% of meiobenthic abundance and 47% of the biomass (Moodley et al., 2000). Foraminifera make a substantial contribution to the carbon cycle, with species such as Ammonia taking up freshly deposited algal carbon. The importance of benthic foraminifera to the sustainability of prawn fisheries is shown by their high abundance in the gut contents of demersal prawns on the continental slope of north-western Australia (Rainer, 1992).

Most foraminifera studies focus on species composition, and the application of these in answering palaeoenvironmental questions such as changes in sea level, salinity, temperature and productivity. There has been little research to date on the ecological role of benthic foraminifera. Most studies are also located in deep-sea environments, with relatively few studies on estuarine foraminifera, particularly within tropical areas. Most studies of estuarine foraminifera have been restricted to the temperate zone in the Northern Hemisphere. The few tropical Australian studies, excluding purely taxonomic studies, include a study of species distributions in the South Alligator River (Northern Territory) (Wang and Chappell, 2001); foraminifera distributions in mangroves in Cleveland Bay (GBR coastline) (Horton et al., 2003); and species composition in the Exmouth Gulf (Western Australia) (Orpin et al., 1999). The only tropical Australian study with information regarding modern foraminifera production rates is that by Wang and Chappell (2001).

Foraminifera biomass

Published values for foraminifera biomass in lagoon and subtidal settings range from 0 to 6 t/km^2, with a range of 0.7 to 7.6 t/km^2 in intertidal estuarine settings (Table 20). The biomass of individual foraminifera in the >63µm size fraction has also been measured, ranging from 8x10^{-6} to 0.003 t/km^2 in shelf sediments (Murray, 1969). This huge range in individual biomass makes it impossible to estimate the biomass of a population based on standing stock alone.

Monthly analysis of biomass and standing stock for benthic foraminifera in the Hamble estuary also revealed that peaks in biomass and standing crop for a species do not always coincide (Murray and Alve, 2000), most likely reflecting different patterns of growth and reproduction.
There are very few estimates of annual production for benthic foraminifera due to the labour-intensive nature of time series studies. Murray and Alve (2000) undertook monthly sampling in the Hamble Estuary in England over a period of 2 years; however they were not able to determine the life spans of species since they appeared to be continuously reproducing, with juveniles present throughout the year. This meant that they were unable to calculate the annual foraminifera production from their data. In a study over two years in the Puerto Deseado intertidal zone, Argentina Boltovskoy and Lena (1969) determined that the majority of species had a reproductive cycle of one month, while the remainder reproduced once each year. By combining the monthly and annual reproduction cycles they were able to calculate an annual production of 4.65 t/km^2 dry weight. This value is equivalent to 23.25 t/km^2 wet weight using the conversion of Korsun et al. (1998).

Table 20: Biomass of living benthic foraminifera (adapted from Murray and Alve, 2000)

Location	Wet biomass ($t \cdot km^{-2}$)	Reference
Lagoon		
Buzzards Bay, USA	0-0.87	Murray (1968)
Abu Dhabi, Persian Gulf	0.01-0.406	Murray (1970)
Subtidal		
Indian River, USA	1-6	Buzas, 1978
Intertidal		
Puerto Deseado, Argentina	2.05 (mean)	Boltovskoy and Lena, 1969
Hamble Estuary, England	0.71-7.6	Murray and Alve, 2000

Benthic foraminifera as a food source

I have been able to locate very little quantitative information regarding the consumption of foraminifera. Information regarding the key predators and incidental consumers is summarised below:

Foraminifera may be consumed actively by predators, or opportunistically by deposit feeders (Murray, 1991). The primary predators of benthic foraminifera include other foraminifera, nematodes, polychaetes, gastropods, scaphopods, crustaceans and fish. Incidental consumers include flatworms, polychaetes, chitons, gastropods, nudibranchs, bivalves, crustaceans, holothuroids, asteroids, ophiuroids, echinoids, crinoids, tunicates and fish (Lipps, 1983).

Foraminifera are a minor component in the diet of *Mugil cephalus* and *M. curema* (Reuda, 2002), and in trumpeter fish (*Pelates sexlineatus*) in seagrass meadows along the coast of New South Wales (Sanchez-Jerez et al., 2002). The foraminifera content of the diet of trumpeter fish varied according to the availability of crustaceans, with higher foraminifera content when crustaceans were limited.

The isopod *Munnopsurus atlanticus,* on the southern margin of the Cap-Ferret Canyon (Bay of Biscay), has been shown to feed extensively on benthic agglutinated foraminifera (Elizalde et al., 1999).

The gut content of three individuals of *Bathymedon longirostris sp. nov.* (Amphipoda: Oedicerotidae) revealed a bulk of calcified foraminiferans, a diet in consonance with their massive mandibles (Jaume et al., 1998).

The dentaliid scaphopod *Fissidentalium megathyris,* collected from Pacific deep-sea sites off central California, feeds almost exclusively on benthic foraminifera (Langer et al., 1995). Individual scaphopods contained up to 188 foraminifera specimens, with an average if 33. Dermersally trawled prawn species on the continental slope of north-western Australia contain between 1.8-15% foraminifera in their stomach contents (Rainer, 1992).

Foraminifera feeding habits

Benthic foraminifera have evolved to live in a diversity of environments, and in the process have also evolved a variety of feeding strategies (Murray1991). Foraminifera in low productivity areas (such as coral reefs and the deep sea) have developed the ability to directly take up dissolved organic material. Active and passive herbivores are common in the photic zone, gathering algae such as pennate diatoms and small chlorophytes, and bacteria. Carnivores will feed on small arthropods, small sea urchins and other foraminifera. Passive suspension feeders also occur, generally living on hard substrates or rooted in soft sediments, and rely on natural currents to transport food particles. In fine-grained sediments beneath the photic zone the majority of foraminifera feed on detritus or bacteria. Actively-feeding individuals of *Ammonia beccarii,* contain live bacteria associated with sediment aggregates, obtained by deposit feeding (Goldstein and Corliss, 1994). This shallow water species also ingests relatively large volumes of organic detritus associated with sediments, but the role of this material in its diet is uncertain.

Foraminifera growth rates

Growth of two common species of large foraminifera from the Red Sea, *Amphisorus hemprichii* Ehrenberg and *Amphistegina lobifera* Larsen, 1976 were examined in laboratory experiments (Lee et al., 1991). A maximum growth rate of 0.037 mm per week was obtained for A. hemprichii. Specimens of *Marginopora kudakajimensis* Gudmundsson from Japan grew best (0.02 mm per week) when cultured in light, in media enriched with nitrate and phosphate changed weekly, and fed.

Foraminifera production

Quantitative information regarding foraminifera production rates and biomass from a variety of sources is summarised in Table 21 and Table 22. Standing stocks for live specimens have mostly been estimated from the total assemblage based on the percent live foraminifera in estuarine to shallow marine sediments (19-300m) on the Gippsland Shelf, southeast Australia (Smith et al., 2001). In calculating the percent live foraminifera I have restricted the data from Smith et al. (2001) to depths between 19 and 45 m to represent shallower water samples, with a percent live value of 2.3%. For deeper water samples I have used values for water depths between 100 and 300 m, with a percent live foraminifera of 1.9%. These percentages are consistent with results from other studies (e.g. Scott and Medioli, 1980).

Seagrass beds provide a habitat for an array of calcareous faunas, such as echinoids, molluscs and foraminifera. A number of studies have estimated calcium carbonate production rates by these epiphytes in a variety of tropical lagoon and shelf settings, and these span a range from 180 g $CaCO3$ m−2 year−1 in Jamaica (Land, 1970) to 2800 g $CaCO3$ m−2 year−1 in Barbados (Patriquin, 1972). Epiphyte faunas in the subtropical setting of southern Mozambique exhibit a lower range of carbonate production of 14 to 51 g m−2 year−1 (Perry and Beavington-Penney, 2005). Of these epiphytes, smaller benthic foraminifera (including *Asterorotalia* cf. *gaimardi* and *Spirillina* sp.) and the soritid *Peneroplis* sp. are a common component of the community.

Sediments collected from the Fly River Delta and Gulf of Papua indicate a range in the standing stock of infauna, ranging from 86-5555 individuals m-2; and 0.10-5.85 g m-2), with lower values in the delta than the gulf (Alongi et al., 1992). The infauna was dominated by nematodes, copepods, foraminifera and small, tube-building, deposit- and suspension-feeding polychaetes and amphipods.

Foraminifera production is affected by the turbidity of the water column. In the South Alligator River, benthic foraminifera were present in very small numbers in very turbid waters associated with the rapid tidal flow (Wang and Chappell, 2001). The distribution of arenaceous[2] versus calcareous foraminifera varies according to pH in estuaries. Waters with a pH > 8 are dominated by calcareous forms, while waters with a low pH are dominantly arenaceous.

Table 21: Average standing stock of benthic foraminifera in a range of environments

Location	***Water depth (m)***	***Benthic foram production***	***Units***
Southern Gulf of Carpentaria[1]	14-20	41±35[*]	#live/g sand
Southern Gulf of Carpentaria[1]	20-30	30±20[*]	#live/ g sand
Southern Gulf of Carpentaria[1]	30-40	19±17[*]	#live/ g sand
Canterbury Bight NZ[2]	395	375[**]	#live/g sand
Florida-Bahamas, brackish waters[3]	0-3	6.9-16[*]	#live/g sand
Florida-Bahamas, open to restricted[3]	0-30	2.3-9.2[*]	#live/g sand

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[2] Arenaceous foraminifera are agglutinated forms with a test composed of quartz grains.

Location	***Water depth (m)***	***Benthic foram production***	***Units***
Florida-Bahamas, platform margin[3]	0-40	1.15-3.45*	#live/g sand
Florida-Bahamas, upper slope[3]	40-200	3.8-11.4**	#live/g sand
South. Alligator R., nearshore marine[4]	?	1.725*	#live/ml sed >62.5µm
South. Alligator R., estuarine[4]	?	0.75***	#live/ml sed >62.5µm
South. Alligator R., channel[4]	?	2.875***	#live/ml sed >62.5µm
Florida, shallow marine lagoon[5]	1	5-170	#live/10 cm^2
Gulf of Elat, Inner shelf[6]	4	17	#live/10 cm^2

*Modern production is calculated based on the % living specimens measured in estuarine to shallow marine sediments (19-45m) on the Gippsland Shelf, southeast Australia (Smith et al., 2001).
**The percent live specimens calculated for depths of 100-300 m (Smith et al., 2001)
***The percent live specimens in channel deposits in the South Alligator River, Northern Australia is 5% (Wang and Chappell, 2001).

1. Post et al. (in prep.)
2. Hayward et al. (2004)
3. Rose and Lidz (1977)
4. Wang and Chappell (2001)
5. Hallock et al. (1986)
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Macro-invertebrates

Table 22: Basic parameters of the Ecopath model of Albatross Bay for macro-invertebrates. Values in bold have been calculated with the Ecopath software; other values are empirically based inputs.

Group name	Trophic level	OI	Biomass ($t \cdot km^{-2}$)	P/B ($year^{-1}$)	Q/B ($year^{-1}$)	EE
Marine small gastropods	**2.55**	**0.527**	**64.153**	2.500	14.000	0.980
Estuarine small gastropods	**2.55**	**0.527**	**0.062**	2.500	14.000	0.980
Estuarine small crustaceans	**2.40**	**0.297**	**0.297**	7.010	27.140	0.980
Marine small crustaceans	**2.35**	**0.284**	**20.520**	7.010	27.140	0.980
Marine worms	**2.31**	**0.273**	**21.412**	6.850	27.400	0.980
Estuarine worms	**2.31**	**0.275**	**0.941**	4.600	15.900	0.980
Marine bivalves	**2.11**	**0.106**	**94.497**	1.209	23.000	0.900
Estuarine bivalves	**2.11**	**0.106**	**9.082**	1.209	23.000	0.900

Table 23: Sources of basic parameter estimates for macro-invertebrates. The values used as inputs in the Albatross Bay model were derived from these sources based on their application to the defined system; rather than being simply extracted.

Group name	Biomass ($t \cdot km^{-2}$)	P/B ($year^{-1}$)	Q/B ($year^{-1}$)	Diet composition
Marine small gastropods	Long and Poiner (1994)	Okey et al. 2004a	Okey et al. 2004a	
Estuarine small gastropods		Okey et al. 2004a	Okey et al. 2004a	
Marine small crustaceans	Long and Poiner (1994)	Okey and Mahmoudi 2002; Okey et al. 2004b	Okey and Mahmoudi 2002; Okey et al. 2004b	Okey 2002; Okey 2004
Estuarine small crustaceans		Okey and Mahmoudi 2002; Okey et al. 2004b	Okey and Mahmoudi 2002; Okey et al. 2004b	Okey 2002; Okey 2004
Marine worms	Long and Poiner (1994)	Long and Poiner 1994 via Huang et al. 2001	Long and Poiner 1994 via Huang et al. 2001	Okey and Mahmoudi 2002
Estuarine worms		Long and Poiner 1994 via Huang et al. 2001	Long and Poiner 1994 via Huang et al. 2001	Okey and Mahmoudi 2002
Marine bivalves		Arnold et al. 2002; Okey et al. 2004b	Arnold et al. 2002; Okey et al. 2004b	Arnold et al. 2002; Okey et al. 2004b
Estuarine bivalves		Arnold et al. 2002; Okey et al. 2004b	Arnold et al. 2002; Okey et al. 2004b	Arnold et al. 2002; Okey 2004b

Marine and estuarine bivalve groups

There were no data to support derivation of biomass estimates for marine bivalves in the Albatross Bay area, so the Ecopath model was allowed to estimate biomass by setting the Ecotrophic Efficiency parameter to 0.9, indicating that 90% of bivalve production is consumed by predators. The P/B value of 1.209 $year^{-1}$ and the Q/B ratio value of 23.00 $year^{-1}$ were derived by Arnold et al. (2002) during construction of the West Florida Shelf model (Okey & Mahmoudi, 2002; Okey et al. 2004). Diet composition for this group was adapted from Arnold et al. (2002) and these values were published in Okey (2004). Marine and estuarine bivalves were split into separate groups to highlight their different diet compositions as prey from both habitats contribute differently in proportion to their overall diet.

Marine and estuarine small crustaceans

There was no data to correlate biomass estimates for small marine and estuarine crustaceans in the Albatross Bay area, therefore the Ecotrophic Efficiency parameter were set at 0.98, indicating that 98% of the proportion of crustacean production is consumed by predators. This allowed the Ecopath model to estimate crustacean biomass. The P/B value of 7.010 $year^{-1}$ and Q/B value of 27.140 $year^{-1}$ were derived by Okey (2002) during the assembly of the West Florida Shelf model (Okey & Mahmoudi, 2002; Okey et al. 2004).Diet composition for this group was adapted from Okey (2002) and published values in Okey (2004). To allow for different diet compositions in their habitats and the proportion that each prey contributes to their overall diet, the small crustaceans were separated into two groups of marine and estuarine.

Marine and estuarine worms

There was no data from which to source biomass estimates for marine and estuarine worms in the Albatross Bay area, to compensate for this the Ecopath model was allowed to estimate biomass by setting Ecotrophic Efficiency at 0.98, indicating that 98% of the proportion of marine and estuarine worm production is consumed by predators. The marine worm P/B value of 6.850 $year^{-1}$ and Q/B value of 27.40 $year^{-1}$ were derived from Long and Poiner (1994) via Huang et al (2001). Estuarine worm P/B value of 4.600 $year^{-1}$ and Q/B value of 15.90 $year^{-1}$ were similarly derived from Long and Poiner (1994) via Huang et al (2001). Diet composition for this group was adapted from Okey et al

(2004a) and published values in Okey (2004). As to indicate the different proportions that each prey contributes within the marine and estuarine environments to the overall worm diet composition, the worms were classified as separate groups.

Marine and estuarine small gastropods

As there was no data from which to source marine and estuarine gastropod biomass in the Albatross Bay area, the Ecotrophic Efficiency was set at 0.98 this indicates that 98% of marine and estuarine small gastropod production is consumed by predators, this allowed the Ecopath model to estimate gastropod biomass. The P/B value of 2.50 year^{-1} and Q/B value of 14.00 year^{-1} was derived from values used in the Galapagos rocky reef model (Okey et al. 2004). Small gastropods were separated into marine and estuarine groups to indicate the proportion that each prey from these separate habitats contributes to the gastropods overall diets.

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Mega-invertebrates

Table 24: Basic parameters of the Ecopath model of Albatross Bay for mega-invertebrates. Values in bold have been calculated with the Ecopath software; other values are empirically based inputs.

Group name	**Trophic level**	**OI**	**Biomass (t·km^{-2})**	**P/B (year^{-1})**	**Q/B (year^{-1})**	**EE**
Octopus	**3.82**	**0.273**	**0.099**	2.370	7.900	0.900
Squid and cuttlefishes	**3.62**	**0.282**	**0.850**	2.370	7.900	0.950
Banana prawn subadults	**3.44**	**0.152**	0.020	3.120	27.181	1.228
Stomatopods	**3.37**	**0.542**	**0.366**	3.500	7.432	0.950
Banana prawn adult	**3.34**	**0.088**	0.079	3.200	19.200	**0.928**
Tiger prawn subadults	**3.32**	**0.039**	0.021	3.200	28.160	3.220
Tiger prawn adult	**3.32**	**0.041**	0.121	2.340	19.200	**0.177**
All other commercial prawns	**3.30**	**0.090**	**0.468**	3.000	25.000	0.900
Large gastropods	**3.28**	**0.059**	0.023	2.800	14.000	**0.462**
Thallasinid prawns (Callianassa)	**3.17**	**0.267**	**1.008**	3.000	25.000	0.950
All other non-commercial prawns	**3.17**	**0.267**	**23.221**	3.000	25.000	0.950
Sand crab	**3.12**	**0.120**	**0.069**	2.800	8.500	0.900
The mud crab	**3.07**	**0.203**	**0.067**	2.800	8.500	0.900
Red mud crab	**3.07**	**0.202**	**0.056**	2.800	8.500	0.900
Banana prawn juvenile	**3.03**	**0.578**	0.011	3.720	43.888	**0.000**
Other large crabs	**2.98**	**0.260**	**5.533**	2.800	8.500	0.900
Spatangoids	**2.93**	**0.458**	2.142	1.400	2.810	**0.168**
Crayfish	**2.87**	**0.448**	**0.010**	3.000	25.000	0.950
Asteroids	**2.77**	**0.703**	0.051	0.490	3.240	**0.148**
Tiger prawn juvenile	**2.59**	**0.504**	0.012	3.400	45.234	**0.069**
Sessile epibenthos	**2.40**	**0.275**	4.985	0.800	9.000	**0.721**
Holothurians	**2.16**	**0.190**	0.065	0.610	3.360	**0.928**
Ophiuroids	**2.13**	**0.118**	**24.847**	1.400	2.810	0.950
Echinoids	**2.01**	**0.019**	0.085	1.650	2.810	**0.791**

Table 25: Sources of basic parameter estimates for mega-invertebrates. The values used as inputs in the Albatross Bay model were derived from these sources based on their application to the defined system, rather than being simply extracted.

Group name	***Biomass ($t \cdot km^{-2}$)***	***P/B ($year^{-1}$)***	***Q/B ($year^{-1}$)***	***Diet composition***
Octopus		Dunning et al. 1994 in Huang et al. 2001	Dunning et al. 1994 in Huang et al. 2001	Okey 2002
Squid and cuttlefishes		Dunning et al. 1994 in Huang et al. 2001	Dunning et al. 1994 in Huang et al. 2001	Okey 2002
Stomatopods	Dell and Sumpton 1999	Meyer and Caldwell 2002	Meyer and Caldwell 2002	Meyer and Caldwell 2002
Banana prawn adult	Loneragan et al. in prep.	Loneragan et al. in prep.	Loneragan et al. in prep.	Robinson, Section 6.9
Tiger prawn adult		Kenyon et al, Section 6.8	Kenyon et al, Section 6.8	Robinson Section 6.9, after Wassenberg and Hill 1987 and others
All other non-commercial prawns		From Somers 1994 in Huang et al. 2001	From Somers 1994 in Huang et al. 2001	
Large gastropods	Long, Pointer and Wassenberg 1995	Okey et al. 2004a	Okey et al. 2004a	
Thallasinid prawns (Callianassa)		From Somers 1994 in Huang et al.2001	From Somers 1994 in Huang et al. 2001	
All other commercial prawns		From Somers 1994 in Huang et al. 2001	From Somers 1994 in Huang et al. 2001	
Sand crab		Okey and Mahmoudi 2002; Okey et al. 2004b	Okey and Mahmoudi 2002; Okey et al. 2004b	Robinson Section 6.9, from Wassenberg and Hill 1997 and Wassenberg unpublished data
The mud crab		Okey and Mahmoudi 2002; Okey et al. 2004b	Okey and Mahmoudi 2002; Okey et al. 2004b	Okey and Mahmoudi 2002; Okey 2004
Red mud crab		Okey and Mahmoudi 2002; Okey et al. 2004b	Okey and Mahmoudi 2002; Okey et al. 2004b	Okey and Mahmoudi 2002; Okey 2004
Banana prawn juvenile				Robinson, Section 6.9 from Round 1999
Other large crabs		Okey and Mahmoudi 2002; Okey et al. 2004b	Okey and Mahmoudi 2002; Okey et al. 2004b	Okey and Mahmoudi 2002; Okey 2004
Spatangoids	Long, Pointer and Wassenberg 1995	Okey et al. 2004a	Okey et al. 2004a	
Crayfish				
Asteroids	Long, Pointer and Wassenberg 1995	Okey et al. 2004a	Okey et al. 2004a	Okey et al. 2004a; Okey 2004
Tiger prawn juvenile				Heales 2000; Heales, Vance & Loneragan 1996; O'Brien 1994; Round 1999
Sessile epibenthos	Long, Pointer and Wassenberg 1995	Okey and Mahmoudi 2002; Okey et al. 2004b	Okey and Mahmoudi 2002; Okey et al. 2004b	Okey and Mahmoudi 2002; Okey 2004

Group name	Biomass ($t \cdot km^{-2}$)	P/B ($year^{-1}$)	Q/B ($year^{-1}$)	Diet composition
Holothurians	Long, Pointer and Wassenberg 1995	Okey et al. 2004a	Okey et al. 2004a	
Ophiuroids	Long, Pointer and Wassenberg 1995	Okey et al. 2004a	Okey et al. 2004a	
Echinoids	Long, Pointer and Wassenberg 1995	Okey et al. 2004a	Okey et al. 2004a	Okey et al. 2004a; Okey 2004

Mega-invertebrate biomass estimates

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Total catch weight (kg) for most of the major mega-invertebrate classes in the Albatross Bay area were derived from the Long; Pointer and Wassenberg (1995) paper, however data for the cephalopods and crabs could not be sourced from this paper. The major classes were divided, according to the classification used in Meglitsch (1972), into the present functional groups in the Ecopath model for Albatross Bay. To obtain biomass estimates as a kg/km² unit, so as to be compatible with the Ecopath model, the total weight of each group was divided by the total swept area, biomass was then converted to tonnes per km². To obtain the total swept area the calculation (0.003km width X 1.5km length X 107 sites = 0.4815km sweep area) was used with figures sourced from the field sample data provided. The burrowing behaviour associated with Stomatopods, Squid, Cuttlefish, and Marine Bivalves suggest that these functional groups were not substantially sampled by the benthic sled; total weight values would therefore underestimate realistic biomass of these classes and as a result were excluded form the Ecopath model.

Octopus, squid, and cuttlefish

Due to the assumed underestimate of 0.012 t/km^2 for octopus, squid and cuttlefish calculated using the method described in section 5.7.1 and the absence of data from which to derive biomass estimates, the Ecopath model was allowed to estimate biomass. By setting the Ecotrophic Efficiency of octopus at 0.9 and the Ecotrophic Efficiency of cuttlefish and squid at 0.98 it indicates that 90% and 98% respectively of the proportion of production by these groups is consumed by predators. A P/B value of 2.37 year^{-1} and Q/B value of 7.9 year^{-1} were derived from Dunning et al. (1994) in Huang et al. (2001). The diet composition of the two groups of octopus and squid and cuttlefish in proportion to their biomass differ comparatively, these diet compositions were adapted from Okey (2002).

Stomatopods

A biomass estimate for stomatopods of the Albatross Bay area was not derived due to a lack of available information for the area. The Ecopath routine was therefore allowed to estimate biomass by setting the Ecotrophic Efficiency at 0.95, indicating that 95% of the stomatopod production is consumed in the system. A P/B value of 3.5 year^{-1} and a Q/B value of 7.432 year^{-1} were borrowed from Meyer and Caldwell (2002) based on data from Panama. Diet composition was also derived form Meyer and Caldwell (2002).

Sand crab

Data from which to source an estimate of total biomass of sand crabs was not available, therefore the Ecotrophic Efficiency was set at 0.9 to indicate that 90% of the proportion of sand crab production is consumed by predators, this allowed the Ecopath model to estimate sand crab total biomass in the Albatross bay area. A P/B value of 2.8 year^{-1} and a Q/B value of 8.5 year^{-1} were derived from the

Ecopath model of the West Florida shelf (Okey and Mahmoudi 2002, Okey et al. 2004) and adapted for the Albatross Bay area.

Due to the raw data for individual weights, total weights and total number of individuals within the gut of sand crabs being obtainable from T. Wassenberg for the Wassenberg and Hill 1987 paper (Feeding by sand crabs) values of each prey item group could be directly entered into the Ecopath model once converted to proportion of biomass consumed. To calculate this biomass value, individual weights and total number of individuals were multiplied to work out the total weights of individuals, or functional groups consumed, which was in turn divided by the combined total weight of all functional groups to establish the proportion of biomass consumed. However the very small sample size of this study may mean that this information is not representative of the sand crab population. As all weights were measured as dry weight, a conversion to wet weight was required, this is set out below:

- dry to wet weight (benthic macrofauna) ratio: 1 to 7.5 (Rowe and Menzel, 1971)
- dry to wet weight (shrimp) ratio: 1 to 7.7 (Bougis 1979 in Cushing 1984)

Mud crab and other large crabs

Crabs have been recognised as being a dominant part of the mega fauna in certain areas; however no data has yet been sourced from which to derive a biomass estimate for the Albatross Bay area. To compensate for this the Ecopath model was allowed to estimate crab biomass by setting the Ecotrophic Efficiency at 0.9, this indicates that 90% of the proportion of mud crab production is consumed by predators. The P/B of 2.8 year^{-1} and a Q/B value of 8.5 year^{-1} are the same as those used for the other two crab groups, these values were derived from the West Florida shelf Ecopath model (Okey and Mahmoudi 2002, Okey et al. 2004b) and adapted for the Albatross Bay area. The diet composition of mud and red mud crabs has been identified as consisting of bivalves, small crabs and perhaps some worms; however values for the Albatross bay area were not available. Therefore, to estimate the diet composition values in proportion to biomass, I used a placeholder diet from West Florida Shelf Model (Okey and Mahmoudi 2002, Okey et al. 2004b).

Large gastropods

Data for the total biomass of large gastropods in the Albatross Bay area were sourced from Long; Pointer and Wassenberg (1995) paper and calculated using the method described in section 5.7.1 with a resulting value of 0.0228 t/km^2. The P/B value of 2.8 year^{-1} and Q/B value of 14.0 year^{-1} were derived from the Galapagos Island model (Okey et al. 2004a). The diet composition in proportion to biomass for large gastropods was estimated using a quantitative judgment by Okey T. for the Albatross bay area, common prey being bivalves, worms and smaller gastropods.

Holothurians

The total biomass for holothurians in the Albatross Bay area was calculated using the methods described in section 5.7.1., using values derived from Long; Pointer and Wassenberg (1995) paper, the calculated holothurian biomass was 0.0650 t/km^2. Both the P/B value of 0.610 year^{-1} and Q/B value of 3.36 year^{-1} were derived from the Galapagos Island model (Okey et al. 2004a). The diet composition and the fraction that each prey item contributes to the holothurians overall diet in the Albatross Bay area was estimated using a quantitative judgment by Okey T. This diet composition consisted of 80% sediment detritus with the remaining 20% being a mixture of meiofauna, forams, microbial heterotrophs and microphytobenthos.

Spatangoids

The total biomass of spatangoids in the Albatross bay area as 2.142 t/km^2 was calculated using the methods described in section 5.7.1. utilising data sourced from Long; Pointer and Wassenberg (1995) paper. The P/B value of 1.40 year^{-1} and Q/B ratio value of 2.81 year^{-1} were derived from the Galapagos Island model (Okey et al. 2004a). The fraction that each food item contributed to the total diet composition of spatangoids was estimated by the judgment of Okey T.; this mainly consisted of marine meiofauna, worms and sediment detritus.

Echinoids

Using the methods described in section 5.7.1. and the data derived from Long; Pointer and Wassenberg (1995) paper, the total biomass for echinoids in the Albatross bay area was calculated as 0.0849 t/km^2.Using values derived from the Galapagos Island model (Okey et al. 2004a) the P/B value was set as 1.65 year^{-1} and Q/B value at 2.81 year^{-1}. The diet composition was estimated on the judgement of Okey T. and roughly based on the estimated diet proposed in the Galapagos Island model (Okey et al. 2004a) and published in Okey (2004). This was composed of predominantly marine macroalgae, marine sediment detritus and microphytobenthos.

Ophiuroids

Data was available from the Long, Poiner and Wassenberg (1995) paper with a total biomass of ophiuroids calculated as 0.0082 t/km^2; according to the method described in section 5.7.1. However, it was expected that this data would severely underestimate this group in the Albatross Bay area, therefore the Ecopath model was allowed to calculate biomass. By setting the Ecotrophic Efficiency as 0.95 signifying that the proportion of ophiuroids production is consumed by predators. Using values derived from the Galapagos Island model (Okey et al. 2004a) the same P/B value of 1.40 year^{-1} and Q/B value of 2.81 year^{-1} were set into the Albatross Bay model. The diet composition and the fraction that each prey item has in the overall diet of ophiuroids were estimated by the quantitative judgement of Tom Okey.

Asteroids

Using values sourced from the Long; Pointer and Wassenberg (1995) paper, a total biomass for asteroids in the Albatross bay area was calculated using methods described in section 5.6.1 as 0.0508 t/km^2. The P/B value of 0.49 year^{-1} and Q/B ratio value of 3.24 year^{-1} were derived from the Galapagos Island model (Okey et al. 2004a). Based on the Galapagos Island model Okey (2004) and Okey et al. (2004a) the diet composition for the asteroids was adapted to best represent the diet of the Albatross bay area, this included microphytobenthos, sessile epibenthos and a variety of small invertebrates.

Sessile epibenthos

Data taken from the Long; Pointer and Wassenberg (1995) paper was used in the estimate of sessile epibenthos total biomass in the Albatross Bay area using the calculation described in section 5.7.1., a total biomass of 4.985 t/km^2 was estimated. P/B and Q/B values were obtained from the West Florida Shelf model (Okey & Mahmoudi, 2002; Okey et al. 2004) these were a P/B value of 0.80 year^{-1} and a Q/B value of 9.0 year^{-1}. Similarly the diet composition in proportion to biomass was also derived from the Florida West Shelf model Okey (2002) and values published in Okey (2004) and adapted to the Albatross Bay area.

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Penaeid prawns of Albatross Bay

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Basic working Ecopath input parameters for the life stages of banana prawns (*Penaeus merguiensis*) and tiger prawns (*Penaeus semisulcatus* and *P. esculentus)* in the defined Albatross Bay area were estimated using a combination of published literature, unpublished data from ongoing stock assessments, and an ontogenetic-stage-based population modeling routine imbedded in the Ecopath input interface. The delineation of life stages used here is presented in Table 26; the parameters are summarized in Table 27; and the interface of the stage-based modeling routine is exemplified in Figure 55. These are followed by a documentation of the derivations of these working input parameters. We note that estimates of biomass, in particular, are uncertain and that this uncertainty has important ramifications for Ecopath with Ecosim model balance and dynamics. Further refinement of these parameters should be a continued focus of research to understand the dynamics of Australia's northern prawn population in a whole ecosystem context and otherwise.

Table 26: Age and size definitions for all prawns in the Albatross Bay model.

Functional group	***Carapace length (mm)***	***Age (mo)***	***Depth range (m)***
Juvenile prawn	< 20	1 to < 4	0 – 1
Sub-adult prawn	20 to 28	4 to < 6	0 – 20
Adult prawn	> 28	≥ 6	10 – 40

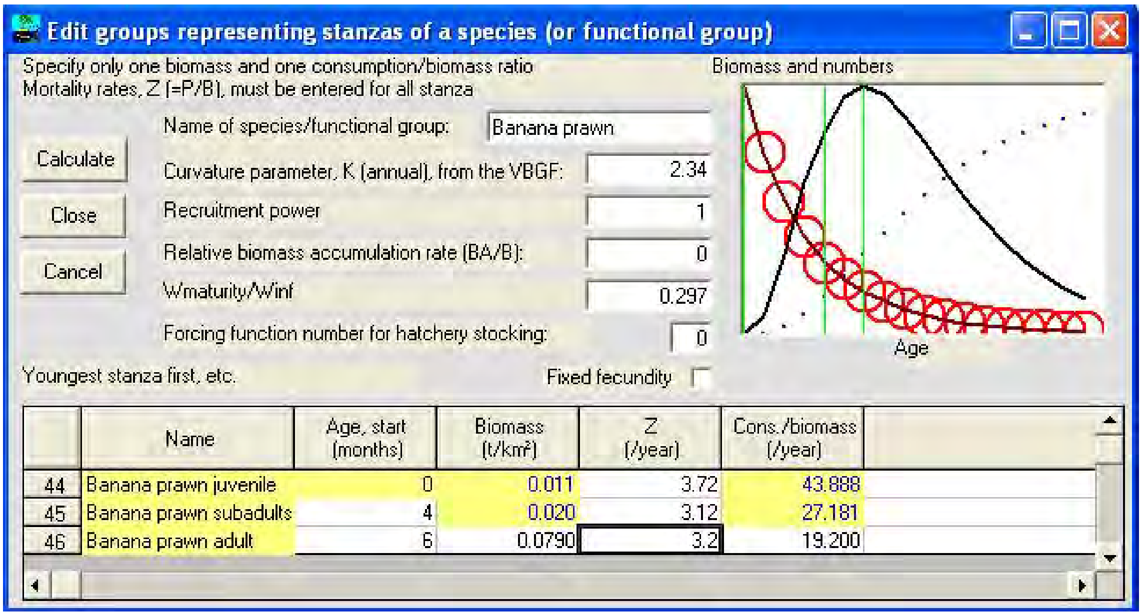
Note: Both banana and tiger prawns settle into nursery areas at 1 to 1.5 months old (after a planktonic larval stage). They become sub-adults after they leave the nursery areas at 3 to 4 months. We consider Banana prawns to become adults at 5 to 6 months, and tiger prawns at 7 to 8 months.

Table 27: Current working prawn parameters in the Albatross Bay model. Bolded values were estimated by Ecopath's stage-based model routine.

Functional group	**Biomass (t·km^{-2})**	**Z (year^{-1})**	**Q/B (year^{-1})**
Banana prawn juvenile	**0.0115**	3.72	**44.0**
Banana prawn sub-adults	**0.0199**	3.12	**27.2**
Banana prawn adult	0.0790	3.20	19.2
Tiger prawn juvenile	**0.0115**	3.40	**45.2**
Tiger prawn sub-adults	0.0211	3.20	**28.2**
Tiger prawn adult	**0.1210**	2.34	19.2

Stage-based prawn model

Single species, stage-based models were imbedded in the overall Ecopath model of Albatross Bay. This ensured biological continuity and sensibility of the information specified for the three life stages of each prawn group. Each of the three life stages—juveniles, subadults, and adults—of each of these prawn species were articulated as separate functional groups in the Ecopath model; but they were coupled with each other ontogenetically in the sense that the biomass from the younger groups flowed into the biomass of the older groups. The input interface of this model is presented in Figure 55



Specify only one biomass and one consumption/biomass ratio
Mortality rates, Z (=P/B), must be entered for all stanza

Name of species/functional group: Banana prawn
Curvature parameter, K (annual), from the VBGF: 2.34
Recruitment power: 1
Relative biomass accumulation rate (BA/B): 0
Wmaturity/Winf: 0.297
Forcing function number for hatchery stocking: 0
Youngest stanza first, etc.
Fixed fecundity ☐

	Name	Age, start (months)	Biomass (t/km²)	Z (/year)	Cons./biomass (/year)
44	Banana prawn juvenile	0	0.011	3.72	43.888
45	Banana prawn subadults	4	0.020	3.12	27.181
46	Banana prawn adult	6	0.0790	3.2	19.200

Figure 55. Ecopath interface for the stage-based model of banana prawns imbedded in the overall Ecopath model of Albatross Bay showing specified growth and maturity input parameters, life-stanza specification, basic input parameters, and a graphical representation of the imbedded model. The red circles represent number of individuals; the dotted line is the average weight of individuals, the black line is the population biomass, and the green vertical lines are the stanza separation.

The curvature parameter, K (annual), for both imbedded models was calculated as the mean of the weekly K values for both males and females of both species of tiger prawns (K=0.043, 0.062, 0.041, 0.034 week^{-1} for females and males of *P. semisulcatus* and *P. esculentus* , respectively), scaled to annual units. The ratio W maturity / W infinity was calculated by converting known lengths at infinity (51.6, 37.5, 44.8, 37.5 mm carapace length, respectively), and assumed lengths at maturity (28.5 mm carapace length) for these respective categories, to weights using specific empirical conversions ($W=0.0027L^{2.764}$, $W=0.003739L^{2.574}$, $W=0.00159L^{2.747}$, $W=0.00265L^{2.648}$).

Adult banana prawns

Biomass

We estimated the biomass of adult banana prawns to be 0.079 t·km^{-2}. This estimate was approximated as the fishery catch plus the estimated prawn biomass consumed by predators, plus 4% of the resulting combined biomass (to account for other mortality); all divided by the estimated total mortality. The average banana prawn catch for the region during 1986 to 1992 was 645 tonnes (see Bishop, this volume). The natural mortality was taken as 118% of the fishing mortality—1.18 is the ratio of the natural mortality to the fishing mortality from an empirical study of this same banana prawn system by Lucas et al. (1979). Based on annual catches of 645 tonnes, the annual banana prawn biomass was estimated to be about 1464 tonnes, which is equivalent to 0.253 t·km^{-2}, when expressed in the total modelled area (5,788 km^{-2}). Dividing by the specified P/B (3.2 year^{-1})—the estimated total mortality—leads to a banana prawn biomass of 0.079 t·km^{-2}. This then represents the averaged biomass density of banana prawns at any given time during the year, which is the expression of biomass required to specify the Ecopath model.

The area that adult banana prawns actually occupy—from about the 10m depth contour to the 40 m depth contour—was estimated at 4,167.67 km^{-2}, representing 72% of the total study area of 5,788 km^{-2}. This value is not used in the estimation of biomass in the specified modelled area of the parameterized Ecopath model; rather, this information is used for specification of the spatially-explicit Ecosim simulations.

P/B

Our P/B estimate for adult banana prawns is 3.2 year^{-1}. The value was derived by examining the effects of a range of mortality estimates (Z), 2.8 to 4.6 year^{-1}, by multiplying the negative exponent of each total mortality rate with a hypothetical population size. This produced values for survivorship after 12 months of about 6% to 0.8%, respectively. Survival of 0.8% (corresponding to a Z of 4.6) seemed too low, but a mortality estimate of 3.2 year^{-1} gave a survival of 4.1%, with a corresponding M of 1.73 and an F of 1.47 based on an M to F ratio of 1.18 from Lucas et al. (1979).

Q/B

We used 19.2 year^{-1} as the ratio of consumption to biomass (Q/B) for adult prawns. The ratio was taken from an independent estimate for adult prawns from the Yucatan continental shelf in the Gulf of Mexico (Arreguín-Sánchez et al. 1993).

Sub-adult banana prawns

Biomass

The biomass of sub-adult banana prawns (0.02 t·km^{-2}) was estimated using the ontogenetic-stage-based population modeling routine imbedded in the Ecopath input interface. It was based on the estimate of adult banana prawn biomass discussed above, and an annual curvature parameter (K) of 2.34, and a $W_{maturity}/W_{inf}$ of 0.297.

The biomass value would be difficult to estimate using survey data as significant areas of the habitat of sub-adult prawns have not been surveyed. While there are survey data on the abundance of 20 – 28 mm CL banana prawns (sub-adults) for the deeper sections of Albatross Bay, there are no historical survey data on the abundance of sub-adult banana prawns in shallow inshore sections of the bay.

Historically, surveys of Albatross Bay have been confined to water depths > 5 m in 1986-1992 and > 8 m in 2002-2006. In conjunction with the 1986-1992 offshore surveys, measurement of the abundance of juvenile and emigrant prawns in the nearby estuary was also undertaken. However, over much of the habitat where the sub-adults might be expected to be found, they have not been surveyed. Near shore regions of Albatross Bay, between the estuary and the 5 m depth contour are difficult to survey using the vessels usually available to researchers: chartered commercial trawlers or 6-8 m work vessels. The zone is too shallow for access by trawler and too exposed for regular access by small workboat.

P/B

Wang and Haywood (1999) suggest that the model for size-dependent mortality provides an estimate of mortality for 15 mm CL juveniles (5 mm CL smaller than our low range for sub-adults) of 0.02 week^{-1}. Over 12 weeks, the values provide an M of 0.24 year^{-1} for large juveniles, lower than we would expect for sub-adults. Currently, the model uses a P/B ratio of 3.12 for sub-adult banana prawns.

Q/B

The ratio of consumption-to-biomass for sub-adult prawns (27 year^{-1}) was calculated by the stage-based model embedded in Ecopath, based on an input for adult prawns of 19.2 year^{-1} that was estimated from the Yucatan continental shelf, Gulf of Mexico (Arreguín-Sánchez et al. 1993).

Juvenile banana prawns

Biomass

The biomass of juvenile banana prawns (0.012 t·km^{-2}) was estimated using the ontogenetic-stage-based population modeling routine imbedded in the Ecopath input interface; it was based on an estimate of adult banana prawn biomass and the other parameters discussed previously.

However, the estimate from the model is two orders of magnitude greater than the juvenile banana prawn abundance estimate of 0.0001479 t·km^{-2} based on data collected by Vance *et al*. (2002) from stake net experiments undertaken at Weipa in the 1990's (se comments to explain this difference below). To obtain this estimate, we noted the highest and lowest estimates of abundance taken over four stake net trials described in Vance *et al*. (2002) (17.5 individuals per 100 m^{-2} and 0.0 individuals per 100 m^{-2}, respectively) and took a mean of the estimates for each mangrove type. The same mangrove habitats were sampled near a 'creek' and near a 'river', so we took a mean number of prawns 100 m^{-2} for the 'creek' and 'river' values for the three mangrove habitat types (*Rhizophora*, 5.625 prawns 100 m^{-2}; *Ceriops*, 5.75 prawns 100 m^{-2}; *Avicennia*, 1.05 prawns 100 m^{-2}). We then weighted the abundance estimates by the proportion of the total mangrove habitat that was comprised of each of the three mangrove types studied in Vance *et al*. (2002). The area of mangroves was obtained from the Queensland Department of Primary Industry GIS. The total area of mangroves in Albatross Bay was 197.8 km^2; comprised of *Avicennia marina* (57.2 km^2), *Ceriops tagal* (42.8 km^2) and *Rhizophora stylosa* (97.8 km^2). We then used the proportion of each mangrove habitat of the total area of all mangroves (i.e. *Avicennia* 0.28925, *Ceriops* 0.21649, *Rhizophora* 0.49426) to arrive at an average abundance of 4.3 prawns 100 m^{-2} for the mangrove habitat as a whole.

To convert to t·km^{-2}, we estimated the average weight of a juvenile prawn to be 0.3 g which is the approximate weight of a 6 mm CL banana prawn, the median size n the mangrove forest. We calculated an estimated banana prawn biomass of **0.00432874** t·km^{-2} at the study site. The mangrove habitat area of Albatross Bay is 197.816 km^{-2} and it represents approximately 3.4177% of the overall modeled area (QDPI GIS data), resulting in a juvenile banana prawn biomass estimate of **0.0001479** t·km^{-2} in the overall Albatross Bay modeled area. Although a few banana prawn postlarvae and even fewer juveniles are caught in habitats other than mangrove forests, their abundance in these habitats is negligible compared to in mangrove forests (Staples *et al*. 1985).

There are several possibilities to explain the discrepancy between the biomass estimate form the Ecopath model and the estimate derived from empirical data. Firstly, in the Embley River estuary, juvenile banana prawns use the *Rhizophora* and *Ceriops* forests (where, on average, they are five times more abundant) much more than the *Avicennia* forest. The *Avicennia* forest occurs highest up the intertidal elevation, near terrestrial forests. Thus, during neap tides these forests are not inundated, so prawns cannot access them. During neap tides, Vance et al. (1996) found a maximum density of juvenile banana prawns of 18.3 prawns 100 m^{-2} in November and 334.5 prawns 100 m^{-2} in March; much higher values than the average they found over all their studies. If these neap-tide values are used as an estimate of abundance, a biomass of juvenile banana prawns of 0.017 $t \cdot km^{-2}$ was estimated; a similar value to the estimate from the Ecopath model.

As well, the higher abundances of juvenile banana prawns in the *Avicennia* forest occurred in the mangroves forests through which a creek meanders, looping back on itself; and sections of *Avicennia* are not far from the creek itself on either side. Banana prawns constantly move throughout the forests on the tidal currents (Vance et al. 2002), so their abundance may vary throughout the forest in all mangrove types during the flood and ebb tides. In contrast, along the river where the mangrove species are zoned in parallel sections along the river, the banana prawn density values in the *Avicennia* forest were very low. The *Avicennia* trees are farthest from the waters edge and inundated for only a short period of time on the spring tides (not on neap tides). These types of *Avicennia* forest may be more extensive than forests among creek meanders, so their aerial extent and low use by banana prawns that use the flood tide to access mangrove forests may not well represent density values for the forests where prawns spend most of their time. Thus, values from Vance et al.'s (2002) study may be low estimates when used for our purposes, as they were made on spring tides.

Secondly, the weight of the juvenile prawns is difficult to estimate. Though the average size of juvenile banana prawns in the forests might be about 6 mm CL, larger and much heavier prawns are common. Vance et al. (1996) found banana prawns in a size range from 4 – 10 mm CL in November, though the average size was smaller at 1-3 mm CL in March. Over the period of Vance et al.'s (2002) studies in the forests adjacent to the creek, banana prawns were generally larger, abundant from 2 to 14 mm CL in the *Rhizophora* forest, with a median value in the Ceriops and *Avicennia* forests of 6-8 mm CL (a range of 4 to 14 mm CL) (Vance et al. 2002). In the forests adjacent to the river, the median size was 17 mm CL (a range of 2 to 21 mm CL). To estimate weight for this study, we used a mean size of about 6 mm CL (~ 0.3 g) as this was the median size found in the mangroves forests of inshore Albatross Bay (Vance et al. 1996, 2002). However, if the weight of a 15 mm CL prawn (~3.7g) is used to estimate banana prawn biomass, a value of 0.006 $t \cdot km^{-2}$ is derived. Moreover, if the weight of a 17 mm CL prawn (~ 7.0 g) is used a value of 0.01 $t \cdot km^{-2}$ is derived. Both values are closer to the biomass estimate from the Ecopath Model.

Future Research

Extensive beam-trawling in a range of estuarine habitats has shown that banana prawns are not found in habitat types other than mangrove forest habitats (Staples et al. 1985). In all probability, a contribution from other habitats to the abundance of banana prawns in Albatross Bay can be discounted. Historically, the abundance of banana prawns in estuarine habitats was measured by catching animals at low tide; in rivers, creeks and remnant water bodies adjacent to and within the mangrove forest habitats. These studies were poor at describing the way the juvenile prawns used the forests at high tide, and at estimating the density of prawns within the forest habitats. Vance et al. (1996, 2002) were the first to attempt to make these estimates; yet our results from the Ecopath model are at odds with their estimates. Our understanding of the way juvenile banana prawns use mangrove forest habitats remains an area where research could be focused.

P/B

We calculated the production to biomass ratio for juvenile banana prawns using Wang and Haywood (1999), who suggested that if we assume constant mortality, the natural mortality of juvenile banana prawns is 0.31 $week^{-1}$. Over a 12 week period in the nursery habitats, natural mortality (M) (and hence P/B for this un-fished staged) would equal **3.72** $year^{-1}$. Wang and Haywood (1999) also suggested that the model for size-dependent mortality provides different estimates of mortality; from a high rate of 0.89 week^{-1} for postlarvae, to a low rate of 0.02 week^{-1} for 15 mm CL juveniles. Over 12 weeks, these values provide an M of 10.68 year^{-1} for postlarvae and an M of 0.24 year^{-1} for large juveniles. The estimated average for all juveniles of **3.72** year^{-1} is very close to an estimated total mortality of 4.08 suggested for adult prawns by Okey and Nance (2002). Furthermore, it is supported by field estimates made from the same data where natural mortality ranged between 0.23 to 0.94 week^{1} (Haywood and Staples, 1993).

Q/B

The ratio of consumption to biomass for juvenile prawns was 45.056 year^{-1}. This value was calculated by the ECOPATH model, given an input for adult prawns of **19.2** year^{-1} that was estimated from the Yucatan continental shelf, Gulf of Mexico (Arreguín-Sánchez et al. 1993).

Adult Tiger prawns

Adult Biomass

The biomass of adult tiger prawns (0.121 t·km^{-2}) was estimated using Ecopath's ontogenetic-stage-based population modeling routine and it was based on the biomass calculation for sub-adult tiger prawns that was provided to the model.

Adult P/B

Currently, the model uses a P/B ratio of 2.34 for adult tiger prawns. These values are much lower than the P/B ratio calculated from published data.

Adult Q/B

The ratio of consumption to biomass for adult shrimp of the West Florida Shelf (19.2 year^{-1}) was taken from an independent estimate for the adult shrimp of the Yucatan continental shelf (Arreguín-Sánchez et al. 1993). This value was used as a placeholder for all prawn groups in the Albatross Bay model.

Sub-Adult Tiger prawns

Sub-adult Biomass

The biomass of sub-adult tiger prawns (0.0211 t·km^{-2}) was derived by estimating the average annual number and weight of tiger prawn recruits to the Weipa tiger prawn fishery. The recruitment model was used to estimate numbers over the period from 1986 to 1992. This method seemed more accurate than using survey data, as extensive nearshore shallow areas (< 5 m deep) of Albatross Bay have not been surveyed.

We estimated the numbers of tiger prawn sub-adults by calculating the number of "recruits" in the Albatross Bay region. Tiger prawn recruitment was calculated using a weekly delay difference model (Dichmont et al. 2003b), as described in Dichmont et al. (2005). The model used the results of the operating model of the Hessian matrix for uncertainty (assuming a catchability, q, from Wang (1999) and the fishing power series Basic High projections (using an average 27 mm carapace length recruit) (Dichmont et al. 2003a). The estimate of numbers was converted to weight using a known length-weight relationship and expressed per km^2 by dividing by the area modeled (5,788 km^2), resulting in a tiger prawn sub-adult biomass estimate of 0.0634 t·km^{-2}. This value was then divided by 3 assuming that the density is present, on average, for 4 months of a year; resulting in a biomass estimate of 0.0211 t·km^{-2}.

There are historical survey data on the abundance of sub-adult tiger prawns (20 – 28 mm CL) for the deeper sections of Albatross Bay; however, the abundance of sub-adult tiger prawns in inshore sections of the bay is unknown. Historically, surveys of Albatross Bay have been confined to water depths > 5 m in 1986-1992 and > 8 m in 2002-2006. In the 1980's and 1990's, the populations of juvenile tiger prawns in the nearby estuary were also surveyed, as well as measurement of the emigration of large juveniles. However, over much of the habitat where the sub-adults might be expected to be found, they have not been surveyed. Nearshore regions of Albatross Bay, between the estuary and coastal seagrass habitats (usually < 1 m depth) and the 5 m depth contour are difficult to survey using the vessels usually available to researchers: chartered commercial trawlers or 6-8 m work vessels. The zone is too shallow for access by trawler and too exposed for regular access by small workboat.

In a sheltered embayment at Groote Eylandt in the western Gulf of Carpentaria, Loneragan et al. (1994) sampled large juvenile and sub-adult tiger prawns offshore from inter-and sub-tidal seagrass beds at depths from 3 to 7 m. Using a 2 m beam trawl with a 12 mm mesh, they caught < 1 prawn 100^{-2}, with a maximum catch of 6 *P. esculentus* 100^{-2}. The size of the prawns increased with depth: from about 10 – 21 mm CL < 2.0 m depth, to about 15 - 21 mm CL at 2.5 m (on the seagrasses); to 15 - 30 mm CL at deeper sites off the seagrass (3.5 - 7 m depth). A large proportion of the prawns were in the 20-28 mm CL size range.

Sub-adult P/B

Currently, the model uses a P/B ratio of 3.2 for sub-adult tiger prawns, which corresponds to 4.1% survival after a year. This was considered to be a reasonable value and used because the production rate is not known.

Sub-adult Q/B

The ratio of consumption to biomass for sub-adult prawns was 28.160 year^{-1}. This value was calculated by the model, given a placeholder input for adult prawns of **19.2** year^{-1} that was estimated from the Yucatan continental shelf, Gulf of Mexico (Arreguín-Sánchez et al. 1993).

Juvenile Tiger prawns

Juvenile Biomass

The estimate of the biomass of juvenile tiger prawns in the study area was 0.0115 t·km^{-2}.

The biomass of juvenile tiger prawns was estimated using the ontogenetic-stage-based population modeling routine of ECOPATH. The input data to the model was the biomass estimate for sub-adult tiger prawns (see above). The value is three times the juvenile tiger prawn biomass that was estimated using empirical data from beam trawl experiments undertaken by Vance *et al*. (1996b) and Loneragan *et al*. (2001) at Weipa in the 1990's; a value of **0.003782** t·km^{-2} (the sum of 0.00020603 for postlarvae, plus 0.00287664 for grooved tigers prawns, plus 0.00069972 t·km^{-2} for brown tigers prawns).

To obtain the empirical value, we estimated the abundance of postlarval and juvenile grooved tiger prawns (*P. semisulcatus*) from the six-year data set of trawls on seagrass beds in the Embley estuary reported in Vance et al. (1996b). They recorded the density estimates over the six year for benthic postlarvae and juveniles. We took a mean over the six years, for both the pre-wet and wet-season abundances. We then took a mean of these two values to provide an estimate of the number of prawns per 1 m^{-2}. We used a net efficiency factor of 0.4 (Loneragan et al. 2001) to estimate the actual abundance of prawns on the seagrass habitats. Also, we noted the highest and lowest estimates of abundance over the six years.

To convert to t·km^{-2}, we estimated the average weight of a benthic postlarvae at 0.03 g, a juvenile prawn at 0.3 g, and made the conversion of g m^{-2} to t km^{-2}, thus producing an estimated tiger prawn biomass estimate of **0.0298125** t·km^{-2} and **0.41625** t·km^{-2} for postlarval and juvenile prawns for the habitat area.

Seagrass habitat covers approximately 40 km^2 in the Weipa Port limits (Roelofs *et al*., 2003). Thus, the area of benthic habitat represented by seagrass is approximately 0.691085% of the overall modeled area, suggesting a grooved tiger prawn biomass estimate of **0.00020603** t·km^{-2} and **0.00287664** t·km^{-2} for postlarval and juvenile prawns in the overall Albatross Bay modeled area.

We estimated the abundance of juvenile brown tiger prawns (*P. esculentus*) from the enclosure study of Loneragan et al. (2001). We took a mean for the pre-wet and late-wet-season for both seagrass types (*Enhalus* and *Halodule*) for each species (i.e. *P. esculentus* and *P. semisulcatus*). (Note that the estimates for *P. semisulcatus* are about half those arising from the Vance *et al* (1996) data. We used a net efficiency factor of 0.4 (Loneragan et al. 2001) to estimate the actual abundance of prawns on the seagrass habitats. To convert to $t.km^{-2}$, we estimated the average weight of a juvenile prawn at 0.3 g and made the conversion of $g\ m^{-2}$ to $t\ km^{-2}$, producing an estimated brown tiger prawn biomass of **0.10125** $t{\cdot}km^{-2}$ at the study site.

The habitat area represented by this study site makes up approximately 0.691085% of the overall modelled area, allowing a juvenile brown tiger prawn biomass estimate of **0.00069972** $t{\cdot}km^{-2}$ in the overall Albatross Bay modeled area.

The discrepancy between the biomass estimated by the model and that estimated by the empirical data may be due to ephemeral algae supporting high abundances of tiger prawn in the Embley River estuary (Haywood et al. 1995, Vance et al 1996b)). Both dense stands of algae and sparse algal beds are found within the estuary. Both habitats support tiger prawn juveniles, often at high densities in the high-biomass algae and usually at low densities among sparse algae and seagrasses (Haywood et al. 1995). We have not included an estimate of the area of algae in our calculations; the algal beds are difficult to quantify and they are seasonal. Similarly, some ephemeral seagrasses in the area probably are not mapped (compare maps in Haywood et al. 1995 and Roelofs et al. 2003), yet they support a sparse distribution of juvenile tiger prawns (Haywood et al. 1995).

Another issue that might affect our estimate of juvenile prawn biomass is prawn size. The size of *P. semisulcatus* of seagrass beds is probably smaller than that of *P. esculentus*. Haywood et al. (1995) showed that 99% of *P. semisulcatus* caught the Embley River estuary at ≤ 10 mm CL; a few were 11-12 mm CL. However, the size range of juvenile *P. esculentus* included individuals up to 16 mm CL. Similarly, at Groote Eylandt, few juvenile *P. semisulcatus* > 10 mm CL were found on the seagrass beds, while juvenile *P. esculentus* > 10 mm CL were common (Loneragan et al. 1994). These data suggest that *P. semisulcatus* probably emigrate from seagrass beds at a smaller size than *P. esculentus*. We have used the weight of a 6 mm CL juvenile (0.3 g) in our calculation as 6 mm CL *P. semisulcatus* were common in the estuary (Vance et al. 1996b). However, larger tiger prawn juveniles that weigh about 1 g or more are probably common in the seagrass habitats (particularly large *P. esculentus*).

Juvenile P/B

Currently, the model uses a P/B ratio of 3.4 for juvenile tiger prawns. These values are similar to the P/B ratio calculated from published data.

We calculated the production to biomass ratio (for both species) using O'Brien (1994) who found natural mortality of juvenile brown tiger prawns in Moreton Bay, south east Queensland to range between 0.06 and 0.29 $week^{-1}$. As Moreton Bay is subtropical, we chose to use the upper estimate of mortality as it closely matches that for the congeneric banana prawn in the tropical Gulf of Carpentaria. Over a 12 week residence in juvenile habitats, the M of 0.29 equals **3.48** $year^{-1}$. These estimates are similar to the M of 5.38 (updated from 4.08) suggested for adult prawns by Okey and Nance (2002).

Juvenile Q/B

The ratio of consumption to biomass for juvenile prawns was 45.234 $year^{-1}$. This value was calculated by the model, given a placeholder input for adult prawns of **19.2** $year^{-1}$ that was estimated from the Yucatan continental shelf, Gulf of Mexico (Arreguín-Sánchez et al. 1993).

Future Research

The abundance and habits of sub-adult prawns (both banana and tiger prawns) in nearshore locations, adjacent to estuarine and inshore nursery habitats has not been adequately quantified. Measurement of the use of these habitats and the timing of emigration through them would be a significant improvement to our ability to make abundance estimates for the Ecopath model.

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Prawn diets

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Abstract

Information was gathered from a variety of published and unpublished sources to estimate the diet composition of Albatross Bay area prawns. The resulting estimates are somewhat uncertain, but they should represent the best possible estimates given the limited information available.

Adult tiger prawn diet

For the purpose of the Albatross Bay Ecopath model, both species of tiger prawns, *Penaeus esculentus* and *P. semisulcatus*, were combined to form the three tiger prawn functional groups—juvenile, sub-adult, and adult tiger prawns. It should be noted that, although the adults of these species consume similar foods, the frequency at which common diet items are consumed does vary (Wassenberg and Hill 1987). Adult tiger prawn diet composition for the Weipa region was calculated using diet summaries presented by Wassenberg and Hill (1987) combined with raw tiger prawn diet data provided by T. Wassenberg (Wassenberg, unpublished data).

Wassenberg and Hill (1987) weighed total foregut contents (mg) and recorded diet composition as percent numerical composition based on the frequency of occurrence of a particular food item. However, the goal of the present exercise is to estimate diet composition for input to the Ecopath model of Albatross Bay, and Ecopath models require diet compositions to be entered as proportion wet weight. Wassenberg's unpublished laboratory book data was used to estimate average weights of each food item in adult tiger prawn foreguts and calculations of proportion wet weight were possible when these average wet weight estimates were combined with percent frequency data in Wassenberg and Hill (1987).

Tabulations of recorded weights of all individuals found singularly within foreguts were made, but were so infrequent that these values could not be used to represent the average weight of food items. Calculations were then carried out using the best estimated average weight of bivalves to estimate the weights of other food items along side bivalves in foreguts. Bivalve average weight was chosen here since, although only appearing ten times singularly within foreguts, most other food items were found singularly less then 6 times making the bivalve average weight the best estimate available. Each food item consumed by adult tiger prawns corresponded to a functional group as set out in the Weipa Ecopath model. By multiplying average weights of individual food items by the number of times they were found in all foreguts analysed, the average weight of that functional group consumed was established. All weight was measured as dry weight, so these were converted to wet weight using the following conversions:

dry to wet weight (benthic primary producers) ratio: 1 to 7.7 (Arreguín-Sánchez et al. 1993)
dry to wet weight (benthic macrofauna) ratio:1 to 7.5 (Rowe and Menzel, 1971)
dry to wet weight (shrimp) ratio:1 to 7.7 (Bougis 1979 in Cushing 1984)

The total weight of each functional group was then divided by the total weight of all food items combined to obtain a proportion value that could be used in the Ecopath model. It is worth remembering that weight estimates were dependent on the estimated average weight of bivalves calculated from only 10 individuals found singularly in foreguts. In addition, the expected large variability of food item weights, leads to the consideration that the resulting estimated average functional group weights are contributed for this exercise are highly uncertain, and possibly inaccurate. They should be considered *possible* average weights rather then actual average weights measured for the present purpose. The accuracy of calculations made here are questionable because Wassenberg and Hill (1987) did not attempt to calculate individual food item weights to begin with, the reason being that most were fragmented.

Additional uncertainties include Wassenberg and Hill (1987) observation that ophiuroids were grossly underestimated due to the method of counting individuals within a tiger prawn foregut; tiger prawns were consuming only the arms of ophiuroids, and thus the typical method of counting ophiuroid discs to estimate individuals was unsuitable. Instead, ophiuroids were recorded as present or absent, rather then as counts of individuals. It was also stated that Crustacea and molluscs were often found as fragments in a foregut and as such there numbers may also be underestimated (Wassenberg and Hill, 1987).

Juvenile tiger prawn diet

Juvenile tiger prawn diet was determined by using numerical composition (%) and mean weight per food item (mg) calculated by Dall et al. (1992) for juvenile tiger prawns in Moreton Bay. Multiplying numerical composition by the mean weight per food item, and then dividing by the total weight of all individuals consumed produced the proportion of wet weight consumed value appropriate for the Ecopath program.

Adult banana prawn diet

Raw data of adult banana prawn diet composition (frequency of occurrence and foregut content weight) of the Gulf of Carpentaria (Wassenberg and Hill 1993) was provided by T. Wassenberg and used to calculate the proportion values for the Albatross Bay Ecopath model. Such values could not be estimated reliably based solely on weights of individuals found singularly within a foregut because of the infrequency of such an occurrence. Instead, diet compositions of banana and tiger prawns (raw data provided by Wassenberg) were compared to determine if the individual weights of food items calculated for tiger prawns could be used reliably for banana prawns. Such comparisons revealed that, although banana and tiger prawns eat similar food items, the weight and frequency at which they are consumed varies.

Banana prawns appear to consume greater numbers of food items than tiger prawns, but at smaller sizes. Based on this observation, the individual weight of food items for tiger prawns were used as a maximum boundary weight for those same food items consumed by banana prawns. In other words, the weight of a particular food item in a banana prawn foregut had to weigh less then that food item in a tiger prawns foregut. With the boundary in place, estimates of food item weights could be made using the weights of those items found singularly within foreguts, few though they were.

Bivalves were the first to be assigned an estimated weight. It is here that further calculations require a lot of guesswork and common sense. The bivalve weight value was altered according to how well the value fit the rest of the data. For instance, a polychaete indicated as the major item in a particular stomach would likely weigh more then the bivalve in that stomach. If, using the assigned bivalve weight and the total gut content weight, the bivalve weighed more then the polychaete, then the assigned value would have to be altered. This value is altered continuously in this way until it fits, as close as possible, most of the data.

Once the best fit for bivalve weight is calculated, the weights of other food items found in foreguts alongside bivalves is recorded and averaged since few, if any, were found singularly. These averaged weights are then altered in the same way as for the bivalves to obtain a value that best fits the data. When altering values, guess work and common sense dictate how they are altered. For example, polychaetes are indicated in the data to be the major food item in most foreguts and thus, common sense would say they weight, on average, more then other food items. Fish scales, on the other hand, would weigh less then other food items since they are found frequently more then five times in a single foregut and up to 101 times. Amphipods, algae and stomatopods were found so infrequently in foreguts, even combined with other food items, that weights could not be calculated based on other food item weights, thus estimated values were assigned.

Many functional groups appeared to be recorded as present or absent in foreguts rather than actual counts of individuals and as such, may be underestimated on a whole. These functional groups included ophiuroids, echinoderms (grouped under ophiuroids), polychaetes, stomatopods, and crustaceans. In the 1987 Wassenberg and Hill paper (Natural diet of Tiger Prawns) it was stated that fragmented Crustacea within a foregut, and the absence of ophiuroid basal discs (used to count individuals), meant these food items were likely to be underestimated. Similar problems with identifying individuals consumed by Banana prawns may have led to the presence/absence recordings of this study. The total average weight of individual prey items (each corresponding to a functional group in the Weipa Ecopath model) were produced by multiplying individual weights by their frequency of occurrence within all foreguts studied. Total average weight was then divided by the total weight of all prey functional groups combined to determine the proportion value for the Ecopath model. Weights were already in wet weight so no conversion was necessary here. The accuracy and precision of the resulting estimates of proportion of total biomass consumed is limited by cases of presence/absence data, by possible underestimations of frequency of occurrence of some food items, and by my assumptions and guestimations of food item sizes. Nevertheless, the resulting estimated diet for adult banana prawns should be the best that is currently possible without further site-specific field studies.

Juvenile banana prawn diet

Round recorded diets of juvenile banana prawns in a subtropical estuary along the Logan River, Moreton Bay of South East Queensland. Prawns were collected from mangroves (Avicennia marina) and adjacent creek habitats (latitude 27˚42’S, longitude 153˚15’E) on the spring tide during February to March 1998. The juvenile stage, as described for the Albatross Bay Ecopath model is defined (as 0-4 months) such that diets from both mangrove and creek sites should be representative of ‘Juvenile banana prawn diet’ and are therefore combined for the model. The proportion wet weight values used in the Ecopath model were estimated by dividing the combined mangrove and creek percent volume for each food item by the sum of all food item percent volumes. Here percent volume was taken as the best available proxy for wet weight.

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Fishes of the Albatross Bay area

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Introduction

The fish fauna of Albatross Bay can be divided into pelagic fish groups and demersal fish groups. The demersal fish fauna of the Gulf of Carpentaria, which includes the Albatross Bay area, has been studied extensively almost since the inception of the Northern Prawn Fishery over 40 years ago. The diversity and high standing biomass of this fish fauna is typical of tropical fish assemblages; well over 360 species of teleosts and elasmobranch species are found there. The fish assemblages differ markedly between Albatross Bay and the adjoining Embley River system, and we have thus treated these two assemblages as separate entities.

The majority of offshore fish surveys in the region have been undertaken using prawn or fish trawls with the specific aim to describe the composition and biomass of trawl bycatch (Blaber *et al*. 1990, 1994, 1995; Stobutzki et al. 2001) and potential prawn predators (Brewer *et al*. 1991). Catches from such surveys can be considered representative of the fish fauna in the region which are dominated by small species representing the families Carangidae (29 spp.), Apogonidae (24 spp.), Scorpaenidae (17 spp.), Leiognathidae and Platycephalidae (13 spp.) (Griffiths et al. 2004). In Australia, the majority of demersal fishes caught by such trawls are of little commercial importance and mostly discarded.

The inshore and estuarine fish surveys of the Embley River were undertaken mainly using gillnets, seine nets and beam trawls with the purpose of both describing the assemblage (Blaber et al. 1989, 1990b) and investigating prawn predation by fish (Salini et al. 1990). This assemblage comprises 197 species, mainly represented by seven taxa: Ariidae, Carcharhinidae, Carangidae, Centropomidae, Haemulidae, Mugilidae and Polynemidae. The most important predators of prawns in terms of biomass are the Queenfish, *Scomberoides commersonnianus* and the Barramundi, *Lates calcarifer*.

The pelagic fish component of the Gulf of Carpentaria has received comparatively little attention, due mainly to the low commercial value of species in the region. Some limited information is available for pelagic fish in northern Australia from early exploratory scientific surveys on the FV *Rachel* (Lyle and Timms, 1984), FRV *Soela* (Okera and Gunn, 1986), aerial tuna surveys (Lyle and Read, 1985) and also Taiwanese gillnet operations that were monitored by scientific observers during 1979-86 (Stevens and Davenport, 1991). Unfortunately, most of the catches were made outside the Gulf of Carpentaria and are not strictly comparable to the Albatross Bay region since demersal fish assemblages have been shown to differ from other regions of the Gulf (Stobutzki et al. 2001). However, some detailed information is being collected currently by CSIRO in a preliminary study on the biology and diets of some ecologically important pelagic fish species in the Weipa region (Griffiths et al. 2004).

The pelagic fishes most common in the Gulf of Carpentaria belong to three families: Scombridae, Carangidae and Istiophoridae. These three families are also characteristic of other tropical pelagic fish assemblages and together comprise over 202 species worldwide (Froese and Pauly, 2005). By far the most dominant species in terms of numbers and biomass that have been caught during trawl surveys in the Albatross Bay region are the small planktivorous pelagic fishes (*Rastrelliger kanagurta*, *Selaroides leptolepis*, *Decapturus* sp.), whilst gillneting and line fishing show the medium piscivorous fishes (*Thunnus tonggol*, *Scomberomorus commerson* and *S. semifasciatus*) to be abundant.

Functional groups and Parameter Estimation

The model parameters for fish functional groups were estimated in a number of ways depending on the group in question. For example, biomass for pelagic and demersal fish had to be calculated differently due to variations in sampling gear. Owing to the high diversity of fishes in the system we also had to estimate biological parameters in a number of ways depending on the animal and data available.

We first built a catalogue of fishes that were documented to be present in the region by collating all existing survey and commercial catch data, which were held mainly by CSIRO and the Queensland Fisheries Service (QFS). Additional information on pelagic fishes was obtained through QFS from observers on the N9 gillnet fishery and by anecdotal information from commercial and recreational fishers in the region.

To assign each species to a specific functional group, we categorised each species in relation to:

- Geographic distribution (offshore or estuary)
- Vertical distribution (benthic, demersal, benthopelagic or pelagic)
- Taxonomic group (elasmobranch or teleost)
- Feeding guild (detritivore, planktivore, insectivore, piscivore, invertebrate eater, scavenger)
- Size (small, medium, large)

In order to develop functional groups for fishes we initially placed most emphasis on trophic similarity of species. However, we found that since some ecologically related species have very different life history strategies (e.g. elasmobranchs vs. teleosts) the P/B and Q/B estimates for each functional group were unrealistic since they were averaged over a wide range of values. As a result, we disaggregated some functional groups. This slightly increased the number of functional groups, but resulted in a far more realistic representation of the fish assemblage. The final list of functional groups is shown in Table 28.

Table 28: Functional groups, biomass (t·km^{-2}), production rate (P/B) and consumption ratio (Q/B) used for the fish component of the Weipa Ecopath model

Functional Group	Biomass	P/B	Q/B
Large pelagic piscivores	0.000057	0.5000	7.7667
Medium pelagic piscivores	0.0125	0.5771	12.3067
Small pelagic piscivores	0.000053	0.8313	14.4000
Large elasmo benthic piscivores	0.0310	0.1225	2.5750
Large teleost benthic piscivores	0.0310	0.5660	6.4600
Small benthic piscivores	0.0600	1.0420	9.8200
Large elasmo benthopelagic piscivores	0.0600	0.4235	4.2765
Large Teleost benthopelagic piscivores	0.00052	0.4508	10.2154
Small benthopelagic piscivores	0.0600	0.8680	9.7400
Large benthopelagic invertebrate feeders	0.0020	0.5467	6.0000
Small benthopelagic invertebrate feeders	1.3200	1.4365	12.4154
Large elasmo benthic invertebrate feeders	0.0800	0.3200	5.8923
Large teleost benthic invertebrate feeders	0.0790	0.5767	6.2833
Small benthic invertebrate feeders	0.5250	1.1814	9.4429
Offshore polychaete feeders	0.1600	1.4500	12.1000
Mollusc feeders	0.1540	0.5150	6.2000
Large pelagic planktivores	0.1120	1.8233	16.1500
Small pelagic planktivores	0.3150	1.8240	16.8300
Scavengers	0.0010	0.4500	6.1000
Estuary large elasmo benthopelagic piscivorous and prawn feeders	5.2300	0.3544	4.4556
Estuary large teleost benthopelagic piscivorous and prawn feeders	5.2300	0.4392	8.3917

Functional Group	Biomass	P/B	Q/B
Estuary large benthic piscivorous and prawn feeders	8.2040	0.3700	4.0667
Estuary large benthopelagic invertebrate feeders	1.2150	0.5063	5.3750
Estuary large benthic invertebrate feeders (mainly rays)	40.3790	0.2733	6.8714
Estuary polychaete feeders	4.7220	1.0433	9.4333
Estuary small benthic invertebrate feeders	1.9280	1.2767	11.1000
Estuary planktivores	1.4180	2.3260	16.4200
Estuary detritivores	5.6640	1.1750	19.3000
Estuary benthic herbivores	0.1280	1.8800	45.7500
Estuary insectivores	0.4080	0.6900	9.5000
Estuary pelagic herbivores	0.9650	1.0833	36.8333
Marine benthic herbivores	0.0251	1.5100	35.1667

Biomass estimates

Due to the gear used to sample the fish fauna, we used different methods to estimate the biomass for demersal and pelagic fishes.

Pelagic fishes

In contrast to many other ecosystems modelled using Ecopath (e.g. Kitchell et al. 2002; Godinot & Allain, 2003; Olson & Watters, 2003), the vast majority of pelagic fishes in northern Australia are not fished commercially and have not been targeted during scientific surveys using appropriate gear such as gillnet or longline. As a result there are no commercial landings or CPUE in the region so we have very little idea of the pelagic fish biomass in Albatross Bay. We were fortunate to opportunistically collect some preliminary data on pelagic fish composition and catch rates in the region onboard a commercial gillnet vessel in 2005. We were also able to access other limited scientific observer data collected on similar vessels in the region. Unfortunately, as is the case with gillnet data, it is difficult to convert catch rates to fish densities or biomass, since the effective fishing area of the net is not known. To overcome this problem we developed a model to estimate the density (and therefore biomass) of scombrids and istiophorids using a number of simple assumptions. Using our model we estimated biomasses as 0.000057 t km^{-2} for large pelagic piscivores, 0.012 t km^{-2} for medium pelagic piscivores, 0.000053 t km^{-2} for small pelagic piscivores, and 0.00052 t km^{-2} for large teleost benthopelagic piscivores.

Demersal fishes

Biomass estimates for demersal fishes were readily available for each species from a number of comprehensive surveys conducted previously in the Weipa region (Blaber et al. 1990), but data from adjacent regions of the Gulf were used if site-specific data were unavailable. We calculated mean catch per trawl (W_i), expressed as kg h^{-1}, using the equation:

$$W_i = \frac{1}{n} \sum_{j=1}^{n} \frac{C_{ij}}{t_j}$$

where C_{ij} = catch (in kg) of Species i in the jth trawl, n = number of trawls, and t_j = duration of jth trawl as a proportion of 1 h.

Biomass (B) expressed as kg ha^{-1} and later converted to t km^{-2}, for each species was calculated as:

$$B_i = \frac{W_i}{Aq_i}$$

where A = the area swept by the trawl in 1 h, and q_i = the catchability of Species i. Catchability (q_i) values were assigned to different species depending on their size and morphology as: 0.3 for small (<225 mm), 0.47 for larger (>225 mm) species and 1.0 for large (>1000 mm) slow-moving species such as rays. See Blaber et al. (1990) for further details. We simply summed biomass estimates for all species to give a total biomass for each functional group.

We were able to derive reliable biomass estimates for most species in 26 functional groups. Only three functional groups, large, medium and small pelagic piscivores, were unable to be estimated using this method. The total estimate of biomass for each functional group is given in Table 28.

Production rates

Owing to the high diversity of the Albatross Bay fish assemblage and their low commercial value in Australia, little biological information is available for the majority of species. Maximum recorded length was often the only biological parameter available for most species and so we resorted to using the simplest empirical equations. Where sample sizes were sufficient in scientific surveys, we assumed the largest recorded fish of each species was L_∞ and used the empirical equation of Pauly (1980) to estimate natural mortality (M). Since the vast majority of species in the region are not fished commercially or recreationally, we assumed that M equals total mortality (Z). We resisted the use of biological parameters from other systems outside Australia since we felt the Albatross Bay system functioned very differently to what has been documented elsewhere.

For species having detailed biological information we used M or Z estimates provided in published studies from the region. Where only growth parameters were available we estimated M as

$$M = 1.60K \text{ (Jensen, 1996)}$$

where K is the von Bertalanffy growth parameter. For some elasmobranch species where maximum age was known, we calculated M by assuming 1% of the population will attain maximum age, which can be represented as:

$$M = -\ln(0.01)/\omega \text{ (Hoenig, 1983),}$$

where ω is longevity in years. For species we knew, or suspected, were fished either as a target or caught incidentally in reasonable numbers as bycatch but fishing mortality (F) was not available, it was assumed that the population would be, at most, fished at MSY. A proxy of fishing mortality at MSY can be assumed to be $F = 0.8(M)$ (Gabriel & Mace, 1999) or $Z = 1.8(M)$.

We assumed there was no immigration or emigration for any species, so that all mortality and prey consumption occurred within the system. An exception was the pelagic fish fauna, which are generally transients in Albatross Bay. For pelagic fishes that are taken commercially only within the system we estimated fishing mortality in relation to the time we felt they were available to be fished in Albatross Bay. For example, if a species is available year round $F = 0.8(M)$; six months $F = 6/12*(0.8(M))$, 1 month $F = 1/12*(0.8(M))$. Such an approach is relevant for Spanish mackerel (*Scomberomorus commerson*) and longtail tuna (*Thunnus tonggol*) since they are generally abundant during the “dry” season. Using the same approach we estimated fishing mortality of species only being captured outside the system in relation to the time they were thought to spend outside the system.

For each functional group we found great variance in the estimated P/B values. Although each species in each functional group was similar in its trophic ecology, their life history strategies were often very different. We incurred this problem with functional groups containing both teleosts and elasmobranchs, which we solved by disaggregating these groups. Where large variance was still evident we excluded outlying values and any values we did not have confidence in based on the quality of biological parameters or the mortality estimation method. We then took the average of the remaining values to obtain an overall value for the functional group.

Average P/B values for each functional group are given in Table 28.

Consumption rates

An estimate of Q/B was made for each species by using the empirical equation of Palomares and Pauly (1998**)**:

$$\log Q/B = 7.964 - 0.204\log W_{\infty} - 1.965T' + 0.083A + 0.532h + 0.398d$$

where W_{∞} is weight (in grams) at age infinity, annual mean water temperature T'= 1000/(°C+273), A is the aspect ratio of the caudal fin = h2/s, h=1 and d=0 for herbivores, h=0 and d=1 for detritivores, and h=0 and d=0 for carnivores.

For species having little biological data, we used maximum length recorded in surveys (assumed L_{∞}) to estimate W_{∞} using a length-weight equation. To provide an overall Q/B value for each functional group we disregarded outlying values or those we had little confidence in. We then took the average of the remaining values. Average Q/B values for each functional group are shown in Table 28.

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Fish diet compositions in the Albatross Bay area

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We obtained quantitative dietary information for 30,010 fish from the Albatross Bay region and the adjoining Embley estuary, which were caught by trawl (Blaber et al. 1994), gillnet, or seine (Salini et al. 1990), and in the case of large pelagic fish, rod and line, longline, and gillnet (Griffiths et al. 2004 and unpublished data). All dietary data, except those for pelagic fish (Griffiths et al. 1994), were recorded as dry weight and were converted to wet weight using a conversion equation specific to each prey type. Where conversion factors were not available for a single prey species, mean conversion factors from that species group were used. The final diet composition matrix is presented in Appendix B.

Diet Records Formatting and Tables Construction

All records that were assigned as empty were removed from the records table. For each of the remaining records, the predator and prey species were each assigned into an Ecopath Functional Group (EFG; numbered from 1 to 99). Unidentified teleosts and invertebrates were assigned to temporary placeholder functional groups (100 and 101) for re-allocation.

Two tables were constructed, containing a list of (1) predator name and functional group and (2) prey name and functional group. As a number of the predator species (54 species) would naturally be assigned to two functional groups because they occur in both inshore and offshore habitats at different life stages, this table had to be split into two tables during this process (inshore, EFG: 28-40, and offshore, EFG: 10-27) to enable accurate aggregations of species and allocation of diets. The dietary data records were accordingly split and assigned into inshore or offshore tables on the basis of the location of the dietary surveys.

Calculation of Diet Proportions into Matrix

The calculation of proportions of prey weights for each prey functional group within each predator functional group was carried separately on four inshore and offshore datasets:

(1) All data
(2) Data subset with abiotics removed
(3) Data subset with abiotics and unidentified teleost and invertebrate EFGs removed
(4) Data subset with abiotics removed and unidentified teleost and invertebrate EFGs re-assigned into all other teleost and invertebrate EFGs on a proportionate basis.

The procedure for proportion calculation on the first three data sets follows;

Prey weights were summed for each prey functional group with regards to each functional group serving as a predator. This was calculated for both of the inshore and offshore tables separately and then both tables were combined by summing the prey weights for identical functional groups. The proportion of each prey functional group consumed by a predator functional group was calculated by dividing each of the weights of the prey functional group over the total prey weight consumed by the predator group.

For the fourth data set, two slightly different approaches were taken.

Method 1:

From the data subset with abiotics removed (2), all unidentified teleosts and unidentified invertebrate prey weights were summed into functional groups 100 and 101 for both of the inshore and offshore tables.

The summed weight for the unidentified teleost functional group (EFG 100) was then proportionally assigned to the teleost prey functional groups within each of the predator functional groups (EFG 10-40). Likewise, the summed weight for the unidentified invertebrate functional group (EFG 101) was proportionally assigned to the invertebrate prey functional groups within each of the predator functional groups.

Once these proportionally assigned weights were added to the weights in each of the prey functional groups consumed by each predator functional group, both inshore and offshore data were combined and summed. Then the proportion of each prey functional group consumed by a predator functional group was calculated by dividing each of the weights of the prey functional group over the total prey weight consumed by the predator group.

Method 2:

The procedure of Method 2 followed that of Method 1 except that when the unidentified teleost and invertebrate prey weights were summed into the Ecopath Functional Groups 100 and 101, they were then proportionally assigned into only the prey functional groups within predator functional groups that contained records of unidentified teleost and invertebrate prey records.

Notes on data inaccuracies

In Method 1, if a predator functional group that contains records of unidentified teleost or unidentified invertebrate prey items but no records of identified teleost or invertebrate prey items then this functional group would not be reassigned any portion of the unidentified teleost or invertebrate prey weight. Instead, the unidentified teleost or invertebrate prey weight would be proportionally reassigned to all other functional groups with identified teleost or invertebrate prey items. In Method 2, these prey weights are not included in the reassigning of the unidentified teleost or invertebrate prey weights to prey functional group within predator functional groups. Rather, the proportions of unidentified teleost or invertebrate prey weights are calculated as if there were no unidentified teleost or invertebrate prey weights for those predator Ecopath Functional Groups.

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Seabirds

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Seabirds of the eastern Gulf of Carpentaria are comprised mostly of terns, boobies, and frigate birds in terms of both biomass and numbers. Densities of each group were estimated from quantitative surveys from the RV *Southern Surveyor* conducted by T.A. Okey (unpublished data) during February-March 2005. Bird density estimates were converted to biomass estimates using average bird weights (http://www.faunarescue.org.au/waterbirds.html) (Table 29).

Table 29: Seabird biomass estimates for the Albatross Bay area

Species	***Mean weight (kg)***	***Biomass (kg·km^{-2})***
Crested terns	0.35	0.34
Common terns	0.12	0.36
Brown Booby	1.10	2.02
Lesser Frigate bird	0.875	0.05
Total biomass		2.77

P/B estimates

Crested terns

Dunlop (1985) gives Z = 0.06 for adults in Western Australia and Crawford et al (2002) found Z = 0.05 for adults in the S African colonies. Underhill et al. (1999) estimated Z = 0.48 for one-year olds, Z = 0.23 for 2-yr olds and Z = 0.2 for 3-yr olds. Adults represent more than 80% of the population (Crawford et al 2002) and so the mean overall mortality becomes Z = 0.09.

Common terns

Feare and Doherty (2004) found Z = 0.16 for adults of the similar-sized Sooty Tern at colonies in Seychelles.

Brown Boobies

Jones (2002) estimated Z = 0.08 for Hawaiian populations of adults of the similar-sized Masked Booby.

Lesser Frigate bird

No published data available on any Frigate bird spp. I suggest using the values for Masked Boobies in Hawaii. Based on the relative contribution of each species to the seabird community, the overall *P/B* (Z) estimate is approximately 0.09.

Q/B estimates

No direct data could be found on consumption rates of each group, but Nagy (1987) provides an estimate for seabirds based on body weight and an assumption of 80% water content of aquatic prey (Table 30). The estimated annual Q/B is the ratio of the extrapolated annual consumption of an individual bird to its average weight. The overall consumption is 93.35 kg·km^{2}·year^{-1} and makes overall Q/B = 48.9 year^{-1}.

Table 30: Consumption rate estimates for the seabirds of Albatross Bay

Species	**Daily consumption (g·d^{-1})**	**Q/B (year^{-1})**
Crested Tern	45.5	47.5
Common Tern	21.4	65.1
Brown Booby	101.9	33.8
Lesser Frigate bird	87.9	36.7

Diet by functional group

The diet compositions used in the Albatross Bay model for these four bird species are based on diet composition estimates (% numbers) from the trawl grounds of the Great Barrier Reef (Blaber et al 1995) (Table 31).

Table 31: Estimated seabird diet compositions for the Albatross Bay model

Species	***Prey functional group***	***Prey group description***	***Percentage of diet (%)***
Crested Tern	20	Small bentho-pelagic invert feeders	53.4
	23	Small benthic invert feeders	30.7
	27	Small pelagic planktivores	15.9
Common Tern	20	Small bentho-pelagic invert feeders	95.0
	27	Small pelagic planktivores	5.0
Brown Booby	4	Turtles	2.0
	12	Small pelagic piscivores	30.1
	20	Small bentho-pelagic invert feeders	6.8
	23	Small benthic invert feeders	28.3
	27	Small pelagic planktivores	32.7
Lesser Frigate bird	12	Small pelagic piscivores	47.0
	20	Small bentho-pelagic invert feeders	9.3
	23	Small benthic invert feeders	7.7
	27	Small pelagic planktivores	36.0

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Turtles

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Data for turtle numbers in the area are somewhat lacking, but a personal communication with Colin Limpus suggested that the combined populations in the modeled area could be as high as 50,000 individuals. Loggerhead turtles have an average weight of around 80 kg, while green turtles average 15-20 kg. Based on these ranges, a conservative biomass estimate of 0.035 $t{\cdot}km^{-2}$ can be derived for the modelled Albatross Bay area. A P/B ratio of 0.192 $year^{-1}$ and a Q/B ratio of 3.5 $year^{-1}$ were adapted from Vaconcellos (2002), as were diet composition values. Additional information can be found in a James Cook University Honours thesis by E.G. Moodie (1979). More information about turtle abundance, biology, and diets is needed to understand their role and vulnerability to trophic changes in the Albatross Bay ecosystem.

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Sea snakes

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Sea snakes are a top predator in the marine ecosystems of northern Australia, and they might structure these systems strongly when their populations attain undisturbed levels. However, sea snakes are particularly vulnerable to prawn trawling and reductions in their populations might have broad ramifications for these ecosystems. The strength of their ecological role has been difficult to assess due to a lack of undisturbed ecosystems in tropical Australia. There are 32 species of sea snakes in northern Australia, but only 13 species are regularly caught in prawn trawls (Milton 2001). Of these species, three species (*Hydrophis elegans, Disteira major, Lapemis hardwicki*) make up about 70% of the sea snakes caught by trawlers in the Northern Prawn Fishery

Biomass

A biomass estimate of 0.0027 $t{\cdot}km^{-2}$ and density estimate of sea snake individuals ($5{\cdot}km^{-2}$) in the Weipa area was derived from catch rates in prawn trawls (Wassenberg et al 1994, Ward 2000, Fry et al 2001), estimates of swept area by each trawl, a mean weight of 0.538 kg, and a catchability of 0.47 (Blaber et al 1990).

Production/Biomass estimates

Table 32 presents derivations of sea snake P/B estimates for the Albatross Bay model. Ward (2001) provided VBG parameters for two of the most common species of sea snake. Using these values, the Beverton-Holt equation was applied to the length data in Fry et al (2001). The Palomares-Pauly equation for natural mortality (M) was also employed, taking 27° C as the mean temperature at Weipa and assuming negligible fishing mortality. However, as most species are less productive than *Lapemis* *hardwicki* or even *H. elegans*, the overall sea snake P/B estimate are likely to be lower than that estimated by the Palomares-Pauly equation.

Table 32: Sea snake population parameters and two derivations of P/B

Species	***L_∞ (cm)***	***K***	***Bev.-Holt-Fry Z (P/B) (year^{-1})***	***Palomares-Pauly P/B (year^{-1})***
Lapemis hardwickii	112	0.41	0.25	0.70
Hydrophis elegans	221	0.17	0.19	0.32

A version of the Beverton-Holt equation that does not use growth parameters and scales the ratio maximum size minus mean size/mean size minus minimum size was also applied to sea snakes in the NPF to get an index of total mortality (Z) (Milton 2001). This produced a mean P/B (Z) value for all species weighted for their relative abundance in Weipa (0.99 year^{-1}). Finally, an equation for estimating Z by Hoenig (1983) relates mortality to longevity. Ward's (2001) figures of longevity (~10 years) produces a Z (P/B) estimate of 0.46 year^{-1}.

Q/B estimates

Diet data in Fry et al (2001) was used to estimate of mean meal size of undigested prey (14.5 g) and an inter-meal period of 1.6 d (1/% with fresh food) to get a consumption·snake·year^{-1} (3.3 kg·snake·year^{-1}). If density is 5·km^2 and biomass is 2·7kg·km^2 then Q/B = 16.5/2.7 = 6.1

Diet composition

Table 33 presents a generalized sea snake diet composition (across all sea snake species) estimated from the data in Fry et al. (2001). Values are based on composition by wet weight.

Table 33: Estimated sea snake diet composition

Prey functional group	***Group #***	***Proportion***
Small bentho-pelagic invert feeders	20	0.179
Small benthic piscivores	15	0.400
Small benthic invert feeders	23	0.394
Small pelagic piscivores	12	0.013

Note: Proportions expressed in wet weight.

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Estuarine crocodile

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Introduction

This functional group consists of only one species – the estuarine crocodile – a relatively abundant and important apex predator in the estuaries of the Weipa region. This is the largest living crocodilian species with a confirmed measurement, and in fact the world's largest living reptile in terms of mass. Adult males can reach sizes of up to 6 or 7 metres, the largest confirmed individual being 6.3 metres. They have a high tolerance for salinity, but are also present in freshwater rivers, billabongs and swamps. Movement between different habitats occurs between the dry and wet season, and as a result of social status; juveniles are raised in freshwater areas, but eventually sub-adult crocodiles are usually forced out of these areas (used for breeding by dominant, territorial adults) into more marginal and saline areas (Britton, 2002).

Estuarine crocodiles take a wide variety of prey, although juveniles are restricted to smaller items such as insects, amphibians, crustaceans, small reptiles and fish (Taylor, 1979). The larger the animal grows, the greater the variety of items that it includes in the diet, although relatively small prey still make up the majority of the diet even in large adults. Prey items include crustaceans (e.g. mud crabs) and vertebrates (e.g. turtles, goannas, snakes, shore and wading birds). Large adults occasionally take much larger prey including buffalo and domestic livestock and wild boar, monkeys. Possums are a noted feature of the diet in the Weipa area.

Following their total protection in the 1980s numbers of estuarine crocodiles has increased and it is estimated that there are at least 100,000 to 150,000 crocodiles in the northern three states of Australia.

Their importance in this study relates to their role as fish predators, consuming a wide range of fish species in the estuaries of the Weipa region.

Biomass estimates

Biomass estimates for the Weipa region are based on counts (spotlight surveys) undertaken by the QNPWS on a regular basis since 1997 (Mark Read, pers. comm.) in the Mission, Hey, Embley and Andoom rivers and estuaries. For the purposes of this study, the counts for October 1997 were used. Counts included the length of the crocodiles and their exact position (GPS). Based on repeat survey trials it is estimated that the surveys sampled not less than 75% of the population. Missing length values were obtained by using the mean length (180 cm) of all animals counted. The weight of animals was obtained by constructing a total length to wet weight relationship using morphometric data from Webb & Messel (1978). The length – weight curve is shown in Figure 56. The total biomass of counted animals was 1338.438 kg and scaling this up for an additional 25% of animals not counted gives an overall biomass of 1784.584 kg. Dividing this weight by the overall area of the Albatross Bay model (5,788 km^2) gives a biomass estimate of 0.0003083248 $t{\cdot}km^{-2}$.

The specified take (bycatch) of crocodiles by the inshore gillnet fishery exceeds the estimated production considerably, and so biomass was left to be estimated by the Ecopath routine by specifying an ecotrophic efficiency of 0.8. The calculated biomass estimate was 0.0033 $t{\cdot}km^{-2}$, over an order of magnitude larger than biomass estimated above. If production rates (P/B) are reasonably correct, and if crocodiles have a stable population, we should expect that there is either an overestimation of the inshore gillnet fishery catch in the present model or an underestimation of crocodile biomass.

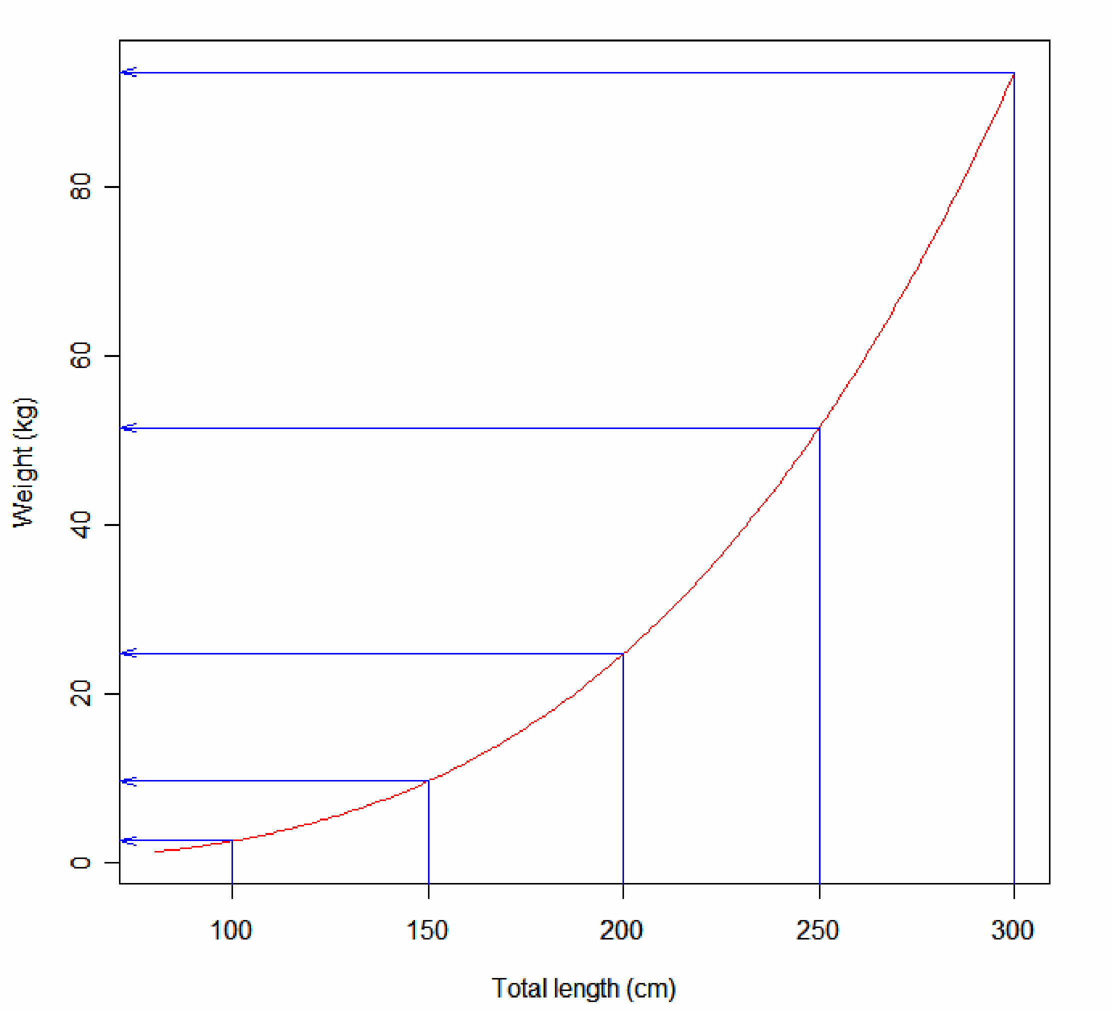

Figure 56. Total length – wet weight relationship for *Crocodylus porosus*

P/B

The production of American Alligator, *Crocodylus acutus,* in a Florida Bay food web model (0.000257579 g C·m^{-2}·year^{-1}) is estimated as consumption (Day et al. 1990) minus egestion (80% assimilation efficiency) minus respiration (Altman and Dittmer 1964, Pandian and Vernberg 1987), and the biomass there is given as 0.000809779 g C·m^{-2} in Jorgenson et al. (1991), resulting in an estimated P/B of 0.31808526 year^{-1}. The Florida Bay model parameters are listed at http://cbl.umces.edu/~atlss/FBay517.html.

Q/B

An estimate of 4% of body weight per week, derived from data in Webb et al. (1978, 1991), resulted in a P/B of 2.08 year^{-1}. However, a Q/B of 5 year^{-1} can be found in Pandian and Vernberg (1987) and Smith (1976). An egestion to consumption rate of 0.2 is from Pough (1973).

Diet composition in proportion of biomass

Almost no data are available on the quantitative diet composition of estuarine crocodiles with the exception of Taylor (1979). Unfortunately this only covers length groups up to 1.2 m. The scant information indicates that the best conservative option is to apportion the diet as 50% fish, spread across all the fish functional groups in the estuaries.

The current crocodile diet in the Albatross Bay model is based qualitatively on the following list of prey items for American Alligator, *Crocodylus acutus* at http://cbl.umces.edu/~atlss/cyp423.html (based on e.g., Delany and Abercrombie 1985, Peterson 1991): Crayfish, Apple Snails, Freshwater Prawns, Aquatic Invertebrates, Terrestrial Invertebrates, Small Herbivorous and Omnivorous Fish, Small Predatory Fish, Large Fish, Turtles, Lizards, Snakes, Salamanders, Large Frogs, Medium Frogs, Small Frogs, Tadpoles, Galliformes, Egrets, Other Herons, Ibis, Mice and Rats, and Rabbits. The following dietary breakdown was derived from Pritchard (1978), Davis and Ogden (1994), and Kushlan (1980): fish (76%), invertebrates (22%), birds (1%), and turtles (1%).

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Mammals Bottlenose dolphin (Tursiops truncatus)

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The number of bottlenose dolphins in the modelled area is highly uncertain, but Colin Limpus was willing to make a rough estimate of 200. Given an average weight of 175 kg per individual, their biomass would be 35,000 kg, or 35 tonnes. This translates to a biomass of 0.00605 $t \cdot km^{-2}$ in the modelled area. A more conservative estimate would be 100 individuals, leading to the value of

0.00303 t·km^{-2} used in the model. More research would be needed to accurately estimate abundance in the area.

A production/biomass ratio of 0.1 year^{-1} was taken from the West Florida Shelf model as described by Vasconcellos (2002), which drew on information from Browder (1993) and Matkin & Hobbs (1999). This value was also published in Okey (2004)

Browder (1993) estimated the consumption/biomass ratio of 41.07 year^{-1} for piscivorous and planktivorous mammals use in the Albatross Bay model. Diet composition for this species was adapted from Vasconcellos (2002).

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Dugong (Dugong dugong)

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Vasconcellos (2002) reports that the annual birth and death rates for manatee are approximately equal at 10%, indicating a P/B ratio of 0.1 year^{-1}. Professor Helene Marsh (James Cook University, personal communication) suggested that it would not be useful to use manatee data in estimating a P/B ratio for dugongs, as they are smaller, longer lived, and slower to breed than manatee. A P/B ratio of 0.08 year^{-1} was specified in the model.

A Q/B ratio for dugongs was derived from Vasconcellos (2002) who reported a daily ration of 10% of body weight in manatee, leading to a Q/B estimate of 36.5 year^{-1}. Dugongs are reported to feed on seagrass exclusively (Department of Environment and Heritage, 2005)

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Fishery Parameter Inputs

Ecopath models require the definition of fleets or gear types that are present in the ecosystem and the specification of landings and discards associated with those gear types (in $t{\cdot}km^{-2}{\cdot}year^{-1}$). This enables a number of static and dynamic analyses to be conducted, and estimates for the Albatross Bay model are summarized in Table 34 and Table 35. Additional fisheries information enables additional types of analyses. Using various types of historical time series information to fit model predictions to observe stock and ecosystem changes should also be attempted to refine and verify model structure and behaviour. The time series information gathered for this project is presented in Table 36. The sections that follow describe the derivation of fisheries estimates.

Table 34: Fisheries catches by fleet for each functional group in the Albatross Bay model. Values are in t/km^2/year

Group Name	**Fishery**								
	Banana trawl	**Tiger trawl**	**Trolling (Spanish mackerel)**	**Offshore Gillnet (Mackerel / Shark)**	**Inshore Gillnet (Shark / Barramundi)**	**Pot (Mud Crab)**	**Recreational**	**Aboriginal**	**Total**
Dugongs								0.013	0.013
Turtles								0.005	0.005
Medium pelagic piscivores			0.002	9.880E-06	0.001		3.470E-06	2.050E-04	0.003
Small pelagic piscivores							7.590E-09		
Sawfishes				6.260E-09					
Large teleost benthic piscivores			3.710E-05		1.930E-06		3.510E-06		
Small benthic piscivores							1.340E-08	5.460E-05	
Large elasmo benthopelagic piscivores			4.260E-05	1.320E-05	7.250E-04		6.120E-07		0.001
Large teleost benthopelagic piscivores			2.160E-05	1.790E-08	7.690E-07		6.050E-06	0.003	0.003
Small benthopelagic piscivores			2.040E-06		1.890E-06		5.210E-06	8.350E-06	
Large benthopelagic invert feeders			6.560E-06	2.970E-08	4.210E-06		3.040E-07		
Small benthopelagic invert feeders			5.880E-07	4.380E-08	2.100E-06		1.510E-07		
Large teleost benth invert feeders			8.410E-06				1.570E-06	5.310E-04	0.001

Group Name	Fishery								
	Banana trawl	Tiger trawl	Trolling (Spanish mackerel)	Offshore Gillnet (Mackerel / Shark)	Inshore Gillnet (Shark / Barramundi)	Pot (Mud Crab)	Recreational	Aboriginal	Total
Small benthic invert feeders			1.830E-05		1.120E-07		2.440E-06	1.140E-05	
Large pelagic planktivores							1.210E-08		
Small pelagic planktivores							8.870E-08	2.090E-04	
Benthic herbivores							3.380E-08		
Estuary lg teleost benthopelagic pisc/prawn feeder			1.460E-05	1.840E-08	3.450E-04		4.340E-06	0.005	0.005
Estuary large benthic pisc/prawn feeders			3.390E-06		3.410E-07		1.680E-08	6.700E-04	0.001
Estuary large benthopelagic invert feeders			6.210E-06	7.200E-09	1.620E-05		1.530E-06	0.001	0.001
Estuary large benthic invert feeders (Rays)					1.590E-07			2.190E-04	
Estuary small benthic invert feeders							7.790E-07	1.710E-04	
Estuary planktivores								1.250E-05	
Estuary detritivores					3.440E-06			9.820E-04	0.001
Estuary benthic herbivores							5.010E-08		

Group Name	Fishery								
	Banana trawl	**Tiger trawl**	**Trolling (Spanish mackerel)**	**Offshore Gillnet (Mackerel / Shark)**	**Inshore Gillnet (Shark / Barramundi)**	**Pot (Mud Crab)**	**Recreational**	**Aboriginal**	**Total**
Estuary insectivores									
Estuary pelagic herbivores					3.110E-06			7.500E-05	
Squid and cuttlefishes			1.890E-07		2.270E-08				
Banana prawn juvenile								4.980E-06	
Banana prawn subadults								4.270E-05	
Banana prawn adult	0.107								0.107
Tiger prawn adult		0.021							0.021
All other commercial prawns		0.011							0.011
Crayfish								3.520E-04	
The mud crab					5.880E-07	4.830E-04	8.560E-08	1.140E-04	0.001
Sand crab						1.110E-07		2.040E-06	
Other large crabs						1.190E-07		2.550E-06	
Estuarine bivalves								2.980E-05	
Sum	**0.107**	**0.0322**	**0.002**	**2.320E-05**	**2.155E-03**	**4.832E-04**	**3.027E-05**	**0.030**	**0.174**

Table 35: Fisheries discards by fleet for each functional group in the Albatross Bay model. Values are in t·km^{-2}·year^{-1}

Group Name	**Fishery**								
	Banana trawl	**Tiger trawl**	**Trolling (Spanish mackerel)**	**Offshore Gillnet (Mackerel / Shark)**	**Inshore Gillnet (Shark / Barramundi)**	**Pot (Mud Crab)**	**Recreational**	**Aboriginal**	**Total**
Dolphins				3.360E-07					
Crocodiles					1.750E-05				
Sea snakes	2.580E-04	0.001							0.002
Large pelagic piscivores				2.020E-07			1.880E-07		
Medium pelagic piscivores	0.001	0.003		1.760E-05			2.550E-05		0.005
Small pelagic piscivores	8.980E-05	6.300E-06		1.290E-07			9.680E-08		
Sawfishes	0.010	0.010		2.590E-07	2.530E-05				0.021
Large teleost benthic piscivores	3.410E-04	0.018		2.010E-08		2.370E-06	1.230E-05		0.018
Small benthic piscivores	0.003	0.123		8.280E-10			3.670E-08		0.126
Large elasmo benthopelagic piscivores	0.017	0.014		1.160E-06	1.890E-04		3.100E-06		0.031
Large teleost benthopelagic piscivores	0.015	0.035		1.300E-06			1.510E-05		0.049
Small benthopelagic piscivores	0.001	0.071			7.220E-05		6.660E-06		0.072
Large benthopelagic invert feeders	2.280E-05	0.003					4.910E-07		0.003
Small benthopelagic invert feeders	0.018	0.823		4.110E-08		1.170E-08	1.060E-06		0.841
Large elasmo benthic invert feeders	0.005	0.005		2.070E-09	2.270E-04	2.330E-07	3.280E-06		0.010
Large teleost benth	5.710E-05	0.017		4.630E-04			4.290E-07		0.017

Group Name	**Fishery**								
	Banana trawl	**Tiger trawl**	**Trolling (Spanish mackerel)**	**Offshore Gillnet (Mackerel / Shark)**	**Inshore Gillnet (Shark / Barramundi)**	**Pot (Mud Crab)**	**Recreational**	**Aboriginal**	**Total**
invert feeders									
Small benthic invert feeders	0.092	0.346					7.580E-06		0.438
Polychaete feeders	8.580E-04								0.001
Large pelagic planktivores	0.006	0.006		1.980E-08			4.550E-07		0.012
Small pelagic planktivores	0.027	0.132					1.670E-07		0.159
Benthic herbivores	2.890E-04				9.740E-07		2.050E-07		
Scavengers	1.180E-04						1.290E-08		
Estuary lg elasmo benthopelagic pisc/prawn feeders						4.660E-07	9.380E-07		
Estuary lg teleost benthopelagic pisc/prawn feeder	0.138			3.640E-07	1.430E-04	6.560E-07	3.900E-05		0.138
Estuary large benthic pisc/prawn feeders					1.420E-06	5.830E-06	1.280E-06		
Estuary large benthopelagic invert feeders	3.110E-05				1.280E-05	7.950E-06	1.500E-05		
Estuary polychaete feeders		0.050			1.270E-05				0.050
Estuary small benthic invert feeders	3.680E-04			1.030E-03			4.550E-07		0.001
Estuary planktivores					8.880E-06	2.330E-09			
Estuary detritivores				2.630E-04	8.940E-06		2.140E-08		
Estuary benthic herbivores		4.650E-04					1.740E-07		
Estuary insectivores				0.029			8.740E-09		0.029
Estuary pelagic				0.009					0.009

Group Name	Fishery								
	Banana trawl	Tiger trawl	Trolling (Spanish mackerel)	Offshore Gillnet (Mackerel / Shark)	Inshore Gillnet (Shark / Barramundi)	Pot (Mud Crab)	Recreational	Aboriginal	Total
herbivores									
Octopus	1.930E-04	5.200E-04							0.001
Squid and cuttlefishes	2.190E-04	0.007							0.007
Stomatopods	2.800E-05	0.003							0.003
All other non-commercial prawns	2.000E-06	0.005							0.005
The mud crab					5.840E-06		1.960E-07		
Red mud crab									
Sand crab	7.090E-04	0.018				1.170E-08			0.018
Other large crabs	2.850E-04					1.610E-06			
Large gastropods									
Holothurians	1.500E-06	0.003							0.003
Spatangoids	3.000E-07								
Echinoids	5.200E-06	1.760E-04							
Ophiuroids	6.000E-07	2.940E-05							
Asteroids	1.260E-05	2.700E-04							
Sessile epibenthos	7.170E-05	0.011							0.011
Marine bivalves	4.570E-05	0.007							0.007
Estuarine bivalves									
Marine small crustaceans	7.350E-05	0.008							0.008
estuarine small crustaceans						4.660E-09			
Marine worms		3.300E-06							
Estuarine worms									
Marine small gastropods	1.000E-07	1.090E-04							
Estuarine small gastropods						1.400E-09			

Group Name	**Fishery**								
	Banana trawl	**Tiger trawl**	**Trolling (Spanish mackerel)**	**Offshore Gillnet (Mackerel / Shark)**	**Inshore Gillnet (Shark / Barramundi)**	**Pot (Mud Crab)**	**Recreational**	**Aboriginal**	**Total**
Large jellies	2.750E-05	5.290E-05							
Small jellies	3.900E-06	8.920E-04							0.001
Sum	**0.338**	**1.719**	**0**	**0.040**	**0.001**	**1.915E-05**	**1.337E-04**	**0**	**2.096**

Table 36: Time series information expressed in the '.csv' format used by Ecosim's time series fitting routine.

title	***Banana catch ($t\cdot km^{-2}\cdot year^{-1}$)***	***Banana effort [a]***	***Banana time index [b]***	***Tiger catch ($t\cdot km^{-2}\cdot year^{-1}$)***	***Tiger effort [a]***	***Tiger CPUE***	***LINE boat days [c]***	***N9 boat days [c]***	***N3 boat days [c]***	***POT boat days [c]***	***REC effort multiplier [c]***
pool code[d]	46	1	46	49	2	49	3	4	5	6	7
type[e]	6	3	0	6	3	0	3	3	3	3	3
1986	0.046899	1	2.594	0.017966	1	0.017966	1	1	1	1	1
1987	0.083687	1.583102	3.22	0.00123	0.010685	0.115162	1	1	1	1	1
1988	0.123919	1.809581	4.127	0.0308	0.994614	0.030967	1	1	1	1	1
1989	0.220054	2.192181	3.475	0.053863	2.242686	0.024017	1	1	1	1	1
1990	0.091512	1.789297	4.047	0.03176	1.281827	0.024777	1	1	1	1	1
1991	0.17597	2.094035	3.771	0.007188	0.25113	0.028624	1	1	1	1	1
1992	0.038215	1.752806	3.672	0.011435	0.556697	0.02054	1	1	1	1	1
1993	0.086631	1.205524	2.187	0.008743	0.389077	0.02247	1.17	1	3	1	1
1994	0.03671	1.313201	5.112	0.034986	1.064862	0.032855	1.02	1	9	3	1
1995	0.105456	1.876469	4.761	0.034102	1.198545	0.028453	3.35	1	10	5	1
1996	0.180512	2.011296	4.557	0.023115	1.745842	0.01324	4.04	1	12	10	8
1997	0.120831	1.731924	3.711	0.04269	1.809333	0.023594	2.93	1	18	15	102
1998	0.029497	0.90316	2.465	0.007775	0.358128	0.021711	2.14	1	10	3	191
1999	0.062846	0.831826	1.794	0.00423	0.252518	0.016752	2.51	4	8	3	242
2000	0.006287	0.421354	3.242	0.026504	1.171259	0.022629	1.13	315	6	5	276
2001	0.010918	0.35991	1.456	0.007838	0.432406	0.018127	1.54	625	8	5	250
2002	0.007301	0.214219	1.018	0.000978	0.052748	0.018532	1.72	345	7	1	262
2003	0.000485	0.099646	1	0.000056	0.003907	0.014415	1.3	251	2	1	256

a. Banana and tiger prawn fishery effort time series were boat days standardized to fishing power changes and scaled relative to 1986;
b. The amount of time needed to take 90% of the catch in the Albatross Bay area, scaled relative to 2003;
c. Time series of effort scaled such that the reliable effort data of later years express recent catches properly when applied to hindcasted placeholder values for the 1986-1992 period (see Section 7.2 of this report);
d. Pool code is the biotic functional group number (high numbers) or the fisheries gear type number (low numbers), as appropriate;
e. Type is the data type used by Ecosim: 0 = relative biomass, 3 = fleet/gear effort, 6 = catches.

Prawn catch and effort in the Albatross Bay target region

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Summary

Annual landings (according to companies' returns) of prawns caught in the Northern Prawn Fishery are not separable into region caught. Therefore, annual catch and effort in the Weipa target region were summarised from a "corrected" dataset of daily logbook records. Doing this requires confidence that the logbook records can be accurately attributed to the target region, which is defined by relatively precise spatial boundaries. The raw logbook records are incomplete in temporal coverage, and some are spatially imprecise, especially in 1986-87. In the "corrected" dataset, the original logbook records were augmented by re-sampling, until the annual total catches matched annual total landings provided independently by companies. Where information on locations and hours trawled was unavailable, values were imputed. The resultant corrected dataset can be used with some confidence to attribute catch and effort to the Weipa target region.

Table 37: Annual catch of Prawns, and effort, from the Weipa target area

	Annual catch, tonnes			Banana trawling*		Banana searching*		Tiger trawling	
	Banana	Tiger	Endeav	Days	Hours	Days	Hours	Days	Hours
1986	255	101	28	340	3612	120	2776	1533	17128
1987	458	7	3	397	5646	148	3460	121	1344
1988	731	166	49	606	8166	137	3164	1591	18701
1989	1205	305	211	743	9136	140	3120	3315	38816
1990	510	182	89	573	6077	76	1708	1815	21089
1991	961	39	22	580	9430	60	1009	355	4128
1992	217	66	34	431	7881	139	2464	710	8376

*Banana trawling and searching can only be separated for units of whole days, in the logbook database for 1986-92. Therefore "banana trawling" may include some hours of searching; banana trawling hours may be overestimated and banana searching hours underestimated.

Commercial logbooks

Skippers who fish in the Northern Prawn Fishery have been required to complete daily logbooks of catch and effort, for many years, as one of the conditions of licensing. During 1986-87, about three quarters of vessels provided complete logbook records. By 1988 the compliance for complete logbook returns reached close to 100%.

Location

The location recorded in the logbooks is that of "the shot with the greatest catch for the day", and for the period 1986-1992 the most precise records were for a 6'x6' grid square. In 1986-89 about 90% of logbook days were recorded at a 6'x6' precision.

Targeted species

Because banana prawns are caught predominantly by day and tiger prawns by night, and different gears are used for each, the catch and effort series have been commonly separated into two parts, assumed to be distinct fisheries. For the present purpose, the two fisheries were defined as follows: when the catch of banana prawns was greater than the catch of all other species, or there was zero catch of any species, the day was defined as a *banana prawn* day. Otherwise, the day was defined as a *tiger prawn* day.

Effort

Typically, when banana prawns are the target, a day contains both searching hours and trawling hours, whereas when tiger prawns are the target, there are no searching hours, and all fishing hours are trawling hours. Banana trawling and searching can be separated, in the logbook database for 1986-92, but only for units of whole days.

Catch

The daily catch is recorded in the logbooks as kg in one of four species groups: Tiger, Banana, Endeavour and King. Species are not distinguished in the logbooks.

Commercial landings

A second, and reliable, source of information about the annual catch of each vessel is the company landings returns, provided to AFMA independently from the logbook records.

"Corrected" logbooks

To overcome some deficiencies of the logbook records, namely, the less than 100% return rate prior to about 1988, and the varying precision of daily locations prior to about 1990, a restricted re-sampling algorithm was applied. Catch and effort records were re-sampled without replacement to accumulate a larger so-called augmented dataset which has the following features:

- The locations at coarse precision have been allocated to one of the 6'x6' nautical mile squares within the known set of a fishing ground, with probabilities proportional to the known fished frequencies.
- The annual total catch for tiger and banana prawns in the augmented dataset is close to the annual total according to the landings, and effort (the number of daily records) is expanded by the number of re-sampled records required to achieve the match to the annual landings totals.
- The re-sampled, augmented part of the dataset retains all the attributes of the original logbook record as sampled.

Details of the methods are given in Dichmont et al 2001 Chapter 3: Augmentation and imputation for the logbook records.

Acknowledgments

The catch and effort data are due to fishers of the Northern Prawn Fishery who provided accurate and complete logbook data, and the AFMA logbook program who collate the current data and provide it to CSIRO in a timely manner.

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Estimated area swept by Albatross Bay prawn trawlers

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An estimation of the total area swept by commercial prawn trawl nets in the identified Albatross Bay area from 1986 to 1992 was needed to estimate the total biomass of prawn trawl bycatch by functional group from that area (see Dell et al, Section 7.1.4). The following methodology was used to derive the estimate of swept area.

Area swept was obtained from the swept area rate of each vessel that fished in the Weipa target area multiplied by hours trawled each year and summed for each year. These estimates of area swept are thus larger than the area of sea floor impacted by the trawl. The area impacted by the trawl would be smaller by a factor that depended on the degree of overlap among trawls, that is, the extent of retrawling over the same ground.

Swept area rate was determined separately for the different target fisheries (banana prawn and tiger prawn), based on characteristics of vessels by year in the two fisheries, accounting for changes in nets and engines (Table 38).

Table 38: Estimated area swept (km^2) in the banana and tiger prawn trawl fisheries

Year	***Banana trawling***	***Tiger trawling***
1986	562	2990
1987	809	201
1988	963	2694
1989	1095	5747
1990	777	3023
1991	1122	606
1992	924	1196

Swept area rate

Swept area rate when targeting tiger prawns was obtained from a deterministic engineering model -- the Prawn Trawl Performance Model (PTPM, described in Chapter 2 of Dichmont et al 2003; and Sterling 2005). The PTPM accounts for the impacts of changes in nets, engines, propellers and kort nozzles, on swept area rate, for each vessel each year. These impacts include improvements in technology, and changes due to regulation of engine size or gear size. For example, in mid-year of 1987 one significant management change was the banning of quad rig in favour of double rig.

Swept area rate when targeting banana prawns was approximated by the following equation:

*rate (metres^2/second) = headline length*number of nets*spread ratio * trawl speed*

where the trawl speed = 2.5 knots and the spread ratio = 0.67 if double rig, or 0.75 if quad rig.

Area swept

Total area swept in the Albatross Bay target region, per year, was obtained from the swept area rate multiplied by hours trawled for each vessel when fishing in that area for the given target species. See Bishop this volume (page for “catch and effort”) for details of hours. Note that trawl hours in the banana prawn fishery may be overestimated due to the limitations of the logbook dataset.

Acknowledgements

I thank the fishers of the Northern Prawn Fishery who provided vessel specifications and Dave Sterling for the swept area rate estimates of the historical NPF fleet.

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Relative fishing power in the banana prawn fishery

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An estimation of changes in relative fishing power was necessary for conducting Ecosim simulations to evaluate alternative causative explanations of observed changes. For these simulations, past ecosystem and fishery changes were reconstructed with all available information. Estimations of fishing power changes are critical for this exercise. The Ecosim model is driven by time series of fishery effort that are standardized for fishing power changes. The temporal trajectories of fishing mortality (of both target and bycatch species) are determined by the time series of standardized effort.

Relative fishing power when targeting banana prawns (Table 39) was estimated by a so-called delta model fitted to the commercial catch and effort data. The delta model refers to a pair of statistical models: firstly, a linear model to estimate harvesting power, and secondly, a logistic model to estimate searching power (Vance et al 2001). Fishing power was the product of harvesting and searching power and the model output was an index of relative fishing power 1970-2000. Low and high sensitivity bounds were also produced, to represent uncertainties due to the difficulty of separating abundance trends from vessel efficiency trends. For the present purpose the Vance et al (2001) relative fishing power series was supplemented for 2001-2004 by assuming the annual increments of relative fishing power when targeting tiger prawns, which had been estimated for the tiger prawn stock assessment (NPFAG in 2005). The rationale for this assumption is based on the arguments that a) any gear cuts and engine changes affected banana prawn fishing power to the same extent as they affected tiger prawn fishing power; b) the impact of TED/BRDs was similar, in relative terms, for the catch of banana prawns as for tiger prawns (see Eayrs and Bose 2001); c) any innovations that improved searching for banana prawns in the last five years cannot be accounted for. We suspect there might be some but are not able to specify details or to estimate any impacts at present.

Table 39: Index of relative fishing power when targeting banana prawns, & low and high sensitivity

Year	***Index***	***Low***	***High***	***Year***	***Index***	***Low***	***High***
1970	0.32	0.58	0.32	1988	2.88	1.93	4.22
1971	0.35	0.60	0.35	1989	2.89	1.95	4.21
1972	0.38	0.61	0.37	1990	2.95	1.90	4.22
1973	0.44	0.66	0.44	1991	3.13	1.99	4.85
1974	0.53	0.72	0.52	1992	3.22	2.02	5.06
1975	0.63	0.79	0.62	1993	3.38	2.11	5.32

Year	Index	Low	High	Year	Index	Low	High
1976	0.69	0.81	0.68	1994	3.39	2.11	5.33
1977	0.80	0.87	0.78	1995	3.53	2.20	5.56
1978	0.93	0.93	0.91	1996	3.58	2.23	5.64
1979	1.00	1.00	1.00	1997	3.84	2.35	6.16
1980	1.12	1.08	1.15	1998	3.70	2.26	5.94
1981	1.24	1.15	1.31	1999	3.70	2.27	5.94
1982	1.42	1.26	1.57	2000	3.57	2.19	5.72
1983	1.72	1.43	2.03	2001	3.78	2.31	6.05
1984	2.08	1.61	2.65	2002	3.69	2.26	5.92
1985	2.31	1.69	3.11	2003	3.69	2.26	5.92
1986	2.57	1.78	3.64	2004	3.70	2.27	5.94
1987	2.72	1.84	3.96				

Source: 1970-2000 Vance et al. 2001; 2001-2004 based on annual increments in relative fishing power for tiger prawns (Dichmont et al 2003).

Acknowledgements

I thank the fishers of the Northern Prawn Fishery who kept and shared accurate and complete logbook data provided the catch, effort, and vessel data. These data were collated and provided by the AFMA logbook program in a timely manner.

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Prawn fishery discard estimates for Albatross Bay

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Abstract

Biomass estimates are described for a wide range of functional groups caught and discarded (mostly dead) as ‘bycatch’ during prawn trawling operations in the Weipa region of the NPF. These estimates were calculated from catch rates collected by either scientific or commercial fishing operations targeting either banana prawns or tiger prawns. They include scientific sampling during 1997 and scientific observers on board commercial vessels in 2004 and 2005. Commercial effort data used in the calculation of biomass estimates were obtained from skippers’ daily logbook records, and adjusted for changes in vessels’ swept area capacity over the years.

Discards from prawn fishing operations

Resource management now encompasses a 'whole of ecosystem' approach and it is no longer acceptable to concentrate solely on the target species of a fishery.

Trawling operations in the Northern Prawn Fishery (NPF) interact with many (> 600) non-target species incidentally captured during the fishing season. This bycatch of the NPF is highly diverse and includes small fish and invertebrates, sea snakes, sea turtles, sharks, rays, sawfish, sponges and other megabenthos (Stobutzki et al. 2001). Bycatch species are discarded from the catch back into the sea and most are either dead or dying (Wassenberg and Hill 1989; Hill and Wassenberg 1990; 2000; Alverson 1997; FAO 2002). Consequently, this group of species represents many functional groups and may have a significant influence on ecosystem dynamics (Table 40).

Biomass estimates

Banana prawn fishery

One of the assumptions of the modelling process is that the data is representative of the 1986 – 1992 period. However, the only suitable bycatch data from the Weipa banana prawn trawl fishery was obtained from CSIRO scientific observers aboard commercial vessels in 2004 and 2005. Consequently this data is likely to under-represent the numbers of large sharks, rays and turtles caught during 1986-1992, due to the use of Trawl/Turtle Exclusion Devices (TED) since 2000 (Brewer et al. 2004). The data came from samples obtained within the model defined region of Weipa and slightly south of the project defined region (up to but not exceeding Lat: 14 degrees 49.21 minutes and Long: 141 degrees 21.08 minutes).

The bycatch data were collected as sub-samples (>10%) of the total catch. The total weight of the bycatch in the net was also weighed before discarding to allow scaling-up for estimates of the total catch of each species from each trawling operation (see details in Heales et al. 2003 a&b). Thus for any given sub-sample from one net, the total bycatch of each species (for both nets in the trawl operation) is:

Wt of species * (Total Bycatch Wt/ Sub-sample Wt) * 2

Here the assumption is that both nets are fishing uniformly and that the bycatch is equally distributed among both nets.

The scaled-up bycatch weights were divided by the trawl time (fractional hours) of each shot to calculate a catch rate (weight per hour fished) for each species within the sample. The catch rates for each species were then averaged across all samples (including those where zero catch was recorded), and taken to represent the weight per hour fished by an average vessel of 2004-5. These rates were standardized to the equivalents for 1986-92 by adjusting for harvest powers of the fleet in 1986-92 relative to the fleet of 2004-5 (See Bishop, Section 7.1.3).

For each species the kilograms caught per year by the fleet in 1986-92 were derived by multiplying the standardized catch rates per hour by the annual hours of commercial trawling for banana prawns in Weipa 1986-92. The annual hours of commercial effort when targeting banana prawns in Weipa were obtained from commercial logbooks, 1986-92 (See Bishop, Section 7.1.1).

Tiger prawn fishery

Discard information from the Weipa tiger prawn season was obtained from a 1997 Southern Surveyor voyage (SS 08/97) that specifically sampled the prawn trawl bycatch from tiger prawn season in each major fishing region within the NPF (Stobutzki et al. 2001). The data from the Weipa region was selected for these analyses. Although this data is five years later than the assumed time frame (1997) for the modelling exercise (1986-1992) the species and their relative contributions to the bycatch should be a reasonably accurate representation of the bycatch from both periods. There were no TEDs or BRDs in the nets during the 1997 survey, as was the case during the period chosen for the Ecopath model.

The tiger prawn bycatch sample data originated from 30 minute scientific survey trawls and the subsample data was scaled-up to represent estimates of the total catch rate for each species from each research-trawling operation. Subsequently, biomass estimates (kilograms caught per year by the fleet in 1986-92) were derived by multiplying the standardized catch rates per km^2 trawled by the annual area actually trawled commercially when targeting tiger prawns in Weipa 1986-92 (See Bishop, Section 7.1.2).

Ecopath estimates

The Weipa target area is 5788 km^2. The kilograms caught per year in Weipa, for each of the banana and tiger prawn fisheries, were converted to tonnes per square kilometre (of the Weipa target area) for each species via:

{(Average kg caught per year / 1000) / 5788} km^2

The tonnes per km^2 values for each species were then summed for each functional group for expression as Ecopath model input parameters (Table 40). Each species was assigned to functional groups according to pre-defined categories (see Table 5, and TROPHOAPPENDIX C). The resulting biomass estimates (tonnes per km^2) for the functional groupings of each fishing season are represented in Table 40.

Table 40: Functional groups and respective biomass estimates from the discards of banana prawn and tiger prawn fishing operations.

Group number	***Functional group***	***Banana season ($t \cdot km^{-2} \cdot year^{-1}$)***	***Tiger season ($t \cdot km^{-2} \cdot year^{-1}$)***
5	Sea snakes	0.0002576	0.0012761
11	Medium pelagic piscivores	0.0011876	0.0032691
12	Small pelagic piscivores	0.0000898	0.0000063
13	Sawfishes	0.0102508	0.0101945
14	Large teleost benthic piscivores	0.0003410	0.0181059
15	Small benthic piscivores	0.0030855	0.1230339
16	Large elasmo benthopelagic piscivores	0.0173733	0.0138089
17	Large teleost benthopelagic piscivores	0.0145281	0.0347512
18	Small benthopelagic piscivores	0.0012360	0.0711231
19	Large benthopelagic invert feeders	0.0000228	0.0027771
20	Small benthopelagic invert feeders	0.0176705	0.8231611
21	Large elasmo benthic invert feeders	0.0053800	0.0047175
22	Large teleost benthic invert feeders	0.0000571	0.0164533
23	Small benthic invert feeders	0.0921437	0.3459734
24	Polychaete feeders (Offshore)	0.0008584	
25	Large pelagic planktivores	0.0061739	0.0057636
26	Small pelagic planktivores	0.0264699	0.1315977
27	Marine benthic herbivores	0.0002891	
28	Scavengers	0.0001179	
30	Estuary lg teleost benthopelagic pisc/prawn feed	0.1384268	

Group number	Functional group	Banana season ($t \cdot km^{-2} \cdot year^{-1}$)	Tiger season ($t \cdot km^{-2} \cdot year^{-1}$)
32	Estuary large benthopelagic invert feeders	0.0000311	
34	Estuary polychaete feeders		0.0497818
35	Estuary small benthic invert feeders	0.0003680	
38	Estuary Benthic herbivores		0.0004646
41	Octopus		0.0005201
42	Squid and cuttlefishes	0.0002193	0.0068319
43	Stomatopods	0.0000280	0.0025283
52	All other non-commercial prawns	0.0000020	0.0052970
56	Sand crabs	0.0007091	0.0175226
57	Other large crabs	0.0002854	
59	Holothurians	0.0000015	0.0030166
60	Spatangoids	0.0000003	
61	Echinoids	0.0000052	0.0001760
62	Ophiuroids	0.0000006	0.0000294
63	Asteroids	0.0000126	0.0002704
64	Sessile epibenthos	0.0000717	0.0105004
65	Marine bivalves	0.0000457	0.0074081
67	Marine small crustaceans	0.0000735	0.0077154
69	Marine worms		0.0000033
71	Marine small gastropods	0.0000001	0.0001088
77	Large jellies		0.0000529
78	Small jellies	0.0000039	0.0008925

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State-managed fisheries in Albatross Bay

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Abstract

Commercial and charter catch and effort information from the Department of Primary Industries and Fisheries, Queensland‘s (DPI&F) Commercial Fisheries Information System (CFISH) database was summarized for the Albatross Bay modelled area. Information on bycatch and discards for these fisheries also came from DPI&F, but approaches to deriving discard estimates differed among the five state-managed fisheries. The following sections describe the methods used to estimate annual catch and discard flow for each of those fisheries. Recreational and Aboriginal fisheries catch and discard estimates are also included in this section, but these estimates rely on assumptions that are less defensible, and thus should be viewed as model place-holders.

Landings from line, gillnet, and pot gear

The average annual landings from four state managed gear types in the modelled area—line trolling, offshore gillnet (N9), inshore gillnet (N3), and pots (crab)—were summarized for the period 1992-2004 by matching the area defined for the Albatross Bay model (Figure 52) with specific 6 x 6 nautical mile commercial fishing grids. There is confidence that these data are accurate from the beginning of this time period (Lew Williams, personal communication, QDPI), though it is possible that early data could include some error as fishers familiarised themselves with the logbooks. Average annual landings for each species (over all years) were used as a basis for back-calculating a convenient starting point (1986-1992) system using effort time series (days per year) corrected for percentage of days covered by these data. Effort in the middle and later years were thus scaled properly so that forward simulations to the present (using Ecosim) would represent effort and landings accurately. The landings estimates were tallied by Albatross Bay Ecopath model functional group and hindcasted to the first year tracked (e.g., 1992) using this corrected effort time series to represent that starting time period. In cases of uncertainty of the history of the fishery prior to data collection, either the earliest landings estimates were used to represent the starting time period or a single day was used as a placeholder, and the relative time series of effort were scaled appropriately. These tallied landings estimates were expressed in $t \cdot km^{-2} \cdot year^{-1}$ for the whole modelled area for entering into Ecopath’s catch interface, and they include both directed catch and other retained ‘byproduct’ catches. The N9 and N3 gillnet fishery results in the Albatross Bay area were separated using information about licences available in CFISH. Both of these fisheries operate in the Albatross Bay area as defined for the model.

Offshore gillnet (N9) fishery discards

Grey mackerel and sharks are the targets of the offshore gillnet fishery in the Gulf of Carpentaria, including Albatross Bay. Discards associated with the N9 fishery were estimated for 2002 using the bycatch information provided in Stapley and Gribble (2004) and Tables 4 and 5 in Appendix 7 (Section 4) of Gribble (2004), combined with the aforementioned CFISH information as well as length-weight relationships provided by Richard Pillans (CSIRO Marine and Atmospheric Research, Cleveland) and those found in FishBase (www.fishbase.org).

The weight of each discarded group observed in the 2002 N9 observer program sampling (Stapley and Gribble 2004) was estimated as the total number of individuals of each species that did not survive discarding (released dead + (0.5 · released alive)) times the average weight, which was estimated by applying average length data provided in Appendix 7 of Gribble (2004) to species-specific length-weight relationships (some of these relationships were from closely related species rather than from the same species). Resulting values were multiplied by 4.182861—the ratio of the total Albatross Bay area grey mackerel catch in 2002 (26963 kg) to the 2002 total observed weight of grey mackerel (6446.065 kg) in this limited observer survey.

The resulting discard estimates for the 2002 Albatross Bay area N9 fishery were then hindcasted to 1986 (and forecasted to 2004) using the proportions of boat days in the Albatross Bay area during each of those years relative to 2002 (derived from CFISH), corrected for the proportions of data collection coverage, which varied among years. Estimated discards for the period 1986-1992 could then be expressed in $t \cdot km^{-2} \cdot year^{-1}$ and characterized for this defined ‘initial state’ model period such that forward projections in time from this period would produce accurate expressions of bycatch when driven by the corrected effort time series used in this back-calculation. This effort time series was applied later to this initial characterization during Ecosim simulations for the purpose of reconstructing fishery and ecosystem changes in our attempts to explain banana prawn catch declines with the information at hand.

Inshore gillnet (N3) fishery discards

The inshore gillnet fishery targets barramundi and sharks, but this fishery is not conducted in the main estuaries of Albatross Bay. The fishery is, however, conducted within the defined modelled area, and so N3 catches and discards do occur in the Albatross Bay Ecopath model.

Discards in the N3 inshore shark / barramundi fishery were estimated from barramundi research netting data, which were collected as part of the DPI&F Long Term Monitoring Program (LTMP) surveys conducted during 2002 and 2004 in the Archer River area. The total number of individuals of each captured species and the average length of those species was extracted from the data series (which represented 213.71 hours of total gear soak time). Total weights for each species captured in those surveys were estimated by applying empirically derived length-weight relationships specific to each species. Some of these length-weight relationships were provided by Richard Pillans (CSIRO Marine and Atmospheric Research, Cleveland) and others were extracted from FishBase (www.fishbase.org); some were from closely-related species. This total weight estimate was then converted to weight per day per boat in the overall modelled area assuming an average gear soak time of 12 hours. These values were then applied to the number of boat days fished in the defined Albatross Bay area with this gear type during 2002 (610 boat days) to estimate discard flows during that year, and then they were hindcasted back to 1986 and forecasted to 2004 using the effort time series recorded from 1992 onwards in CFISH. This effort time series (boat days per year) was corrected for the proportion of days covered by these data. These bycatch items were organized by functional group and the species within each functional group were tallied for an estimate of bycatch per functional group for the starting point system of interest, and expressed in $t \cdot km^{-2} \cdot year^{-1}$. The hindcasted values were used to specify the starting point system flows.

In later Ecosim simulations, the effort time series was scaled such that the initial 1986-1992 time period equalled 1 such that a time series of boat days projected to the present would accurately represent estimated changes in bycatch throughout the period with the highest confidence represented by the middle and later years. We note that Peverell et al. (2004, pages 116-117) presents ratios of catch to incidental catch (non-marketable species), and these patterns are consistent with the results of the derivations presented herein.

Mud crab fishery discards

Mud crab landings estimates for the defined area and the period in question were derived according to the methods described earlier for the line and gillnet fisheries. The discards associated with these catches were derived from the LTMP mud crab surveys conducted between 2000 and 2004. The total number of each bycatch species or group in the 403 pot lifts in these surveys were tallied and multiplied by estimated mean weights of individuals captured by crab pots to estimate the total weight of each group in the overall survey. Rough estimates of average weights for fishes were provided by Dr. Steve Blaber and those for invertebrates were provided by Mark Tonks and Quinton Dell (CSIRO Marine and Atmospheric Research, Cleveland) while considering the gear and the mesh size. Total weight per boat day was then estimated by dividing the estimated total weight in the survey by 403 pot lifts and multiplying by the average number of pots per day per operator in the Gulf of Carpentaria fishery (6.042 pots$\cdot$day^{-1} derived from information in Gribble et al (2004)). This total weight per boat day was expressed in t$\cdot$km$^{-2}\cdot$year^{-1} for each year by multiplying these values by the number of boat days for each year (corrected for percentages of days per year covered by the sampling). Resulting estimates were tallied by Ecopath functional group and hindcasted to the first year tracked (1993) using this corrected effort time series, and this value was used to represent the modelled starting time period (1992-1996). The time series used to drive changes in effort in the Ecosim model was re-set to one for this time period.

Recreational fishery discards

The scale of recreational fishing effort in the Albatross Bay area is uncertain because quantitative information is very scarce. No detailed information about private boat operators and shoreline participants was available for Albatross Bay, though such information is available for the far northern region. Our approach was to extrapolate from CFISH data representing one monitored commercial charter boat (1995 onwards) using rough place-holder assumptions. Thus, while information on the composition of commercially-caught organisms in the area is reasonable (one boat is somewhat representative of the effort in this case), the overall estimates of quantity relies on rough assumed multipliers of charter boat effort.

The number of individuals of each species recorded as caught in this dataset were tallied by year and summed across years 1999-2004 for an estimate of the average catch per monitored boat for this period. Mean annual catch per monitored boat was derived multiplying the average number of individuals by the average weights of individuals of each species. These weights were derived from the database provided by Shane Griffiths (CSIRO Marine and Atmospheric Research, Cleveland), or based on 25% of the maximum weight for each species listed in FishBase (www.fishbase.org). This mean catch by mass was multiplied by four, assuming that charter boat effort represents 25% of the sportfishing effort in the Albatross Bay area.

The resulting estimate of total annual catch was expressed again in terms of one boat day (t$\cdot$km$^{-2}\cdot$year^{-1}) in order to specify an hypothetical catch starting point to which a boat day effort time series (derived from the same data set and scaled to 1 as a starting period) could be applied. This has the effect of scaling the time series so that effort is properly expressed during the years that the data represent. A parallel approach was taken with respect to the released component of the catch to derive discard rates for the recreational fishery.

Aboriginal subsistence fishery

Estimated annual catches of key species taken by indigenous fishers in Queensland was taken from Coleman *et al.* (2003; Table 6.3). These estimates were multiplied by 0.157—the ratio of the indigenous population in Weipa and Napramum (975) to those in the Queensland area (6205) (Monaghan 2004, Table 14a), in order to very roughly estimate indigenous fisheries catches in the Albatross Bay area. Fish that were classified as ‘miscellaneous fishes’ in Coleman *et al.* (2003) were proportionally allocated to the identified fish groups for the purpose of this estimate. Mean weights were then applied to this estimate of numbers of individuals caught to derive estimates of catch weight, and these were expressed as t$\cdot$km$^{-2}\cdot$year^{-1} in the overall modelled area. Mean weights for these species were provided by Shane Griffiths, Mark Tonks, Quinton Dell, Steve Blaber and Toni Cannard (CSIRO Marine and Atmospheric Research, Cleveland). The resulting estimates of total annual mean weights of each species were tallied into Ecopath functional groupings specified for this model, and these estimates were then applied to the initial 1986-1992 model time period and this catch was assumed to be static throughout subsequent Ecosim runs (no effort time series was applied to these rough aboriginal catch estimates). Discard estimates were not calculated, as discards were assumed to be minimal.

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The Ecopath Approach

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The Ecopath approach

Ecopath trophic models describe the state of energy flows in a food web. They are designed to include all biotic components of an ecosystem, and biomass wet-weight (used here) is almost always the currency, though some have modelled nutrients. Polovina (1984) developed *Ecopath* to study coral reefs at French Frigate Shoals. A variety of dynamic capabilities have since been added (e.g., Christensen and Pauly 1992, Walters et al. 1997, Walters et al. 1999, Christensen et al. 2000, Pauly et al. 2000). Scores of applications of *Ecopath with Ecosim* can be found at: http://www.ecopath.org/, along with the freely distributed software and documentation. Although the formulations and basic concepts are accessible in these venues, the general approach is summarized here.

The Ecopath master equation (Equation 2-1) expresses the law of conservation of mass or energy and it indicates the basic input parameters. This equation balances a group's net production (terms to the left of the equal sign) with all sources of mortality, migration, or change for that group (terms to the right). More specifically, it says that the net production of a functional group equals the sum of (1) the total mass (or energy) removed by predators and fisheries, (2) the net biomass accumulation of the group, (3) the net migration of the group's biomass, and (4) the mass flowing to detritus.

Equation 2-1. $B_i \cdot (P/B)_i \cdot EE_i = Y_i + \Sigma B_j \cdot (Q/B)_j \cdot DC_{ji} + BA_i + NM_i$

B_i and B_j are biomasses of prey ($_i$) and predators ($_j$) respectively;

P/B_i is the production/biomass ratio, equivalent to total mortality (Z) in most circumstances (Allen 1971);

EE_i is the ecotrophic efficiency; the fraction of the total production of a group utilized in the system;

Y_i is the fisheries catch per unit area and time (i.e., Y = F*B);

Q/B_j is the food consumption per unit biomass of j;

DC_{ji} is the contribution of i to the diet of j;

BA_i is the biomass accumulation of i (positive or negative); and

NM_i is the net migration of I (emigration less immigration).

The implied thermodynamic constraints of this equation underscore the power of *Ecopath* models as a focal point for refinement of ecosystem information. The need to reconcile energy production and demand among components of the food web narrows the possible ranges of parameter estimates for particular groups. Inclusion of a biomass accumulation factor and migration factor in the general *Ecopath* equation distinguishes *Ecopath* modeling as an 'energy continuity' approach rather than a strictly 'steady state' approach. Conservation of energy (*continuity*) is assumed for every identified component of the ecosystem, and the whole system. This basic constraint enables representation of changes in populations (i.e., functional groups) when expressed in dynamic form (See Section 9 Methods II: Ecosim dynamics).

Model construction procedure

The following eight steps to constructing an *Ecopath* model are modified from Okey and Mahmoudi (2002):

1. **Define the ecosystem in space and time** – The spatial extent of the system and the represented time period must be clearly defined. Parameter estimates are expressed in annual units, but any time period can be represented.
2. **Define functional groups** – Myriad species comprise interaction webs, but these species must be aggregated into related groupings that make sense in terms of ecological function, and the questions of interest.
3. **Estimate basic parameters** for each functional group. These parameters are shown in Equation 2-1, and documenting these derivations makes up the bulk of this volume.
4. **Estimate fisheries information** – Landings, discards, discard fates, and economic information is derived and entered for each fisheries gear type. Effort and catch time series should also be specified such that the catches and discards in the initial modelled period is expressed properly over time.
5. **Estimate additional *Ecopath* parameters** – Detritus fates, assimilation rates, multi-year trends, spatial and temporal distributions, and habitat associations.
6. **Enter parameters** into the windows-based input interfaces (see www.ecopath.org).
7. **Characterize model pedigree** by ranking parameter quality (i.e., confidence).
8. **Balance the model** according to thermodynamic constraints.

A variety of procedures for evaluating and refining model structure and behaviour should be applied after initial balancing of the preliminary model. The current preliminary model has gone through three identifiable iterations since initial place-holder model construction, thus allowing refinement of the model each time. Considerable uncertainties persist in the present preliminary iteration becauus of liminations of empirical data and the model should continue to be refined in future projects as scientists, managers, and fishers endeavour to understand the mechanisms of prawn dynamics. Derivation procedures differed among functional groups, and thus specific procedures are presented throughout this document.

The most useful ecosystem models are those that distil broad knowledge and information held by broad communities of experts, and those that include these experts in the collaborative investigations and insights that emerge from joint ownership and cooperation. The benefits of constructing Ecopath with Ecosim models through broadly collaborative approaches has been demonstrated repeatedly by the present author and his colleagues during the last eight years (Okey and Pauly 1999a, b, Okey and Pugliese 2001, Okey and Mahmoudi 2002, Okey et al. 2004a, Okey et al. 2004b). These benefits include scientific community ‘buy-in’ and participation, broad ownership and interest in the resulting model, enhanced opportunities for iterative refinement, testing, and verification, further collaboration and consilience in the scientific and management communities, synthesis of disparate ecological information into an informative research and planning framework, and other opportunities.

Albatross Bay model description

The spatial, temporal, and biological scope of the model was defined during project workshop I, and this definition was refined thereafter. The scope of the Albatross Bay model is currently defined in five ways:

- Time: 1986-1992
- Vertical: 12º10’30” S and 13º S latitudes
- Horizontal: Top of estuaries to 40 m isobath (two subsystems)
- Area: 5,788 km^2 area
- Biological functional groups (99 groups in 8 broad categories an two linked subwebs representing estuarine and offshore habitats):
  - 2 marine mammal
  - 3 reptile (1 exclusively estuarine)
  - 4 bird
  - 33 fish (12 estuarine)
  - 9 prawn (2 explicitly estuarine and 2 outmigrating)
  - 32 other invertebrate (8 exclusively estuarine)
  - 7 primary producer (3 exclusively estuarine)
  - 2 microbe (one estuarine)
  - 7 detritus (3 estuarine)

At Workshop II, experts helped refine the straw-man Albatross Bay model, and they helped to balance the model trophodynamically in order to prepare the model for simulations so that the project questions could be explored with the Ecopath/Ecosim approach. The Albatross Bay Ecopath model includes several design features for ensuring optimal usefulness given the nature of the questions of interest in this project:

- *Linked subsystems* – The estuary ecosystem and the offshore system that are linked to each other ecologically, especially with respect to organisms that move from one system to the other either ontogenetically or as adults. The two subwebs are articulated at their bases and naturally more linked at middle and upper trophic levels;
- *Embedded stage-based models* – The model contains two stage-based sub-models describing the population dynamics of both Banana prawn and Tiger prawn categories, as partitioned into juvenile, sub-adult, and adult group, each with different diets, predators, habitats, and population characteristics;

- *Fisheries information* – Landings information by fleet and functional group are specified in the model, as is discard catch information and the fate of that discard. The model accounts for seven fleets that operate in the area:
  - Banana prawn trawl
  - Tiger prawn trawl
  - Line (Spanish mackerel)
  - Net (Mackerel / Shark)
  - Gillnet (Barramundi)
  - Pot (Mud Crab)
  - Recreational
- *Fish biomass and diet information* – The model contains rigorous diet and bycatch estimates for all the fish groups in the model. This is unusual for Ecopath models, and critical for addressing hypotheses related to the relative influence of fish predation mortality of prawns versus fisheries mortality of prawns.
- *Prawn diet information* – The model contains diet information for all the stages of the main prawn functional groups. These diets were collected from the literature as well as from the unpublished data of prawn experts at CSIRO Marine and Atmospheric Research in Cleveland, Queensland.
- *Time series data* of catches, effort, CPUE, and indices of abundance – The Albatross Bay model benefits from available time series data sets so retrospective forecasted predictions (from the 1987-1992 period) can be driven by changes in effort and compared with indices of abundance and catch.

Ecological model refinement

The existing Albatross Bay model is considered preliminary. Most parameters in the model need to be reviewed, checked, and further refined before the model can be used for rigorous quantitative prediction in the sense of reconstructing past ecosystem changes accurately. Nevertheless, the qualitative results of quantitative simulations—e.g., the relative magnitudes of predicted changes—can be examined using this preliminary iteration of the model to help understand the overall effects of fisheries and other stressors, to gain insights into the causes of recently observed catch declines, and to improve understanding of system structure, functions, and interactions.

Fish biomasses and diet compositions are relatively rigorous as the result of somewhat comprehensive site-specific studies of the fish fauna of the Albatross Bay area. It is fortuitous that this information exists, as it provides the model with a good grounding of the predation pressure of fishes on prawns. The input parameters of other functional groups in the system—both at high and low trophic levels—are are far less certain, and these parameters will need to be re-examined iteratively and prioritized so that research efforts in the system can be optimized in the context of understanding the whole Albatross Bay banana prawn ecosystem.

Other necessary refinements include improved estimations of fisheries catch and discard information for all the fleets, for the time period in question, where possible. Time series information will also need to be continually refined. Information on habitats and spatial aspects of the system and functional groups will enable spatially-explicit explorations of potential future spatial policies, but spatial refinements and analyses are outside the scope of the present project. Finally, specification of economic (and social) parameters in the model will allow innovative explorations of alternative management strategies. Such capabilities of this approach will potentially be a useful decision support system.

Types of simulations that are possible

In addition to the main goal of constructing a preliminary Ecopath model for the Albatross Bay Ecosystem, the temporal dynamic simulation routines of Ecosim were the natural focus of this preliminary exploration. The main exploratory mode of Ecosim allows users to examine simulated multi-species (functional group) effects of user-specify simulated changes to fishing mortality (increases or decreases) either by a fleet or to a particular functional group. This allows dynamic exploration of ‘what if’ questions and the trophically-dominant dynamics and relationships in the system, all through a user-friendly gaming interface. Other types of basic fisheries analyses (in a whole food-web context) include analyses of predicted community compositions at different levels of fishing. Both trophic and non trophic interactions can be explored using these simulations, as can the interactions of biological and physical forces in shaping the environment. A time-series fitting routine within Ecosim is a more sophisticated type of analysis that is designed for reconstructions of ecosystem changes by specifying historical fisheries time series information. Here, time series representing the various explanations for catch declines are added to the model until the observed changes in the system are explained by the model, thus providing an overall (most likely) explanation of the relative roles of the various specified factors in causing the observed catch declines.

The Spatial dynamic simulation capabilities of Ecosim are not explained here because these are beyond the scope of the current project. However, these spatially-explicit simulations can be conducted once the Ecopath model is constructed and the Ecospace routine is parameterised with some more information on habitat and spatial aspects of the ecosystem.

Alternative management strategies / Decision support systems – Once the model of Albatross Bay is adequately refined, and once economic and social information is specified in the model, a policy optimization procedure can be used to adjust fishing strategies over time among all the fleets to achieve a pre-specified (pre-value-weighted) policy objective for the ecosystem wherein ecological, economic, and social values are weighted. This is a quantitative approach to finding an overall fishing policy solution that will optimize the system’s value given the emergent influence of each fleet, and given the trophodynamic constraints in a whole-system context. This is an integrated and automated Decision Support System for finding the right mix of alternate management strategies. It can be used on its own, or in conjunction with other Decision Support Systems. This analysis was also beyond the scope of the present project.

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Ecopath Static Analyses

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Four quantitative descriptions of the static Ecopath model of the Albatross Bay area are presented in this section: (1) a ‘pedigree’ assessment of the quality of the input data (Table 41); (2) a series of indices and flow estimates that summarize the characteristics of the modeled ecosystem (Table 42); (3) a brief description of the banana prawn sub-web (Figure 57); a comparison of major sources of banana prawn mortality (Figure 58); and (4) an assessment of the relative impacts exerted on banana prawns by each of the functional groups in the model, as the model is currently specified (Figure 59). This latter analysis is featured in this section as providing preliminary insights into the relative influence of particular functional groups on banana prawns. The results of dynamic simulations presented later provide more such preliminary insights.

Evaluation of the quality of input data

Ecopath’s data pedigree routine enables qualitative evaluation of the quality of each input parameter, which is converted to quantitative estimates of data confidence in the form of pedigree indices that can then be used to calculate an overall model pedigree, which also takes into account the number of living biological groups. Data pedigree is data quality as judged by particular criteria that are standard in Ecopath models (shown in Appendix G3). These ratings are converted to confidence intervals estimates (+/- %) for use in probability analyses that address uncertainty; to generally evaluate relative quality of the model; or to reveal and prioritize relative data gaps and needs for marine science program planning. Overall pedigree values for models constructed with poorly collected data of low precision that are not locally-based are close to 0, while those constructed with high quality and locally collected data exhibit overall pedigree values closer to 1.The overall Ecopath data pedigree index of the present iteration of the Albatross Bay Ecopath model is 0.413 (with 92 living biological groups; the measure of fit (t* is 4.3). This ranking is better than many models, but it indicates that the Albatross Bay model could be refined further to increase its usefulness for management and policy applications. Table 41 shows the estimated confidence intervals (+/- %) for each parameter estimate, based on qualitative ranking categories. Note that the confidence is reasonably high for many of the fish group estimates (confidence intervals are relatively low), whereas confidence is low for many other groups.

Table 41: Estimated confidence intervals (+/- %) surrounding the Ecopath input parameter estimates, based on the qualitative ratings of data pedigree defined in TROPHOAPPENDIX D.

Group	B	P/B	Q/B	Diet	Catch
Dolphins	80	20	20	80	50
Dugongs	80	40	40	60	50
Crocodiles	80	40	40	50	50
Turtles	80	40	40	80	50
Sea snakes	30	50	10	30	50
Lesser frigates	30	40	50	30	---
Brown boobies	30	40	50	30	---
Crested terns	30	20	50	30	---
Common terns	30	40	50	30	---
Large pelagic piscivores	50	50	50	30	50
Medium pelagic piscivores	50	50	50	30	50
Small pelagic piscivores	80	50	50	30	50
Sawfishes	30	50	50	30	50
Large teleost benthic piscivores	30	50	50	30	50
Small benthic piscivores	30	50	50	30	50
Large elasmo benthopelagic piscivores	30	50	50	30	50
Large teleost benthopelagic piscivores	30	50	50	30	50
Small benthopelagic piscivores	30	50	50	30	50
Large benthopelagic invert feeders	30	50	50	30	50
Small benthopelagic invert feeders	30	50	50	30	50
Large elasmo benthic invert feeders	30	50	50	30	50
Large teleost benth invert feeders	30	50	50	30	50
Small benthic invert feeders	30	50	50	30	50
Polychaete feeders	30	50	50	30	50
Large pelagic planktivores	50	70	70	30	50
Small pelagic planktivores	50	70	70	30	50
Benthic herbivores	30	50	50	80	50
Scavengers	30	50	50	30	50
Estuary lg elasmo benthopelagic pisc/prawn feeders	30	50	50	30	50
Estuary lg teleost benthopelagic posc/prawn feeder	30	50	50	30	50
Estuary large benthic pisc/prawn feeders	30	50	50	30	50
Estuary large benthopelagic invert feeders	30	50	50	30	50
Estuary large benthic invert feeders (Rays)	30	50	50	30	50
Estuary polychaete feeders	30	50	50	30	50
Estuary small benthic invert feeders	30	50	50	30	50
Estuary planktivores	30	50	50	30	50
Estuary detritivores	30	50	50	60	50
Estuary benthic herbivores	30	50	50	30	50
Estuary insectivores	30	50	50	30	50
Estuary pelagic herbivores	30	50	50	30	50
Octopus	80	20	20	30	50
Squid and cuttlefishes	80	20	20	30	50
Stomatopods	80	40	40	30	50
Banana prawn juvenile	80	20	80	30	50
Banana prawn subadults	80	70	80	50	50
Banana prawn adult	50	20	60	30	50
Tiger prawn juvenile	80	20	80	30	---
Tiger prawn subadults	80	70	80	50	---
Tiger prawn adult	50	20	60	30	50

Group	B	P/B	Q/B	Diet	Catch
All other commercial prawns	80	60	60	80	50
Thallasinid prawns (Callianassa)	80	60	60	80	---
All other non-commercial prawns	80	60	60	80	50
Crayfish	80	70	70	80	50
The mud crab	80	60	60	80	50
Red mud crab	80	60	60	80	---
Sand crab	80	60	60	30	50
Other large crabs	80	60	60	80	50
Large gastropods	30	60	60	80	---
Holothurians	30	50	60	80	50
Spatangoids	30	70	70	80	50
Echinoids	30	40	60	80	50
Ophioroids	80	60	60	80	50
Asteriods	30	60	60	80	50
Sessile epibenthos	30	60	60	60	50
Marine bivalves	80	60	60	60	50
Estuarine bivalves	80	60	60	80	50
Marine small crustaceans	80	60	60	80	50
Estuarine small crustaceans	80	60	60	80	50
Marine worms	80	40	60	80	50
Estuarine worms	80	40	60	80	---
Marine small gastropods	80	60	60	80	50
Estuarine small gastropods	80	60	60	80	50
Marine meiofauna	80	60	60	80	---
Estuarine meiofauna	80	60	60	80	---
Marine forams	80	60	60	60	---
Estuarine forams	80	60	60	60	---
Large jellies	80	40	60	80	50
Small jellies	80	40	60	80	50
Marine zooplankton	30	10	40	50	---
Estuarine zooplankton	30	10	40	50	---
Marine ichthyoplankton	80	60	60	80	---
Estuarine ichthyoplankton	80	60	60	80	---
Insects	80	40	40	30	---
Marine microbial heterotrophs	80	40	40	60	---
Estuarine microbial heterotrophs	80	40	40	60	---
Marine phytoplankton	30	30	---	---	---
Estuarine phytoplankton	30	30	---	---	---
Microphytobenthos	80	40	---	---	---
Seagrass	10	10	---	---	---
Estuarine macroalgae	80	40	---	---	---
Marine macroalgae	80	40	---	---	---
Mangroves	80	70	---	---	---

The Albatross Bay ecosystem can be summarized in a number of ways: comparison of this ecosystem with other ecosystems; comparisons of a past ecosystem with a present ecosystem; and assessments of system efficiency, structure and function, and mean trophic level of the catch (Table 42). For example, the mean trophic level of the catch is estimated to be 3.77. This is 0.43 trophic levels higher than the Banana prawn trophic level because the bycatch that is captured along with the prawns in this system has a higher mean trophic level than prawns. The estimated trophic levels of prawn groups are higher than normally estimated for prawns because prawn diets are relatively well specified in the Albatross Bay model, and because prawns in this system are larger than in many other "shrimp" systems throughout the world.

Table 42: Summary of basic flows and indicies in the Albatross Bay Ecopath model*

Index	***Flows (t·km-^{2}·year^{-1})***
Calculated total net primary production	4728
Net system production	2613
Sum of all production	6126
Sum of all consumption	5764
Sum of all exports	4232
Sum of all respiratory flows	2116
Sum of all flows into detritus	10365
Total system throughput	22476
	Biomass (t·km^{-2})
Total living biomass	199
	Value
Total annual primary prod./total biomass	24
Total biomass/total annual throughput	0.01
Total primary production/total respiration	2.24
Connectance index	0.14
Mean trophic level of the catch	3.77
System omnivory index	0.24

Note: Flows and biomass expressed in wet weight

The throughput of biomass from detritus is estimated to be twice that from primary producton (Table 43), but the input parameters for most primary producer groups and all detritus groups in the model are highly uncertain and are considered placeholder values. This is a conspicuous limitation of the current model (and of the general knowledge about the ecosystem), as ‘bottom up’ hypotheses cannot be rigorously evaluated without improved knowledge in this area. The other major (general) limitation of the Albatross Bay model, in terms of understanding prawn dynamics, is the lack of rigorous information about higher trophic level organisms. This limits a full exploration of ‘top down’ control dynamics in the system.

Table 43: Flows from primary production and detritus in the Albatross Bay model*

TL	***From primary production***					***From detritus***				
	Consumed	Export	To detritus	Respiration	Throughput	Consumed	Export	To detritus	Respiration	Throughput
VI	0.1	0	0.2	0.6	1.0	0.4	0.5	0.8	2.0	3.2
V	1.0	0.1	2.2	4.6	7.9	3.2	0.2	6.6	12.9	22.9
IV	7.9	0.3	16.3	24.7	49.1	22.8	0.4	46.1	63.3	132.6
III	49.1	0.3	84.0	90.8	224.2	132.3	0.4	300.0	287.7	720.4
II	223.6	0.1	901.6	820.4	1946.0	719.7	0	1128.4	808.2	2656.3
I	1945.5	0	2782.6	0	4728.1	2656.0	4230	0	0	11979.4
Sum	2227.3	0.7	3787.1	941.2	6956.4	3534.5	4231	1482.0	1174.3	15515.3

Note: Flows are expressed in t·km^{-2}·year^{-1}. System imports are not presented.

Many predators consume adult banana prawns, and adult banana prawns consume a variety of prey (Figure 57). Accurate specification of prawn sub-webs, i.e. the trophic relationships of prawns to their predators and prey, was emphasized (given priority) during the construction of the Albatross Bay model so that the prawn dynamics would be specified adequately.

Stomatopods can impose a very large proportion of the overall banana prawn mortality (Figure 57 and Figure 58) when even just 5% of the stomatopod diet is specified to be adult banana prawn. This 5% specified in the present model is based on the best available diet information from similar systems used during model construction. A preliminary sample of stomatopod gut contents was analyzed because these model results imply that predation of prawns by stomatopods (or other similar predators) might be key to understanding prawn dynamics in the Gulf of Carpentaria, and because the notion of strong predation by stomatopods is consistent with fisherman observations and other anecdotal information. This special analysis indicated that stomatopods might consume prawns exclusively, at least during certain times of the year and from particular localities (M. Robinson, University of Queensland, unpublished data), implying that the specified 5% of the diet allocated to prawns is a considerable underestimate and that stomatopods would have a much bigger impact than that specified by the current iteration of the model.

Stomatopods impose this high mortality because the Ecopath algorithm calculated a very large stomatopod biomass in the Albatross Bay area based on the high demand for stomatopods in the fish diets specified in the model. Although it is quite possible that stomatopod biomass was somehow overestimated in the diets of fish predators, considerable downward adjustment would still impose a huge mortality on prawns with only a small stomatopod preference for prawns. We conducted some of the analyses presented in this report without specifying a prawn diet for stomatopods, as there were no available site-specific data about stomatopod diets (or abundance) from the Albatross Bay area or from anywhere in Northern Australia during the time of model construction. Other simulations with 5% of the stomatopod diet as prawn biomass, based on information from other regions. These simulations indicated that stomatopods were key to the prawn dynamics, but other ‘vampires from the basement’ emerged when we ‘underemphasized’ the role of stomatopods.

The issue of unknown or emerging predators is a critical one for Australia’s Northern Prawn Fishery, and this is but one example of important and fruitful avenues of research that are indicated by the current trophodynamic model. Improved information about predators such as stomatopods and octopods will be used to refine the model to improve its performance and usefulness in the coming years.

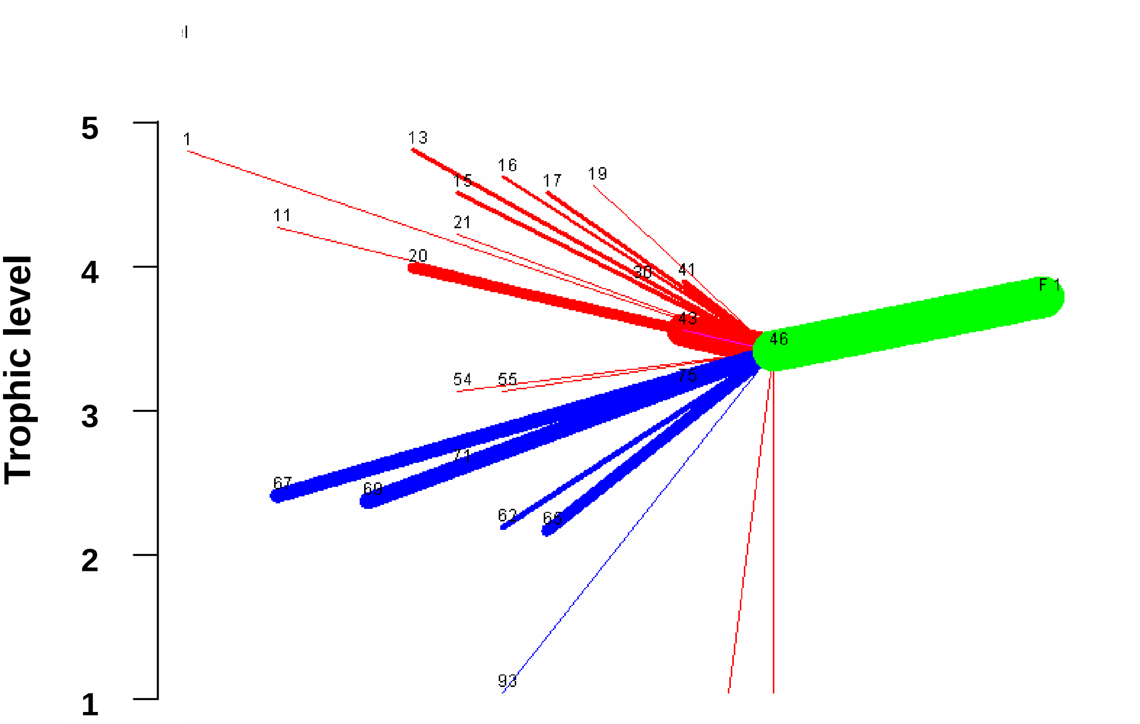

Figure 57: The adult banana prawn sub-web of the Albatross Bay area, Gulf of Carpentaria. Line thickness indicates relative magnitude of flows. Red lines are flows to predators (and detritus), blue lines are flows from prey, and the green line is the flow to the fishery. Numbers refer to the functional groups shown inTable 44. In this figure, vertical position indicates trophic level, but horizontal position is arbitrary, so the length of connector lines means nothing.

Table 44: Predators and prey of adult banana prawns in the Albatross Bay model. The numbers refer to the functional groups shown in Figure 57.

Predator	Prey	Group name
1		Dolphins
11		Medium pelagic piscivores
13		Sawfishes
15		Small benthic piscivores
16		Large elasmo benthopelagic piscivores
17		Large teleost benthopelagic piscivores
19		Large benthopelagic invert feeders
20		Small benthopelagic invert feeders
21		Large elasmo benthic invert feeders
30		Estuary large teleost benthopelagic pisc/prawn feeder
41		Octopus
54		The mud crab
55		Red mud crab
43		Stomatopods
	62	Ophiuroids
	65	Marine bivalves
	67	Marine small crustaceans
	69	Marine worms
	71	Marine small gastropods
	75	Marine forams
	93	Discards

Note: Refer to Appendix G3 for the species compositions of fish groups.

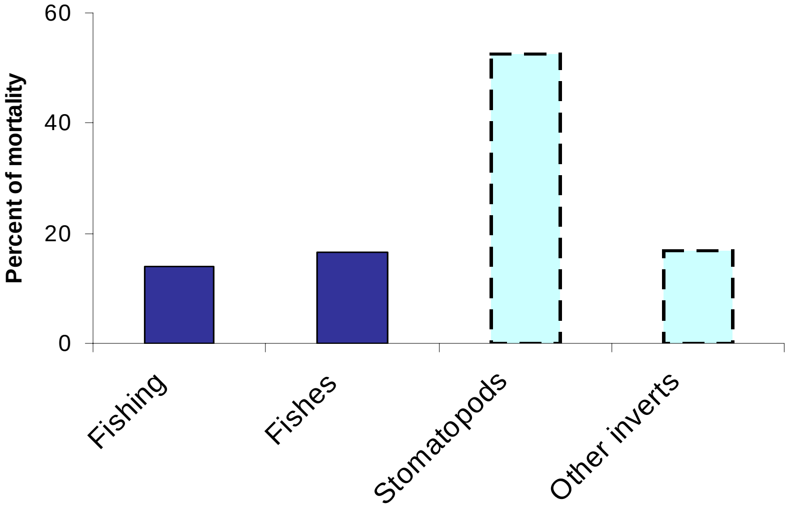

Figure 58. Relative mortality imposed on adult banana prawns in the Gulf of Carpentaria by major consuming groups. Dashed (lighter) bars indicate high uncertainty in those functional groups. The stomatopod bar is the result of adult banana prawns making up only 5% of the overall stomatopod diet (see text).

An analysis indicating the possible relative magnitudes of direct and indirect trophic impacts of each functional group in the system on the three identified life stages of prawns (in a steady state context) Figure 59 indicates those species that might be strong facilitators of banana prawn biomass (the larger bars above zero) and those that might have strong negative effects on banana prawn biomass (larger bars below zero). The large positive bars towards the lower end of the figure (lower trophic levels) represent prawn food items, which obviously have a positive trophic effect on banana prawn life stages. Strongly positive bars towards the top of the figure (high trophic levels) generally represent predatory facilitators of banana prawns, whereas strongly negative bars at upper-mid trophic levels represent "vampires from the basement"—predators of banana prawns that later analyses indicate emerge significantly when key apex predator groups are removed. Competitive effects are indicated by both positive and negative bars at middle trophic levels.

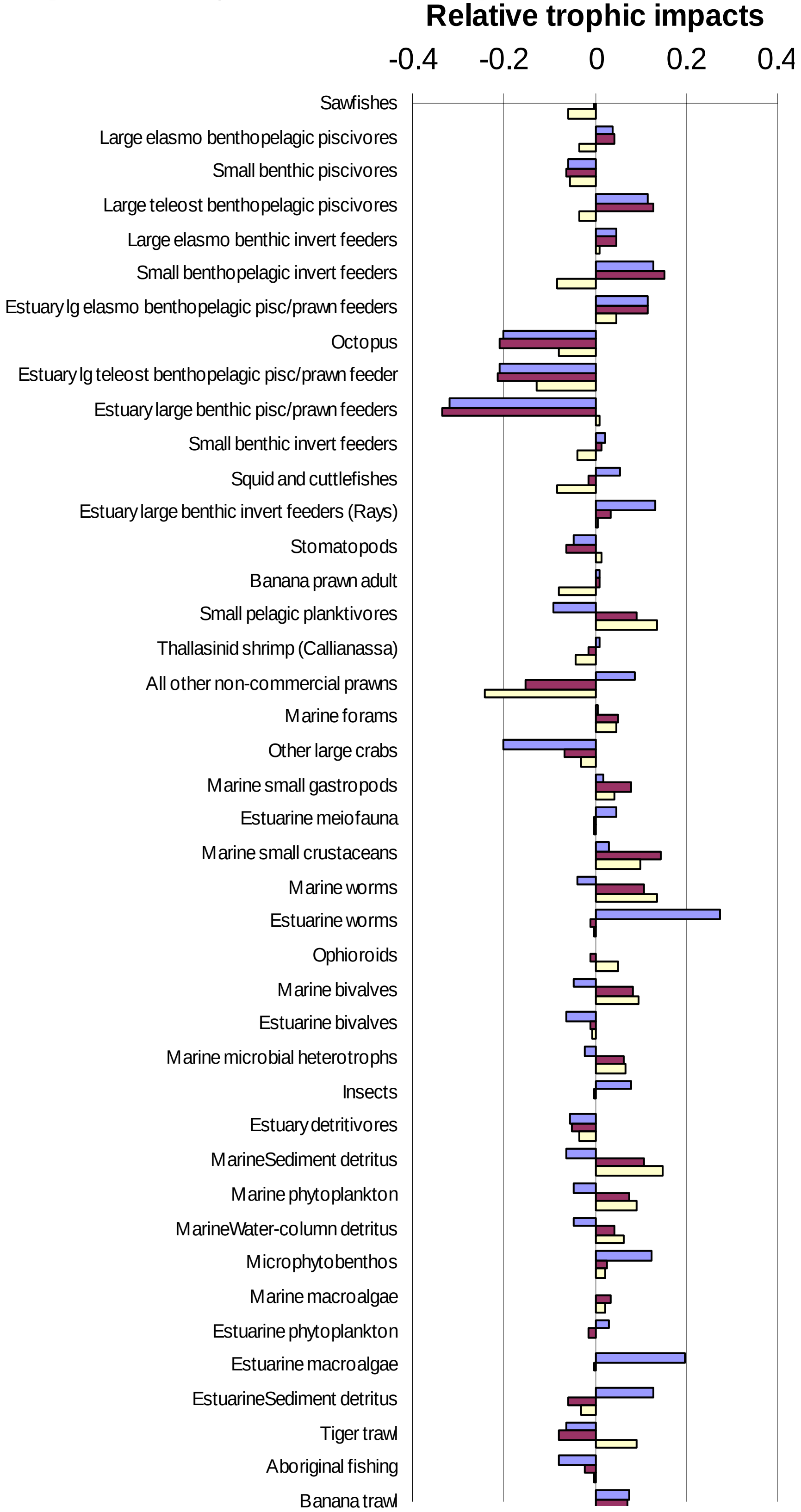

Figure 59: Estimated relative trophic impact of each functional group in the Albatross Bay model on banana prawn juveniles (blue), subadults (red), and adults (white). This static ‘trophic impacts’ analysis indicates that functional groups with values above zero provide beneficial trophic effects (i.e., facilitate prawn group biomasses), whereas groups with values below zero tend to reduce prawn group biomasses. The version of the model depicted here does not include stomatopods feeding on

prawns, and so does not show the overwhelmingly large negative effect of stomatopods on banana prawns. Groups not indicated to cause ≥ 5% change were excluded from this figure.

This static analysis of mixed trophic impacts is a useful screening tool for choosing profitable dynamic simulation strategies. It is based on the approach developed by Leontief (1951) and later applied to ecological systems by Hannon (1973), Hannon and Joiris (1989), and Ulanowicz and Puccia (1990). It also serves as a form of ordinary sensitivity test (Majkowski 1982).

Ecosim dynamics

Ecopath was refined considerably with the dynamic simulation routines *Ecosim* and *Ecospace* (see Walters et al. 1997, Walters et al. 1999, Pauly et al. 2000, Walters et al. 2000). In *Ecosim*, information in the static *Ecopath* file is re-expressed in a dynamic formulation (***Equation 9-1***).

Equation 9-1.

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ji} + I_i - \left(M0_i + F_i + e_i\right) \cdot B_i$$

dB_i/dt is the change in the biomass of group i (B_i) over time, g_i is the efficiency of the conversion of food into growth, Q_{ji} is the rate of consumption by predators j of prey group i, I_i is the immigration rate, $M0_i$ is the natural mortality rate, F_i is the fishing mortality rate, and e_i is the emigration rate.

The dynamics and sensitivity of Ecosim models is largely controlled by the consumption rates (Q_{ji}) (Equation 9-2), which are limited by the proportion of a given predator group's prey that exist in a vulnerable state. Prey vulnerability is controlled within the expression of consumption rate by a user-specified (or calculated) transfer rate of prey movement between vulnerable and invulnerable pools (v_{ij} and v'_{ij}), thus representing the universal community stabilizer of prey refugia. The consumption rate (Q_{ji}) expressed in Equation 9-2 includes the prey vulnerability parameters.

Equation 9-2.

$$Q_{ji} = \frac{v_{ij} \cdot a_{ij} \cdot B_i \cdot B_j \cdot T_i \cdot T_j \cdot S_{ij} \cdot M_{ij} / D_j}{v_{ij} + v'_{ij} \cdot T_i \cdot M_{ij} + a_{ij} \cdot M_{ij} \cdot B_j \cdot S_{ij} \cdot T_j / D_j}$$

a_{ij} is the rate of effective search for prey i by predator j, T_i and T_j are the relative feeding times of prey i and predator j, S_{ij} is the user-defined seasonal and long-term environmental forcing effects, M_{ij} is the non-trophic mediation forcing effects, and D_j represents the effects of prey handling time by predators, which further limits consumption rates. See Walters et al. (1997), Christensen and Walters (2004), and the Ecopath with Ecosim user's guide (Christensen et al. 2004) for more information. Download the software from www.ecopath.org.

Parameters v_{ij} and v'_{ij} represent prey vulnerabilities, or the rate of exchange of biomass between two prey behavioral states: a state in which all predators have full access to prey and a state in which prey have full refuge from predators. Prey use refugia in real ecosystems. Thus, not all prey biomass is vulnerable to predation at any given time, and predator-prey relationships are limited by behavioral and physical mechanisms. *Ecosim* is designed so that the user can specify the type of trophic control (Lotka-Volterra type vs. donor control) that mediates any interaction in the food web. Maximum consumption rates are hypothesized, and thus the rate of exchange of biomass (v_{ij}) that a predator normally exerts. For low predator biomass or high prey vulnerability (v_{ij}) the functional relationship approximates a mass-action flow, or Lotka-Volterra type interaction implying a strong 'top-down' effect. For high predator biomass or low prey vulnerabilities the functional relationship approaches a donor-controlled (bottom-up) flow rate so v_{ij} is the maximum possible instantaneous mortality rate that j can cause on i (see Walters et al. 1997).

Prey vulnerabilities can be specified by adjusting the proportion of prey in vulnerable and invulnerable states (pools) via adjustment of the v values, which are scaled such that pure Lotka-Volterra (top down) type control and pure donor control. In the real world, this mixture of trophic control is mediated by temporal or spatial refugia, or by the relative primacy of physical and biotic forces in regulating communities, i.e., predator-prey interactions. For the basic gaming simulations presented in this report, vulnerability of prey was scaled between 1.2 and 10 (Ecosim default range) in proportion to the trophic level of the predators (Christensen et al. 2004).

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Simulation results and discussion

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Simplified trawl impact scenarios

Preliminary simulations using Ecosim’s gaming interface and simple hypothetical trawling strategies indicted that banana prawn (*Penaeus merguiensis*) biomass in the Albatross Bay area would have declined considerably with either increases or large decreases in 1986 banana prawn trawling rates (directly through stock overfishing), and it would have declined considerably with increases in tiger prawn trawling rates (indirectly through ‘ecosystem overfishing’).

A simulated gradual linear doubling of banana prawn trawling from 1986 levels would have decreased banana prawn biomass by ~90% (Figure 60a). This prediction manifests (in the model) as direct impacts (i.e., stock overfishing). The simulations also show that a gradual doubling of tiger prawn trawling from 1986 levels would have decreased banana prawn biomass by ~70% (Figure 60b), but in this case the effect manifests indirectly through increased predation of banana prawns caused by a fishery-initiated shift in the Albatross Bay biotic assemblage (ecosystem overfishing). A gradual doubling of both banana and tiger prawn trawling fishing caused a ~98% decrease in banana prawn biomass through combined stock overfishing and ecosystem overfishing (Figure 60c).

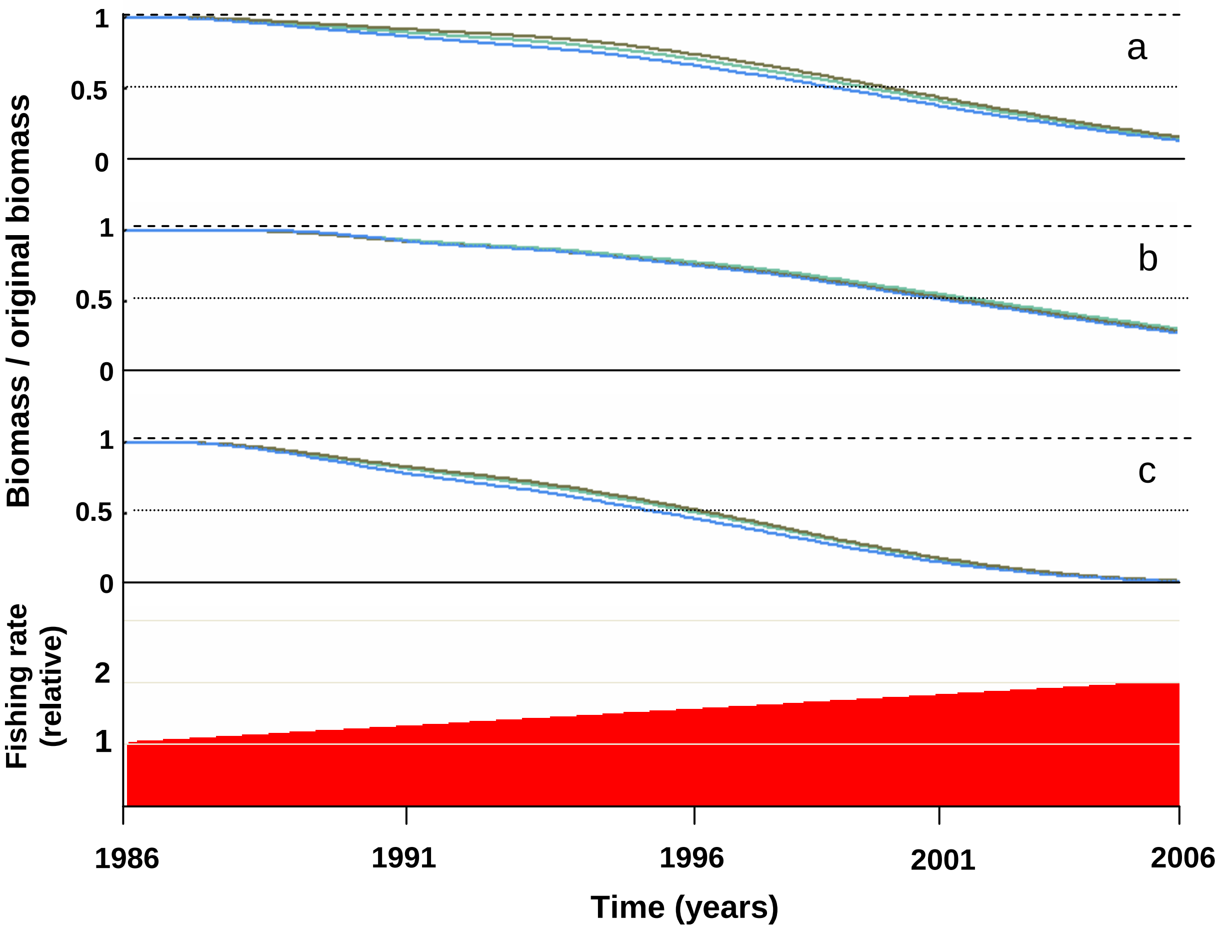

Figure 60: Predicted biomass trajectories of juvenile (green line), sub-adult (brown line), and adult banana prawns (*Penaeus merguiensis*) (blue line) in response to an hypothetical gradual doubling of (a) banana prawn trawling, (b) tiger prawn trawling, and (c) both from the 1986 level.

A simulated gradual linear decrease in prawn trawling in the Albatross Bay area from 1986 levels to zero by 2006 (whether banana prawn trawling, tiger prawn trawling, or both combined) lead to predicted increases in banana prawn biomass for about 12 years, followed by considerable declines in biomass (to ~40% of 1986 levels) in cases where banana prawn trawling was eliminated (Figure 61). Stated another way, the simulation indicates that anywhere between 50% and 75% of the 1986 fishing rate (by banana prawns or both fleets) would lead to noticeable increases in banana prawn biomasses. Fisheries economic analyses should therefore indicate that fleet efficiency and profitability would be considerably enhanced at these considerably lowered fishing rates.

Elimination of tiger prawn trawling lead to sustained moderate increases in banana prawn biomass (b). Again banana prawn trawl impacts manifest mostly directly (i.e., stock overfishing), whereas tiger prawn trawl impacts manifest indirectly (i.e., ecosystem overfishing).

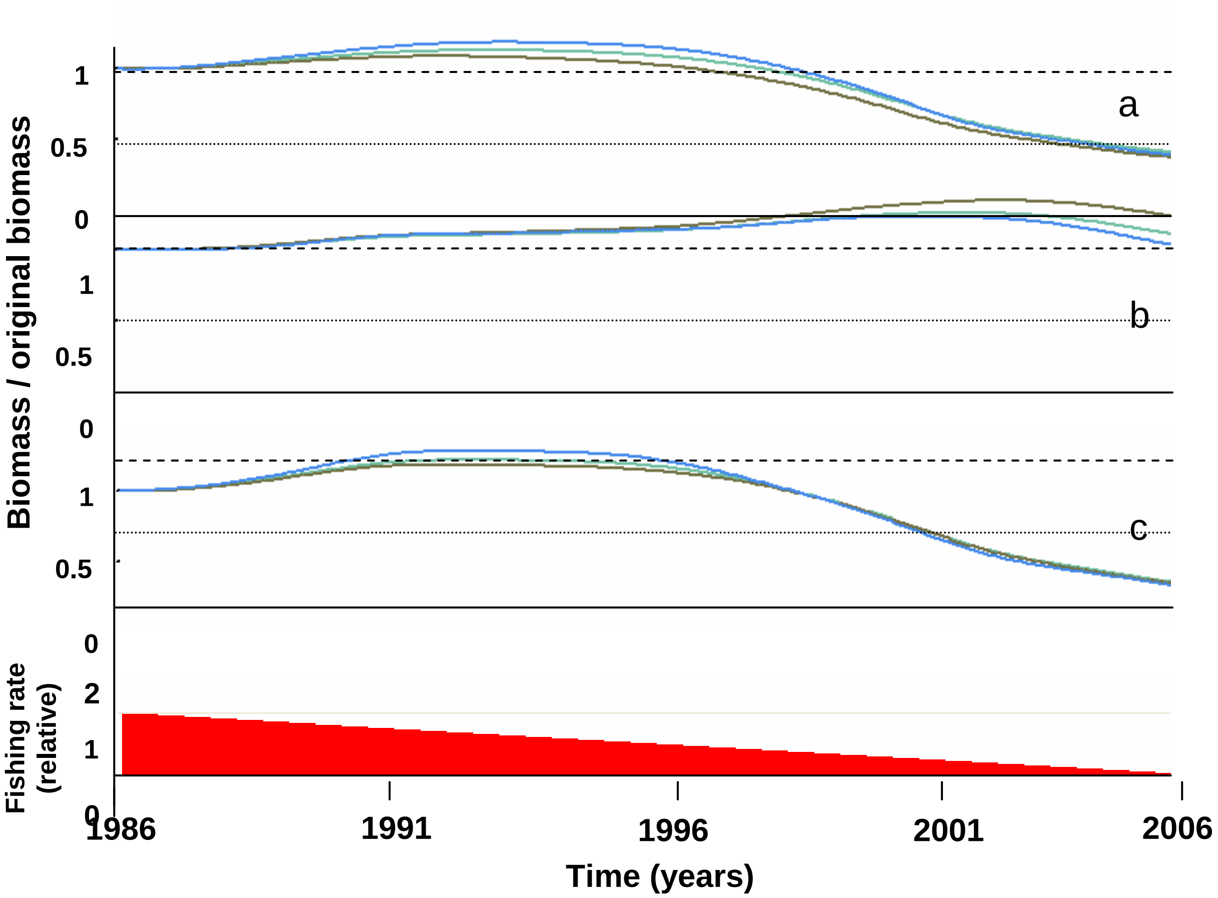

Figure 61: Predicted biomass trajectories of juvenile, sub-adult, and adult banana prawns (*Penaeus merguiensis*) in response to a gradual removal of (a) banana prawn trawling (b) tiger prawn trawling, and (c) both from the 1986 level.

A simulated trajectory of prawn trawling, i.e., a gradual doubling of fishing rate from 1986 to 1989 followed by a steady rate until 1996 and then a gradual decrease to zero in 2006, led to expected decreases during the early years of the simulations followed by signs of recovery after either banana or tiger prawn trawling rates decreased sufficiently in the most recent years of the simulation (Figure 62 (a) and (b)). Banana prawns failed to recover in the simulation of both prawn trawl fleets were exposed to the same scenario. This fishing strategy is an hypothetical caricature of the actual history of fishing rates in this system, which is considerably variable, but the results seem reasonable given this preliminary simplification, as they illustrate plausible outcomes of such a simplified “target-based” strategy.

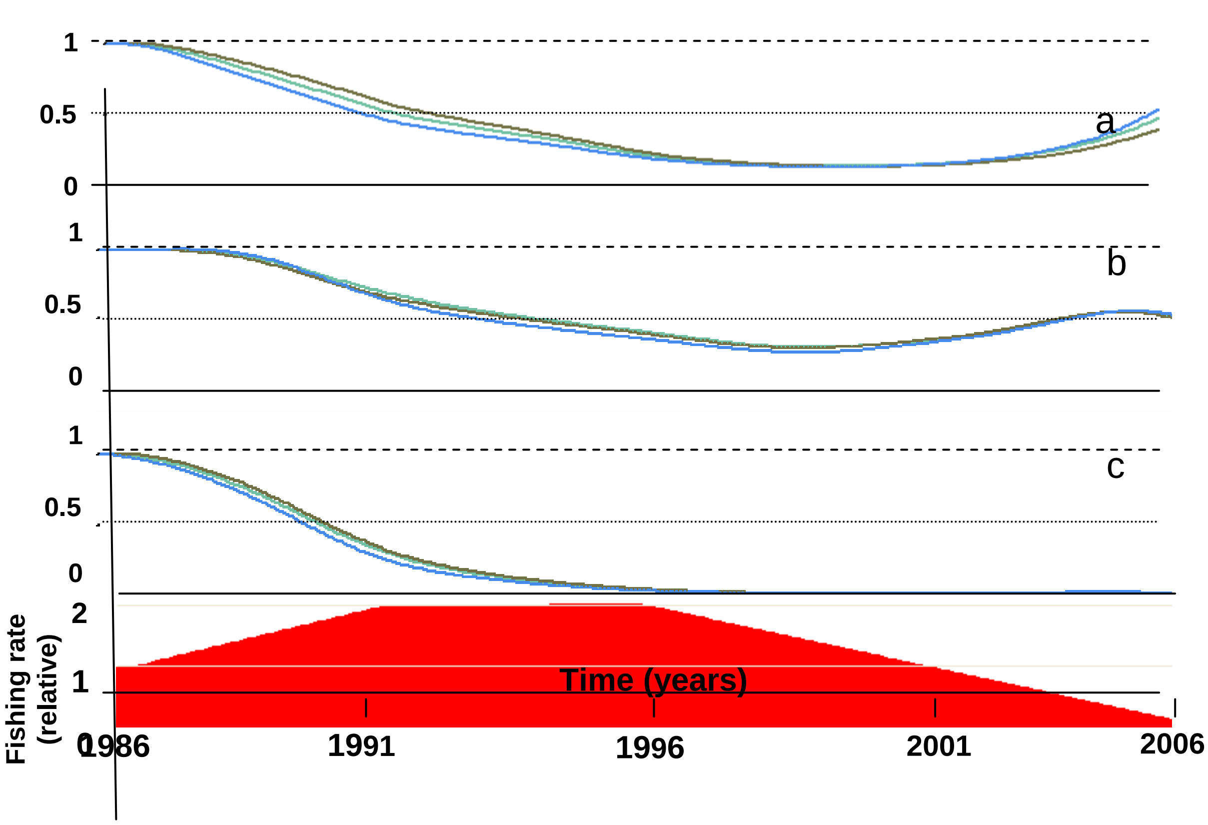

Figure 62: Predicted biomass trajectories of banana prawn (*Penaeus merguiensis*) juveniles (green line), sub-adults (brown line), and adults (blue line) in response to caricatured trawling rate history scenario shown in bottom panel: a gradual doubling from 1986 to 1989 then a gradual decrease from 1996 until the present.

Examination of the broader community effects of a gradual doubling of both banana prawn and tiger prawn trawling rates from 1986 levels (Figure 63) indicates that Albatross Bay area prawn trawl fisheries modify the structure of the biological community strongly—reducing the biomasses of a broad array of functional groups (mostly those at upper to mid trophic levels) while allowing another suite of functional groups to increase (mostly at mid to lower trophic levels).

A closer examination of this broad pattern of community modification reveals predicted impacts that are consistent with the general life habits, life history characteristics, and bycatch rates of the various functional groups. For example, sea snakes, offshore sharks, and other large offshore benthic and benthopelagic piscivore and invertivore groups decreased, whereas some pelagic fish groups and cephalopods increased with increased prawn trawling. Crabs decreased, whereas less vulnerable and faster growing scavengers, herbivores, and planktivores increased.

In general, this simulation exemplifies the potential usefulness of this modelling approach. The present iteration of the Albatross Bay model produces simulations that provide qualitatively useful insights. Future refined iterations of the model can provide accurate and prescriptive simulations if further investments are made to continue developing and refining this model.

If these preliminary simulations are accurate qualitatively (e.g., considerably decreased banana prawn trawling decreases banana prawns) one implication is that prawn trawl fisheries are ‘productive’ *because* this form of fishing modifies the overall ecosystem to the benefit of prawns through, for example, the reduction of the predators and competitors of prawns through bycatch. The humans in this system reduce their own competitors non-selectively and this generally tends to increase prawn biomass until a ‘tipping point’ of fishing rate beyond which prawns begin to become overfished directly, or until the non-selective modification of the resident assemblage favours species that are effective predators of prawns, or until both effects manifest. This is indicated by the combination of direct and indirect effects revealed through the simplified scenarios, and by the evidence presented previously (and below) that certain apex predators, which are vulnerable to prawn trawling, facilitate banana prawns by controlling key “vampires from the basement”. Obviously, the 1986 Albatross Bay community was not ‘pristine’ or un-fished, and indeed it appears that the 1986 banana prawn trawling rate was higher than optimal for banana prawn biomass (Figure 61 (a) and (c)), but simulations using this as a starting point still provide very useful insights.

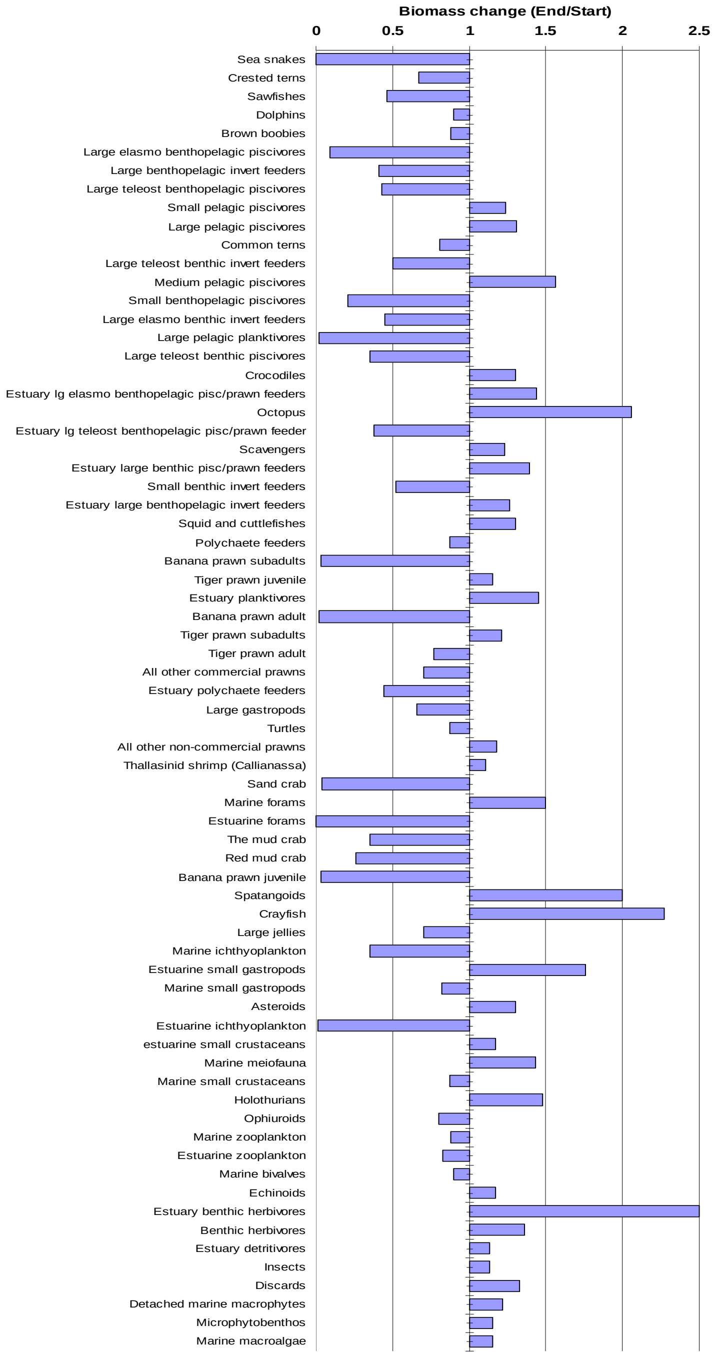

Figure 63: Predicted changes in each functional group in the Albatross Bay model 20 years after a gradual linear doubling of both banana prawn and tiger prawn trawling rate from 1986 levels (Scenario c in Figure 60). Groups are presented in order of descending trophic level and only those groups that were predicted to change greater than ten percent are presented.

It is not surprising that a fishery with high rates of bycatch, such as Australia's Northern Prawn Fishery, would encounter unexpected and indirect ecological outcomes of fishing. Examination of preliminary Albatross Bay Ecopath model simulations indicates that the depletion of certain apex predators (e.g., via trawl bycatch) reduces banana prawn biomass by, for example, enabling the emergence (increase in biomass) of organisms that impose mortality on banana prawns. Such indirect trophic effects, or 'trophic cascades', might well be common in marine ecosystems, albeit difficult to see or detect without empirically-based trophodynamic models and empirical studies to evaluate their existence and strength. The present trophodynamic modeling approach is ideally suited to highlight such trophic cascades, especially those that are strong and conspicuous.

Vampires from the basement

"Vampires from the basement" are species that might compete with humans for food and whose populations increase unexpectedly when ecosystems are perturbed by fishing, thus causing ecological outcomes unwelcome to human users of the system (C. Walters, personal communication). If fishing reduces or removes biotic components in an ecosystem, other biota are likely to replace those that were removed because of the sudden availability of 'excess' exploitable energy (e.g., prey biomass). The perturbation of complex ecosystems can result in surprising increases of sometimes unexpected species as energy flows are redirected through the modified ecosystem linkages.

Note that two versions of the Albatross Bay model were used for this series of simulations—one that does not include banana prawns in stomatopod diets (the following three subsections) and one that does (the 'Stomatopod') subsection.

Octopus

Banana prawns decline in the Albatross Bay model if we simulate the removal of benthic sharks and rays (the 'Large elasmobranch benthic invertebrate feeders' functional group) by imposing high bycatch fishing mortality directly on that group (Figure 64). In this simulation, banana prawns declined because octopus increased as the result of removing this group.

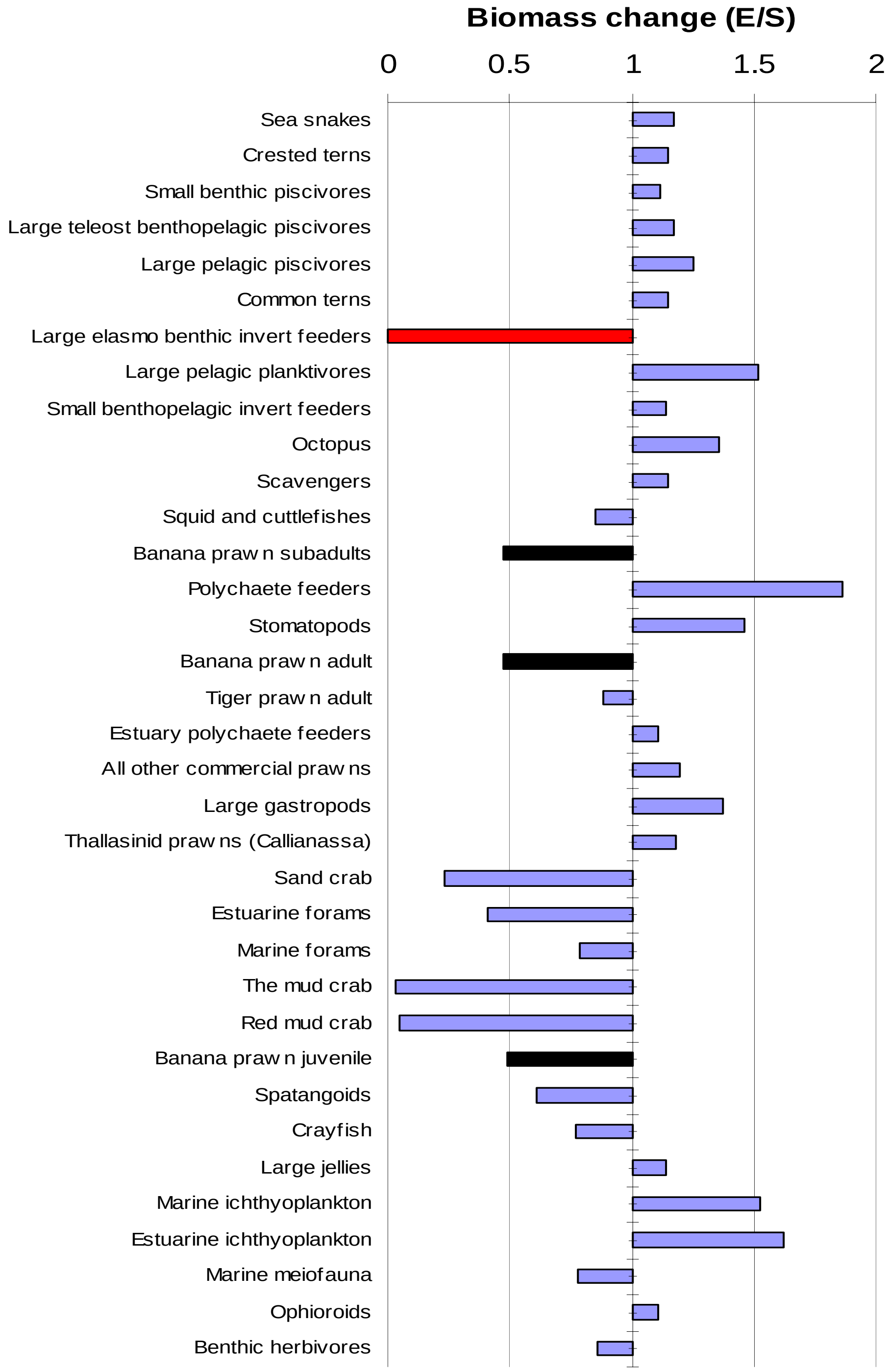

Figure 64: Simulated results of removing ‘Large elasmobranch benthic invertebrate feeders’ from the Albatross Bay ecosystem. The red bar indicates the functional group that was removed; the solid black bars represent banana prawn life stages. Functional groups are presented in order of descending trophic level and only those groups that were predicted to change greater than ten percent are presented.

It is important to note when interpreting Figure 64 that the bars represent relative change and do not indicate absolute biomass or consumption rates. Thus, one must examine the dynamics of both the relative changes in flows and the absolute flows in order to gain insights into emergent causality in these simulations. Examples of such diagnostics provided in the Ecosim routine include changes in mortality components, feeding time, consumption rates, predation mortality, and percent prey, in addition to changes in biomass, etc.

This trophic cascade manifests, not because rays are removed, but because the depletion of sicklefin weasel shark (*Hemigaleus microstoma)*—a component of this functional group and a specialist octopus-eater—enabled a considerable increase in octopus biomass, which in turn increased the mortality on banana prawns enough to cause a considerable decline. This mechanism of banana prawn biomass decline is quantitatively plausible based on the information in the model because prawn trawling is predicted to easily deplete benthic sharks and rays ('Large elasmobranch benthic invertebrate feeders'). This simulation reveals a plausible mechanism of banana prawn biomass declines driven indirectly by prawn trawling, an affect that could not be accounted for by single-species fisheries models.

The sicklefin weasel shark facilitates banana prawn populations by controlling an apparently important predator of prawns – even if this shark controls only one critical life stage of that predator – i.e., juvenile octopuses. When we simulate the removal of that shark species, banana prawns are predicted to decline as the result of increased predation pressure. Prawn trawling adversely affects this particular shark directly as bycatch, so at least in this one example the incidental capture of non-target species is indicated to reduce banana prawn populations indirectly and in a non-trivial way. Such simulations indicate possibilities, or hypotheses, that are plausible, thereby pointing the way toward approaches that can be developed to test these hypotheses. This indicates a trophic cascade that can be examined explicitly using this modeling framework, as opposed to simply speculating about its existence based on knowledge about the system, or as opposed to never thinking of this potentially real dynamic at all. Verification of such a mechanism could be accomplished through either experimental studies or field sampling designed to check the relative abundances and refine the modeling analyses.

Octopuses of the Albatross Bay area presumably impose much of their banana prawn mortality on sub-adults during or just after movement of these prawns from the estuaries to the offshore areas, thus potentially explaining why January prawn "recruitment" surveys often indicate moderate to high prawn biomass while April catches have been very low during recent years. If octopuses have indeed been more abundant during these recent years, they would impose their increased prawn mortality on the fishing grounds between January and April of each year. The bycatch / shark / octopus explanation is plausible and should be evaluated further using simulation and direct empirical studies.

The removal of the 'Small benthopelagic invertebrate feeding fishes' functional group—the other main predator of octopus—also causes a predicted collapse of all banana prawn life stages because its removal enables octopus to increase considerably, which imposes prolonged increased mortality on sub-adult and adult banana prawns, though slow increases in benthic sharks and rays ('Large elasmobranch benthic invertebrate feeders') eventually begins controlling octopus in this simulation. However, the 'Small benthopelagic invertebrate feeding fishes' functional group is not predicted or observed to have declined as the result of prawn trawling, so this simulation does not indicate a likely explanation for the recent declines in banana prawn catches. The starting fishing mortalities and predation mortalities of each bycatch functional group are specified for the 'starting period' in the Ecopath model and those mortality rates change over time during Ecosim dynamic simulations. During these simulations, there was never any indication that the 'Small benthopelagic invertebrate feeding fishes' functional group declined as the result of any of the simulations.

Simultaneous vampires

When we simulate the removal of 'Large teleost benthopelagic piscivores' (trevallies, snappers, and barracuda) from the Albatross Bay model, banana prawn biomass is predicted to decline dramatically (by 90%). This decline manifests because of increases in three predators of juvenile and subadult banana prawns: 'Estuary large benthic fish/prawn eating fishes', octopus, and stomatopods. The removal of this functional group also enables increases of three groups that feed on adult prawns ('Small benthic piscivores, small benthopelagic invertebrate feeders, and octopus), but the decline is caused principally by the aforementioned predation on the juvenile and subadult life stages. This simulation represents another plausible explanation for the recent observed declines in banana prawn catches, as the biomass of 'Large teleost benthopelagic piscivores' is predicted to be affected strongly (decreased) by prawn trawling (Figure 63). The present simulation is also consistent with the observed moderate to high January biomasses of banana prawn “recruits,” since much of the predation on these prawns might occur between January and April given the life history of banana prawns.

Barramundi

Sharks are indicated by yet another simulation to facilitate prawns in the Albatross Bay area, in this case due largely to their control of barramundi. If we simulate the removal of the ‘Estuary large elasmobranch benthopelagic pisc/prawn feeders’ (estuary carcharhinid sharks), banana prawn biomass is predicted to decline (by 70%) because of increases in barramundi biomass and subsequent mortality of juvenile and sub-adult life stages of banana prawns. This simulation indicates the importance of estuarine sharks in facilitating and maintaining prawn populations. However, the estuary sharks group is not indicated to have declined as the result of prawn trawling (because they reside principally in the protected estuaries). Other evidence indicates that estuary shark populations in the Albatross Bay region might be healthy for the time being due to inshore fishery restrictions. This estuary shark / barramundi explanation, therefore, should not be considered a highly plausible explanation for the recent observed declines in banana prawn catches, even though it does stand out as an issue for future management. Management that maximizes barramundi populations would, according to the current Albatross Bay model, tend to degrade banana prawn resources, and *vice versa*. All of the examples presented thus far indicate trade-offs between species, but the barramundi example is easiest to visualize: You can have lots of Barramundi, or you can have lots of prawns, but it might not be possible to have both.

Stomatopods

Early simulations using straw-man versions of the Albatross Bay model indicated that stomatopod mortality might overwhelm other sources of banana prawn mortality (fishes and fishery), even when very low proportions of stomatopod diet is comprised of banana prawns (see e.g., Figure 58). This high mortality imposed by stomatopods on prawns is indicated by high biomasses of stomatopods from fish diet information, even when the high end of stomatopod production rate estimates are used in the model in order to minimize the estimated stomatopod biomass. The stomatopod sub-web is among the most complex functional group sub-webs in the Albatross Bay model (Figure 65). This sub-web shows the empirically-based high demand for stomatopods by fish predators, which necessitates the calculated high stomatopod biomass. The relative flows from prawn groups to stomatopods are very small, but the biomass of banana and other commercial prawn groups are specified to be small compared relative to that of stomatopods making the effect strong even though the flows are not large.

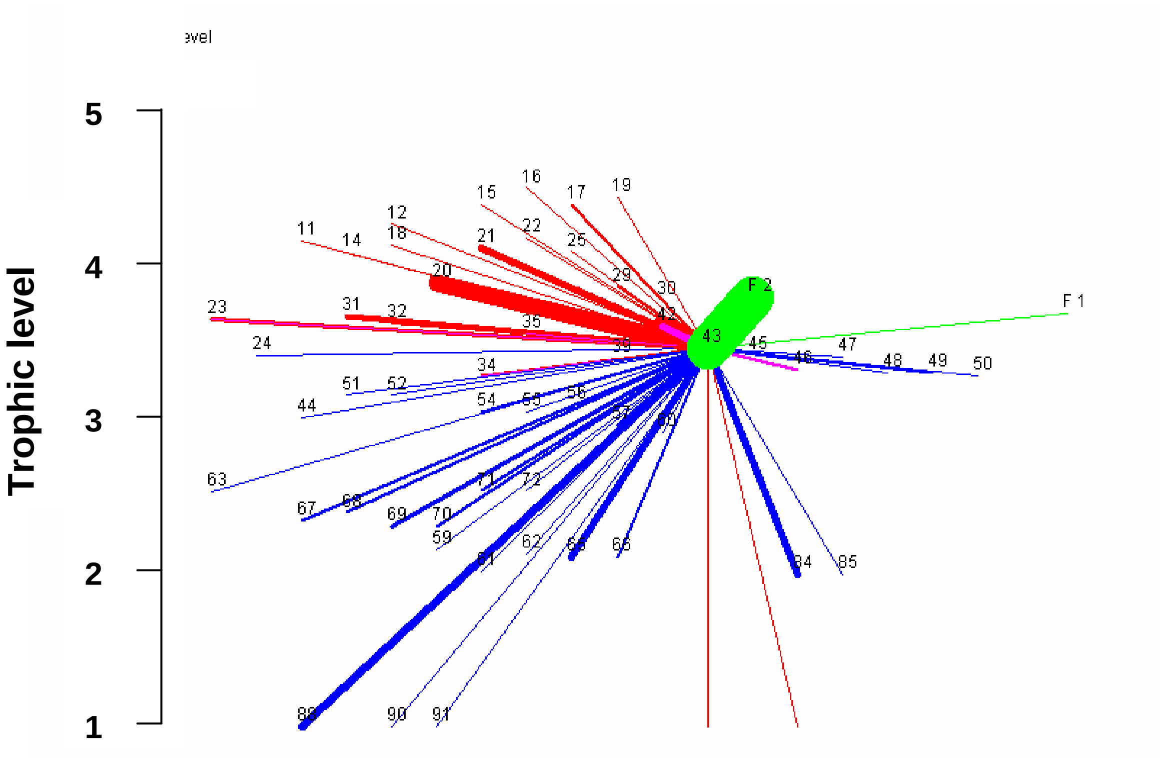

Figure 65: The stomatopod sub-web of the Albatross Bay area, Gulf of Carpentaria. Line thickness indicates relative magnitude of flows. Red lines are flows to predators (and detritus), blue lines are flows from prey, and the green lines are bycatch flows to the fisheries. F1 is the banana prawn trawl fishery and F2 is the tiger prawn trawl fishery. The flows of stomatopods to fish predators (red lines) is reasonably well known for the Albatross Bay area, whereas the stomatopod diet composition used here is borrowed from other systems and based on the author's judgement.

The simulations described in the previous sub-sections were conducted using a version of the Albatross Bay model in which stomatopods were not specified to consume banana prawns because of the high uncertainty of stomatopod diets in the Albatross Bay area, and in the Gulf of Carpentaria. Subsequent preliminary work has indicated that prawns might be the exclusive component of stomatopod diet, at least during some portions of the year (Melissa Robinson, University of Queensland, personal communication). The simulations described in the present sub-section were conducted with a version of the Albatross Bay model in which 5% of the stomatopod diet consisted of adult banana prawns, 1% consisted of sub-adult banana prawns, and 1% consisted of juvenile banana prawns.

Banana prawns are predicted to decline by 60% when offshore carcharhinid sharks ('Large elasmobranch benthopelagic piscivores') are removed from the system, and this is mediated ultimately by stomatopods (no figure). This decline is manifested in the model through a six-link trophic cascade (including humans). This cascade can be simplified as a chain of strong interactions. The removal of carcharhinid sharks causes an increase in the biomass of 'Small benthic piscivores' (*Saurida* spp. and *Platycephalus* spp.), which causes a decrease in squid and cuttlefish, which in turn causes an increase in stomatopods, which then causes a decline in juvenile and sub-adult banana prawn biomass, which is finally predicted to cause adult banana prawn biomass to decline.

The plausibility of such an indirect (and seemingly unrealistically long) trophic cascade is justified because some of the predator functional groups are affecting their prey biomass by consuming early life stages of their prey, and this can be examined more explicitly in future iterations and refinements of the model. Other issues detract from the plausibility of this particular trophic cascade mechanism of banana prawn decline. For example, squid and cuttlefish might decline if the Albatross Bay system were bounded, but it is an open system in reality, and so the current iteration of the model might overestimate the impact of small benthic piscivores on squid and cuttlefish biomass, which in reality might typically replenish from a more oceanic meta-population, and this might be true for several other functional groups. These issues too can be adjusted and refined in future iterations of the model. Observed increases, rather than decreases, of squid and cuttlefish in this system might also discredit this simulation/hypothesis.

In addition to obvious implications about the critical role of carcharinid sharks in structuring and regulating the Albatross Bay ecosystem (and potentially facilitating banana prawns), this simulation indicates the potentially central role of stomatopods in helping to structure and regulate this system, even if the entire cascade is qualitatively incorrect. Stomatopods influenced banana prawns very strongly in this simulation through only 2% of their diet at the most since the main effect manifested through juvenile and sub-adult banana prawns rather than adults (5% of the stomatppod diet was on adult banana prawns). It is very likely that banana prawns make up considerably more than 7% (2% + 5%) of the stomatopod diet, and that could mean that stomatopods (and sharks) are the key(s) to understanding banana prawn (and tiger prawn) dynamics.

Removal of ‘Large teleost benthopelagic piscivores’ (trevallies, snappers, and barracuda) from this “Stomatopod feeding” version of the Albatross Bay model causes a predicted 99% decline in banana prawn biomass through the very same trophic cascade described above for the removal carcharhinid sharks. This indicates, as discussed previously in the context of the “non-stomatopod feeding”, that the trevallies-snappers-barracuda functional group is also a key facilitator of banana prawns. This could be wrong, but it is what the current versions of the Albatross Bay model indicates presently.

The removal of the ‘Small benthic invertebrate feeding fishes’ functional group also causes banana prawns to decline (by ~20%), primarily by enabling increases in stomatopods, which impose increased mortality on juvenile and sub-adult banana prawns.

Time series fitting

In addition to driving the Ecosim simulations with the simplified fishing scenarios described above, simulations were also driven by quantitatively derived historical time series of effort in the seven fishing fleets as a way to attempt reconstruction of past ecosystem and fishery changes more accurately and precisely than the simplified scenarios could. The goal of this effort was to impose these historical time series of effort to the existing catches and discards in the 1986-1992 base model (left hand panels of Figure 66 and Figure 68) in order to fit the resulting predicted biomass trajectories with observed catch trajectories and indices of biomass. Two different indices were used (The banana prawn index is the relative time required to capture 90% of the banana prawn catch, and the tiger prawn index is catch per unit effort.) because catch per unit effort was even more variable for banana prawns, and not viewed as useful. To accomplish the best fit to the observed data, Ecosim uses an optimization routine to search for the combination of prey rates that will reduce the sum of squares of the divergences of predicted from observed (Christensen et al. 2004). The simulated banana prawn biomass trajectory followed rough index of biomass that was used, in the roughest sense, but the fit to the highly variable observations was poor (Figure 66).

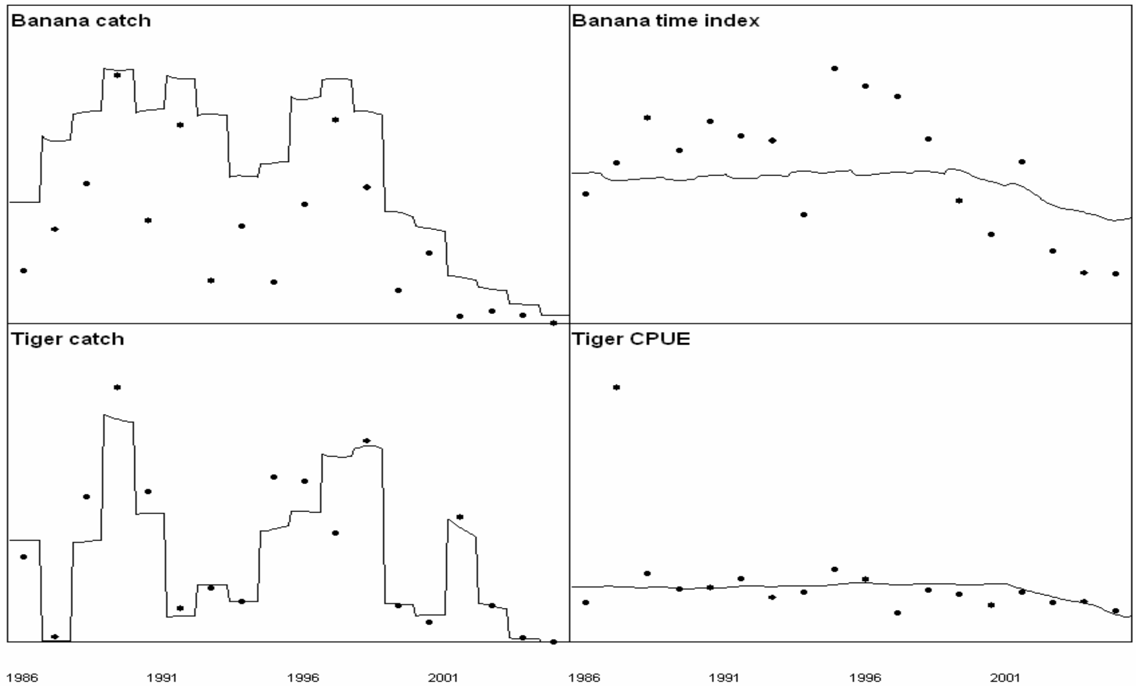

Figure 66: Predicted trajectories of catches and biomasses of banana prawns and tiger prawns (lines) fitted to historical observations of catches and biomass indices (dots), driven by historical changes in fisheries effort. The banana prawn index (upper right panel) is the relative time required to capture 90% of the banana prawn catch. The tiger prawn index (lower right panel) is catch per unit effort.

These results indicate that historical fishing effort, within the context of the trophodynamic interactions specified in this version of the Albatross Bay Ecopath model, can only partially explain the "observed" decline in banana prawn and tiger prawn biomass in recent years and in the very roughest of ways. The Ecosim fitting routine can also be set to search for anomalies of error in fitting, which could be considered anomalies of primary production (Figure 67), which can then be used to drive biomass trajectories in combination with the fisheries time series in order to improve the fit of those trajectories to the observed data. This is used as a big 'error term' that is called a production anomaly. This production anomaly error term improved this preliminary poor fit only slightly (Figure 68).

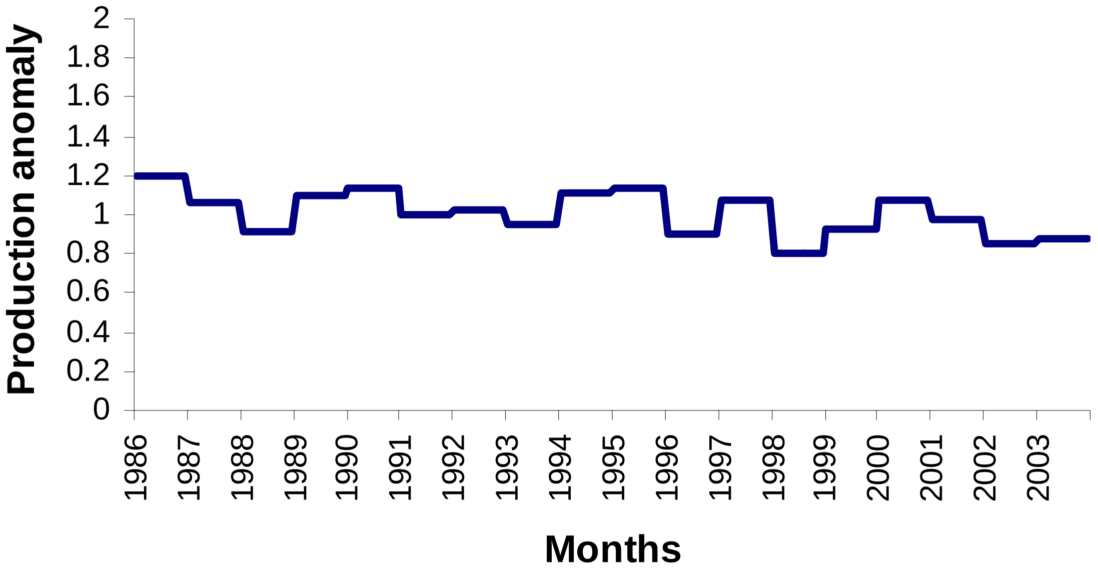

Figure 67: Anomaly produced during a search for error in fitting predicted biomass trajectories to "observed" biomasses in Albatross Bay using historical fisheries information. This error anomaly was used as an anomaly of production to try to improve this fit.

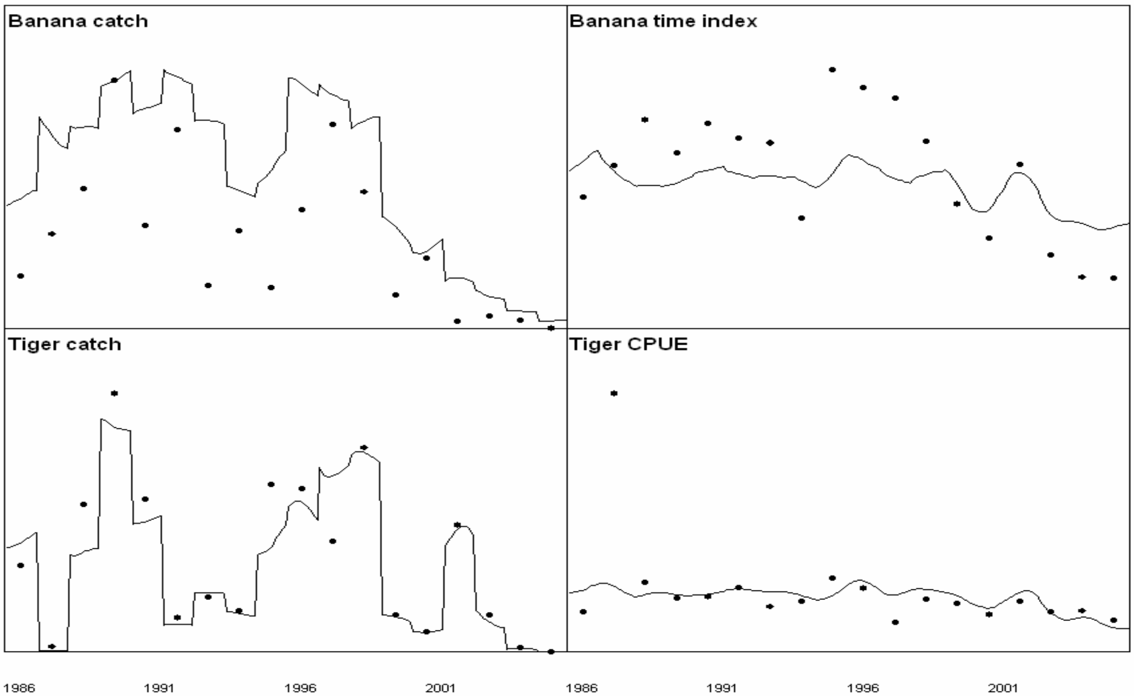

Figure 68: Predicted trajectories of catches and biomasses of banana prawns and tiger prawns (lines) fitted to historical observations of catches and biomass indices (dots), driven by a combination of historical fisheries effort and a produced anomaly of "primary production" error.

Ecological model refinement

It is challenging to construct a static trophodynamic model of a tropical marine ecosystem and to refine it to the point where begins to provide useful and insightful results that relate to management of the human activities in the system, such as the predominant fisheries. Sections 8 and 10 illustrate this usefulness in the sense that system structure and flows can be summarized quantitatively and the dynamics and functionality of the system can be characterized such that the results of simulations might be considered reliable, at least qualitatively.

The existing Albatross Bay model is considered preliminary. Most parameters in the model need to be further reviewed, checked, and refined before the model can be used for rigorous quantitative prediction in the sense of reconstructing past ecosystem changes accurately. Nevertheless, the qualitative results of quantitative simulations, e.g. the relative magnitudes of predicted changes, can be examined using this preliminary iteration of the model to help understand the overall effects of fisheries and other stressors, to gain insights into the causes of recently observed catch declines, and to improve understanding of system structure, functions, and interactions.

It is even more challenging to reconstruct ecosystem changes in a complex tropical ecosystem such that the results of simulations are quantitatively accurate and precise. This was beyond the scope of the present study, which was scoped to construct a preliminary trophodynamic model as a framework for understanding the food web and ecosystem and to conduct preliminary simulations to gain insights into the banana prawn dilemma at hand. A reconstruction of ecosystem changes was attempted nevertheless. Although considerable time was devoted to refining model input parameters to develop this analysis, the present author does not consider present results of the time series fitting analysis to be reliable. Rather, they serve here as an example of the types of analysis that can be conducted if investments are made to refine this simulation approach and the underlying model further. If such an investment is made the reliability of this approach to accurately reconstruct ecosystem changes can be improved considerably, though some basic problems are beyond the control of a desktop modeling exercise. Several problems prevent straightforward time series fitting simulations.

One major category of problems with the time series fitting is the apparent high temporal (e.g., inter-annual) variability in populations (e.g. prawn populations) and in fishery catch and effort. This high variability is difficult to simulate or reconstruct using the present iteration of the Albatross Bay Ecopath model while minimizing an erosion of model reliability. That is to say, high variability probably magnifies the effect of imprecision in the response speed of biotic groups to changes in fishing, predation, or resources. This problem could result from the underlying behavior of the Ecopath with Ecosim model formulation, but since the approach features variable speed splitting and other features that account for biological components that change at different speeds, the reliability of this model can probably be improved vastly by parameterizing the dynamics more carefully and correctly during future iterations of model refinement. Another major problem is the lack of reliable biomass indices (i.e., observed biomass) to fit the predicted biomass trajectories against. A third problem is the lack of adequate time series of primary production, river flow rates, and other important physical variables in the system that could be specified as a time series that forces selected biotic components in the model.

Fish biomasses and diet compositions are comparatively rigorous in the Albatross Bay model as the result of comprehensive site-specific studies of the fish fauna of the Albatross Bay area. It is fortuitous that this information exists, as it provides the model with a good grounding of idea the predation pressure of fishes on prawns. The input parameters of other functional groups in the system – both at higher and lower trophic levels – are far less certain, and these parameters will need to be re-examined iteratively and prioritized so that research efforts on the system can be optimized to understand the whole Albatross Bay banana prawn ecosystem.

Other necessary refinements include improved estimations of fisheries catch and discard information for all the fleets, for the time period in question, where possible. Estimates of temporal (time series) changes in primary production, biomass, and fisheries information will also need to be refined continually. Information on habitats and spatial aspects of the system and functional groups will enable spatially-explicit explorations of potential future spatial policies, but spatial refinements and analyses are outside the scope of the present project. Finally, specification of economic (and social) parameters in the model will allow innovative explorations of alternative management strategies. Such capabilities of this approach will potentially be the foundation for an explicit and integrated decision support system.

Trophodynamics conclusions

Given those caveats and limitations, the preliminary simulations and other analyses presented in this report indicate that the prawn trawl fisheries of the Albatross Bay region modify the resident biological community considerably, even without considering impacts on biogenic habitat. The simulations indicate that this considerable modification occurs through both direct impacts on populations of marine organisms and indirectly through trophic cascades. They also indicate that changes in catch rates of banana prawns and tiger prawns, within the magnitudes actually experienced over the past 20 years, can cause depletions of banana prawn biomass that would be severe enough to cause decreases in catch rates like those actually encountered during the last few years.

An intriguing result is that banana prawn biomasses were predicted to decrease considerably from 1986 levels with either increases or large decreases in prawn trawl catch rates, and the only apparent way to increase it marginally is by marginal decreases in prawn trawl catch rates, or with a complete reduction in tiger prawn trawl catch rates, or both. This result indicates that, up to a point, prawn trawling generally facilitates prawn biomass in this system, purely through the modification of the biological community in ways that benefit prawns—i.e., through trophic interactions. Beyond a certain point of fishing intensity, the effect of prawn trawling inhibits prawn biomass through both direct exploitation and indirect trophic effects.

An additional series of explorations and simulations indicates the presence of key banana prawn facilitators. The removal of these facilitating species/biotic groups causes the emergence of certain species (vampires from the basement) that cause considerable declines in banana prawns in the Albatross Bay ecosystem model. The presence of these trawler-facilitator-vampire-prawn cascades indicate plausible mechanisms for explaining how prawn trawling can indirectly cause sudden and persistent declines in banana prawn biomasses and catches that are surprising, in addition to direct impacts on prawn stocks. Other cascades and mechanisms might well exist in this system, and those highlighted might well be weaker than indicated by this preliminary series of analyses. Further refinement of the Albatross Bay model is needed to answer these questions with confidence.

It is nevertheless clear from this series of simulations that the present modeling approach holds considerable potential for understanding the Albatross Bay marine ecosystem (and by extension more of Australia’s northern ecosystems); the impacts of Australia’s prawn (and other) fisheries; and for informing fisheries and conservation policies. Although the present model and example simulations provide general insights about the impacts of Australia’s northern prawn trawl fisheries, they represent only the first step towards the development of a working trophodynamic Ecopath model that produces predictions that could be accurate and precise enough to be used explicitly for purposes such as quota setting.

Even though some lines of evidence that emerged from this modeling exercise support the notion that overfishing caused banana prawn declines, the present lack of quantitatively reliable reconstructions of ecosystem changes (i.e., explicit time series fitting using environmental variables or catch histories) prevents us from concluding whether or not the recent history of fishing actually did cause such biomass declines. Refinement of the present model might well enable a compelling discernment of at least some of the possibilities in addition to providing Management Strategy Evaluation type bio-economic modeling, policy optimization routines based on trade-offs in maximizing disparate values in the system, spatially-explicit approaches to simulating fishery dynamics and the effects of closed areas, and other implications of human activities in these complex ecosystems.

TROPHOAPPENDIX A: Albatross Bay model contributors

The list presented below includes all of the individuals who contributed in some way to the scoping, development, or construction of the Albatross Bay Ecopath model.

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TROPHOAPPENDIX B. Diet composition matrix for the albatross Bay Model

	Prey \ Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	Dolphins																					
2	Dugongs																					
3	Crocodiles																					
4	Turtles			0.008				0.02														
5	Sea snakes																					
6	Lesser frigates											2E-06										
7	Brown boobies																					
8	Crested terns																					
9	Common terns																					
10	Large pelagic piscivores																					
11	Medium pelagic piscivores	0.02										9E-04					0.001					
12	Small pelagic piscivores	0.02				0.013	0.47	0.301				0.009					0.005	1E-05		0.007	0.006	
13	Sawfishes																					
14	Large teleost benthic piscivores	0.02										1E-05				0.003	0.005	0.001		0.016		
15	Small benthic piscivores	0.02				0.3									0.003		0.09	0.046	0.009	0.02	0.002	0.005
16	Large elasmo benthopelagic piscivores																					
17	Large teleost benthopelagic piscivores	0.01															1E-04	0.003				
18	Small benthopelagic piscivores	0.02													0.011	0.01	0.01	0.022		0.004		
19	Large benthopelagic invert feeders	0.001																				
20	Small benthopelagic invert feeders	0.001				0.179	0.093	0.068	0.534	0.05		0.068	0.021	0.801	0.115	0.216	0.221	0.251	0.241	0.089		0.005
21	Large elasmo benthic invert feeders																			0.164		
22	Large teleost benth invert feeders	0.03														0.005	0.006					
23	Small benthic invert feeders	0.02				0.394	0.077	0.283	0.307			0.011			0.011	0.05	0.08	0.047	0.007	0.091	0.005	0.018
24	Polychaete feeders															0.03	0.04	0.047		0.004	0.034	0.114
25	Large pelagic planktivores	0.2			0.007																	
26	Small pelagic planktivores	0.187			0.007	0.014	0.36	0.328	0.159	0.95	0.706	0.721	0.583		0.03	0.293	0.07	0.092	0.17	0.168	0.006	2E-05
27	Benthic herbivores															0.003		0.01				
28	Scavengers																					
29	Estuary lg elasmo benthopelagic pisc/prawn feeders															0.005						
30	Estuary lg teleost benthopelagic pisc/prawn feeder			0.077								0.005				0.005	0.008					
31	Estuary large benthic pisc/prawn feeders			0.077								0.004				2E-04	0.012	0.02		0.003	0.001	
32	Estuary large benthopelagic invert feeders			0.077													0.001			0.009		
33	Estuary large benthic invert feeders (Rays)			0.038																		
34	Estuary polychaete feeders			0.038												0.011	0.004	0.006		0.011		
35	Estuary small benthic invert feeders			0.076								0.002				0.02	0.023	0.005	0.002	0.009	0.001	3E-05
36	Estuary planktivores	0.02									0.222	0.069	0.394		0.01	0.022	7E-04	0.008	0.026		0.006	
37	Estuary detritivores			0.076								0.055				0.027	0.054	0.02		0.004	0.012	0.01
38	Estuary benthic herbivores			0.076								1E-03					0.004			0.001		
39	Estuary insectivores			0.038																		
40	Estuary pelagic herbivores			0.076								0.03				7E-04	0.001			0.006		
41	Octopus	0.001											4E-05		0.004	1E-05	0.022	0.008	1E-03	0.019	0.013	0.045
42	Squid and cuttlefishes	0.4									0.072	0.016			0.061	0.217	0.114	0.12	0.053	0.01	0.082	0.006
43	Stomatopods											0.001	1E-04		0.056	0.004	0.072	0.024	0.003	0.028	0.035	0.145
44	Banana prawn juvenile																					
45	Banana prawn subadults																					

	Prey \ Predator	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
1	Dolphins																					
2	Dugongs																					
3	Crocodiles																					
4	Turtles																					
5	Sea snakes																					
6	Lesser frigates																					
7	Brown boobies																					
8	Crested terns																					
9	Common terns																					
10	Large pelagic piscivores																					
11	Medium pelagic piscivores								0.001	0.009												
12	Small pelagic piscivores								0.034	0.015												
13	Sawfishes																					
14	Large teleost benthic piscivores		7E-04						0.006	3E-04												
15	Small benthic piscivores	0.011	0.005						0.007	0.005	5E-06	0.006										
16	Large elasmo benthopelagic piscivores																					
17	Large teleost benthopelagic piscivores								0.03	9E-04	0.01											
18	Small benthopelagic piscivores		0.002						0.002	3E-04												
19	Large benthopelagic invert feeders																					
20	Small benthopelagic invert feeders	0.285	0.05						0.04	0.055	0.009	0.09				0.069					0.06	
21	Large elasmo benthic invert feeders																					
22	Large teleost benth invert feeders								0.006	0.002											0.003	
23	Small benthic invert feeders	0.003							0.023	0.03	0.005				0.029						0.01	
24	Polychaete feeders	0.075							0.01	0.007	0.02				0.028						0.02	
25	Large pelagic planktivores																					
26	Small pelagic planktivores	0.012	0.02		0.604				0.16	0.206	0.042	0.013				0.111						0.36
27	Benthic herbivores									0.003											0.007	
28	Scavengers	0.001																				
29	Estuary lg elasmo benthopelagic pisc/prawn feeders									0.003												
30	Estuary lg teleost benthopelagic pisc/prawn feeder								0.04													
31	Estuary large benthic pisc/prawn feeders		1E-03		0.013				0.03	0.002												
32	Estuary large benthopelagic invert feeders									3E-04												
33	Estuary large benthic invert feeders (Rays)																					
34	Estuary polychaete feeders								0.002	0.002												
35	Estuary small benthic invert feeders	0.014	0.001		0.002				0.062	0.005	0.005	0.003	0.009		0.009							
36	Estuary planktivores				0.181				0.006	0.042	0.01				0.019							
37	Estuary detritivores								0.381	0.366	0.069	5E-04										
38	Estuary benthic herbivores									0.004												
39	Estuary insectivores																					
40	Estuary pelagic herbivores								0.051	0.04	0.03											
41	Octopus	0.008	0.003								0.002	0.001			1E-04							
42	Squid and cuttlefishes	0.055	1E-04		7E-04				0.018	0.027	0.003	0.011							3E-05			0.01
43	Stomatopods	0.022	0.028		0.004				0.037	0.006	0.043	0.011		0.014	0.003				0.003			0.05
44	Banana prawn juvenile								0.001	0.003	0.005				0.0003	0.00007			0.003		0.010	0.001
45	Banana prawn subadults							0.002	0.001	0.003	0.005				0.0003	0.00007			0.003		0.010	0.001

	Prey \ Predator	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62
1	Dolphins																				
2	Dugongs																				
3	Crocodiles																				
4	Turtles																				
5	Sea snakes																				
6	Lesser frigates																				
7	Brown boobies																				
8	Crested terns																				
9	Common terns																				
10	Large pelagic piscivores																				
11	Medium pelagic piscivores																				
12	Small pelagic piscivores																				
13	Sawfishes																				
14	Large teleost benthic piscivores																				
15	Small benthic piscivores																				
16	Large elasmo benthopelagic piscivores																				
17	Large teleost benthopelagic piscivores																				
18	Small benthopelagic piscivores																				
19	Large benthopelagic invert feeders																				
20	Small benthopelagic invert feeders																				
21	Large elasmo benthic invert feeders																				
22	Large teleost benth invert feeders																				
23	Small benthic invert feeders	0.002																			
24	Polychaete feeders	0.002																			
25	Large pelagic planktivores																				
26	Small pelagic planktivores																				
27	Benthic herbivores																				
28	Scavengers																				
29	Estuary lg elasmo benthopelagic pisc/prawn feeders																				
30	Estuary lg teleost benthopelagic pisc/prawn feeder																				
31	Estuary large benthic pisc/prawn feeders																				
32	Estuary large benthopelagic invert feeders																				
33	Estuary large benthic invert feeders (Rays)																				
34	Estuary polychaete feeders	0.003																			
35	Estuary small benthic invert feeders	0.001																			
36	Estuary planktivores																				
37	Estuary detritivores																				
38	Estuary benthic herbivores																				
39	Estuary insectivores																				
40	Estuary pelagic herbivores																				
41	Octopus																				
42	Squid and cuttlefishes	0.1																			
43	Stomatopods				0.003																
44	Banana prawn juvenile	0.002																			
45	Banana prawn subadults																				

	Prey \ Predator	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85
1	Dolphins																							
2	Dugongs																							
3	Crocodiles																							
4	Turtles																							
5	Sea snakes																							
6	Lesser frigates																							
7	Brown boobies																							
8	Crested terns																							
9	Common terns																							
10	Large pelagic piscivores																							
11	Medium pelagic piscivores																							
12	Small pelagic piscivores																							
13	Sawfishes																							
14	Large teleost benthic piscivores																							
15	Small benthic piscivores																							
16	Large elasmo benthopelagic piscivores																							
17	Large teleost benthopelagic piscivores																							
18	Small benthopelagic piscivores																							
19	Large benthopelagic invert feeders																							
20	Small benthopelagic invert feeders																							
21	Large elasmo benthic invert feeders																							
22	Large teleost benth invert feeders																							
23	Small benthic invert feeders																							
24	Polychaete feeders																							
25	Large pelagic planktivores																							
26	Small pelagic planktivores																							
27	Benthic herbivores																							
28	Scavengers																							
29	Estuary lg elasmo benthopelagic pisc/prawn feeders																							
30	Estuary lg teleost benthopelagic pisc/prawn feeder																							
31	Estuary large benthic pisc/prawn feeders																							
32	Estuary large benthopelagic invert feeders																							
33	Estuary large benthic invert feeders (Rays)																							
34	Estuary polychaete feeders																							
35	Estuary small benthic invert feeders																							
36	Estuary planktivores																							
37	Estuary detritivores																							
38	Estuary benthic herbivores																							
39	Estuary insectivores																							
40	Estuary pelagic herbivores																							
41	Octopus																							
42	Squid and cuttlefishes																							
43	Stomatopods																							
44	Banana prawn juvenile																							
45	Banana prawn subadults	0.002																						

	Prey/Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
46	Banana prawn adult	0.001										0.001		0.138		0.008	0.024	0.009		0.012	0.005	0.002
47	Tiger prawn juvenile																					
48	Tiger prawn subadults																					
49	Tiger prawn adult	0.001										4E-04			7E-06		0.012	0.011		0.005	6E-04	0.01
50	All other commercial prawns											6E-05			0.004	5E-04	0.021	0.016		0.002	0.002	0.014
51	Thallasinid prawns (Callianassa)			0.008											0.03	2E-04	1E-03	0.006	0.161	0.001	0.2	0.073
52	All other non-commercial prawns			0.008								9E-04			0.03	0.014	0.034	0.03	0.077	9E-04	0.057	0.136
53	Crayfish			0.038								1E-05			0.024		7E-05	0.001	0.002		6E-04	0.003
54	The mud crab	0.001		0.008	0.058																	
55	Red mud crab	0.001		0.008	0.058																	
56	Sand crab	0.001			0.058							3E-05					0.001		9E-04	0.161		
57	Other large crabs	0.001		0.008	0.058							0.001	9E-04		0.498	0.001	0.023	0.104	0.011	0.134	0.205	0.319
58	Large gastropods	0.001		0.023																		
59	Holothurians														0.025			5E-04			0.001	0.004
60	Spatangoids																					
61	Echinoids														7E-04	5E-04	2E-04	5E-05			0.002	5E-05
62	Ophiuroids														1E-04		9E-04	0.002		1E-04	0.006	4E-04
63	Asteroids																				4E-05	
64	Sessile epibenthos				0.23										0.002	1E-05	7E-06	6E-05	7E-04	3E-05	0.001	5E-04
65	Marine bivalves	0.001			0.214																	
66	Estuarine bivalves	0.001												0.061	0.002	1E-04	0.001	0.006	0.005	0.003	0.02	0.002
67	Marine small crustaceans														0.003		7E-06	5E-04	1E-04	1E-04	0.044	7E-05
68	estuarine small crustaceans											3E-04	6E-04		0.012	0.001	0.003	0.007	0.027	0.019	0.024	0.028
69	Marine worms												4E-04		0.017	0.05	0.01	0.068	0.026	4E-05	0.183	0.014
70	Estuarine worms														2E-04		5E-05	2E-05			0.004	1E-04
71	Marine small gastropods														0.003	2E-05	2E-04	7E-04	2E-04	4E-04	0.003	0.002
72	Estuarine small gastropods																					
73	Marine meiofauna																					
74	Estuarine meiofauna																					
75	Marine forams																				8E-07	
76	Estuarine forams																					
77	Large jellies				0.08																	
78	Small jellies				0.02																2E-06	
79	Marine zooplankton	0.001										4E-04	6E-04		0.031	0.003	0.022	0.008	0.178	2E-04	0.04	0.044
80	Estuarine zooplankton																			2E-06	6E-05	
81	Marine ichthyoplankton																					
82	Estuarine ichthyoplankton																					
83	Insects											1E-06			0.017		0.001		4E-06		3E-06	
84	Marine microbial heterotrophs																					
85	Estuarine microbial heterotrophs																					
86	Marine phytoplankton																					
87	Estuarine phytoplankton																					
88	Microphytobenthos				0.05																	
89	Seagrass		1									1E-04			3E-04			9E-07		7E-06		
90	Estuarine macroalgae				0.08															3E-06	3E-06	
91	Marine macroalgae				0.08							2E-05										
92	Mangroves														2E-04	2E-05					3E-06	
93	Discards	0.005																				
94	Detached Marine macrophytes																					
95	Detached Estuarine macrophytes (estuarine)																					
96	Estuarine Water-column detritus											3E-04										
97	Estuarine Sediment detritus																					
98	Marine Water-column detritus																					
99	Marine Sediment detritus																					
	Import	0.015		0.25		0.1																
	Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

	Prey/Predator	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
46	Banana prawn adult									0.005											0.033	
47	Tiger prawn juvenile																					
48	Tiger prawn subadults								0.002	0.008	0.002	0.004	0.001								0.02	
49	Tiger prawn adult																					
50	All other commercial prawns		0.006						0.002	0.006	5E-04	0.002		0.001	0.003						0.01	
51	Thallasinid prawns (Callianassa)	0.058	0.03		9E-04				5E-04	0.015	0.039	0.009		0.009					0.032		0.01	
52	All other non-commercial prawns	0.005	0.053		5E-04	0.5		0.1	0.005	0.09	0.01	0.006		0.009	0.096				0.003		0.01	
53	Crayfish	2E-04			2E-05																0.01	
54	The mud crab																				0.04	
55	Red mud crab																				0.04	
56	Sand crab								0.002	0.003											0.04	
57	Other large crabs	0.241	0.15	0.088	0.091			0.485	0.029	0.021	0.326	0.291	0.347	0.033	0.236	0.066			0.599		0.25	
58	Large gastropods																				0.006	
59	Holothurians	9E-04	0.002						3E-04		0.001			2E-04								
60	Spatangoids																				0.01	
61	Echinoids	0.025	4E-04		5E-06				8E-04			0.004			0.003							
62	Ophiuroids	0.006	0.03		1E-05						3E-05	4E-04			0.014							
63	Asteroids										5E-05											
64	Sessile epibenthos	0.009	9E-04		7E-05				5E-06	2E-05	0.009					4E-05					0.11	
65	Marine bivalves		0.06					0.1													0.1	
66	Estuarine bivalves	0.033	0.03		0.002				3E-04	0.001	0.03	0.433	0.286	0.005	0.036	0.005					0.02	
67	Marine small crustaceans	0.003	0.14	0.53	0.001			0.1													0.02	0.06
68	Estuarine small crustaceans	0.007	0.06		0.034				5E-04	0.005	0.006	0.077	0.003	0.021	0.017	0.009			0.002		0.01	
69	Marine worms	0.051	0.12	0.198	3E-04			0.1	0.002	0.001	0.205	0.016	0.328	0.599	0.412	0.007					0.06	0.02
70	Estuarine worms		0.01																		0.01	
71	Marine small gastropods	0.006	0.05	0.184	3E-04			0.1	3E-04	0.001	0.01	0.006	0.013	0.001	0.004	2E-04			1E-04		0.02	
72	Estuarine small gastropods		0.006																		0.01	
73	Marine meiofauna		0.04					0.01													0.01	
74	Estuarine meiofauna		0.005																		0.005	
75	Marine forams		0.04		2E-05			0.005							7E-05							
76	Estuarine forams		0.01																			
77	Large jellies																					0.01
78	Small jellies																					0.01
79	Marine zooplankton	0.068	0.046		0.018	0.08			0.007	0.007	0.091	0.009	0.013	0.281	0.035	0.046			0.019			0.47
80	Estuarine zooplankton				2E-04	0.02										0.677						
81	Marine ichthyoplankton																					0.01
82	Estuarine ichthyoplankton																					
83	Insects									1E-06	0.001	6E-05		0.017		0.002			0.112			
84	Marine microbial heterotrophs																					
85	Estuarine microbial heterotrophs				0.048															0.1		
86	Marine phytoplankton					0.3																
87	Estuarine phytoplankton					0.1														0.7		
88	Microphytobenthos						0.1										0.15					
89	Seagrass								2E-04	1E-03	3E-04	0.003	5E-05									
90	Estuarine macroalgae									5E-04	3E-04	5E-05			0.037	3E-05						
91	Marine macroalgae						0.8															
92	Mangroves	2E-05	4E-05						2E-04	9E-04	0.005	5E-04	1E-04	0.01	0.018	0.008			0.226			
93	Discards																				0.007	
94	Detached Marine macrophytes						0.05											1				
95	Detached Estuarine macrophytes (estuarine)																					
96	Estuarine Water-column detritus									5E-05	1E-04						0.1			0.2		
97	Estuarine Sediment detritus																0.75					
98	Marine Water-column detritus										0.006											
99	Marine Sediment detritus						0.05															
	Import																				0.02	
	Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	

	Prey/Predator	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
46	Banana prawn adult									0.005											0.033	
47	Tiger prawn juvenile																					
48	Tiger prawn subadults								0.002	0.008	0.002	0.004	0.001								0.02	
49	Tiger prawn adult																					
50	All other commercial prawns		0.006						0.002	0.006	5E-04	0.002		0.001	0.003						0.01	
51	Thallasinid prawns (Callianassa)	0.058	0.03		9E-04				5E-04	0.015	0.039	0.009		0.009					0.032		0.01	
52	All other non-commercial prawns	0.005	0.053		5E-04	0.5		0.1	0.005	0.09	0.01	0.006		0.009	0.096				0.003		0.01	
53	Crayfish	2E-04			2E-05																0.01	
54	The mud crab																				0.04	
55	Red mud crab																				0.04	
56	Sand crab								0.002	0.003											0.04	
57	Other large crabs	0.241	0.15	0.088	0.091			0.485	0.029	0.021	0.326	0.291	0.347	0.033	0.236	0.066			0.599		0.25	
58	Large gastropods																				0.006	
59	Holothurians	9E-04	0.002						3E-04		0.001			2E-04								
60	Spatangoids																				0.01	
61	Echinoids	0.025	4E-04		5E-06				8E-04			0.004			0.003							
62	Ophiuroids	0.006	0.03		1E-05						3E-05	4E-04			0.014							
63	Asteroids										5E-05											
64	Sessile epibenthos	0.009	9E-04		7E-05				5E-06	2E-05	0.009					4E-05					0.11	
65	Marine bivalves		0.06					0.1													0.1	
66	Estuarine bivalves	0.033	0.03		0.002				3E-04	0.001	0.03	0.433	0.286	0.005	0.036	0.005					0.02	
67	Marine small crustaceans	0.003	0.14	0.53	0.001			0.1													0.02	0.06
68	Estuarine small crustaceans	0.007	0.06		0.034				5E-04	0.005	0.006	0.077	0.003	0.021	0.017	0.009			0.002		0.01	
69	Marine worms	0.051	0.12	0.198	3E-04			0.1	0.002	0.001	0.205	0.016	0.328	0.599	0.412	0.007					0.06	0.02
70	Estuarine worms		0.01																		0.01	
71	Marine small gastropods	0.006	0.05	0.184	3E-04			0.1	3E-04	0.001	0.01	0.006	0.013	0.001	0.004	2E-04			1E-04		0.02	
72	Estuarine small gastropods		0.006																		0.01	
73	Marine meiofauna		0.04					0.01													0.01	
74	Estuarine meiofauna		0.005																		0.005	
75	Marine forams		0.04		2E-05			0.005							7E-05							
76	Estuarine forams		0.01																			
77	Large jellies																					0.01
78	Small jellies																					0.01
79	Marine zooplankton	0.068	0.046		0.018	0.08			0.007	0.007	0.091	0.009	0.013	0.281	0.035	0.046			0.019			0.47
80	Estuarine zooplankton				2E-04	0.02										0.677						
81	Marine ichthyoplankton																					0.01
82	Estuarine ichthyoplankton																					
83	Insects									1E-06	0.001	6E-05		0.017		0.002			0.112			
84	Marine microbial heterotrophs																					
85	Estuarine microbial heterotrophs				0.048															0.1		
86	Marine phytoplankton					0.3																
87	Estuarine phytoplankton					0.1														0.7		
88	Microphytobenthos						0.1										0.15					
89	Seagrass								2E-04	1E-03	3E-04	0.003	5E-05									
90	Estuarine macroalgae									5E-04	3E-04	5E-05			0.037	3E-05						
91	Marine macroalgae						0.8															
92	Mangroves	2E-05	4E-05						2E-04	9E-04	0.005	5E-04	1E-04	0.01	0.018	0.008			0.226			
93	Discards																				0.007	
94	Detached Marine macrophytes						0.05											1				
95	Detached Estuarine macrophytes (estuarine)																					
96	Estuarine Water-column detritus									5E-05	1E-04						0.1			0.2		
97	Estuarine Sediment detritus																0.75					
98	Marine Water-column detritus										0.006											
99	Marine Sediment detritus						0.05															
	Import																				0.02	
	Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	

	Prey/Predator	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85
46	Banana prawn adult																							
47	Tiger prawn juvenile																							
48	Tiger prawn subadults	0.02																						
49	Tiger prawn adult																							
50	All other commercial prawns	0.02																						
51	Thallasinid prawns (Callianassa)	0.02																						
52	All other non-commercial prawns	0.02																						
53	Crayfish																							
54	The mud crab																							
55	Red mud crab																							
56	Sand crab																							
57	Other large crabs																							
58	Large gastropods																							
59	Holothurians	0.001																						
60	Spatangoids																							
61	Echinoids																							
62	Ophiuroids	0.01																						
63	Asteroids																							
64	Sessile epibenthos	0.229																						
65	Marine bivalves																							
66	Estuarine bivalves																							
67	Marine small crustaceans	0.01	0.015			0.01		0.01																
68	estuarine small crustaceans	0.01	0.005				0.01		0.01															
69	Marine worms	0.01	9E-04			0.04		0.01																
70	Estuarine worms	0.01	1E-04				0.04		0.01															
71	Marine small gastropods	0.05																						
72	Estuarine small gastropods	0.05																						
73	Marine meiofauna		0.02	0.01		0.07		0.1		0.1		0.01												
74	Estuarine meiofauna		0.01		0.01		0.07		0.1		0.1		0.01											
75	Marine forams									0.1														
76	Estuarine forams										0.1													
77	Large jellies		0.005																					
78	Small jellies		0.005													0.2								
79	Marine zooplankton		0.002											0.77		0.34	0.3	0.02		0.5				
80	Estuarine zooplankton		5E-04												0.77		0.02		0.02		0.01			
81	Marine ichthyoplankton		1E-04													0.01	0.01							
82	Estuarine ichthyoplankton																							
83	Insects																							
84	Marine microbial heterotrophs		0.261	0.1		0.19		0.15		0.2		0.35		0.23		0.05	0.05	0.1		0.06				
85	Estuarine microbial heterotrophs		0.05		0.1		0.24		0.15		0.2		0.35		0.23		0.01		0.1		0.4			
86	Marine phytoplankton		0.211	0.23		0.1		0.22								0.3	0.3	0.63		0.25			0.005	
87	Estuarine phytoplankton		0.03		0.23		0.1		0.22								0.02		0.63		0.28	0.01		0.005
88	Microphytobenthos	0.3	0.04	0.12	0.12	0.08	0.08	0.09	0.09	0.3	0.3	0.2	0.2					0.05		0.07	0.21	0.02	0.005	0.005
89	Seagrass					0.001	0.05												0.001			0.02		
90	Estuarine macroalgae	0.01					0.12				0.1											0.05		0.035
91	Marine macroalgae	0.01				0.169				0.1													0.035	
92	Mangroves																							
93	Discards		3E-04			3E-04																	1E-04	
94	Detached Marine macrophytes	0.01				0.199		0.05																
95	Detached Estuarine macrophytes (estuarine)	0.01					0.15		0.05													0.1		
96	Estuarine Water-column detritus		0.07				0.07		0.05								0.09		0.249		0.05	0.1		0.5
97	Estuarine Sediment detritus	0.09	0.07		0.13		0.07		0.32		0.2		0.44								0.05	0.7		0.454
98	Marine Water-column detritus		0.1	0.13	0.41	0.07		0.05								0.1	0.2	0.2		0.06			0.5	
99	Marine Sediment detritus	0.09	0.104	0.41		0.07		0.32		0.2		0.44								0.06			0.455	
	Import		0.001			0.001																		0.001
	Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

TROPHOAPPENDIX C. Species Composition of fish functional groups

Functional group No.	Weipa Functional Group
10	**Large pelagic piscivores**
10	*Istiphorus platypterus*
10	*Makaira indicus*
10	*Xiphias gladius*
11	**Medium pelagic piscivores**
11	*Acanthocybium solandri*
11	*Grammatorcynus bicarinatus*
11	*Grammatorcynus bilineatus*
11	*Gymnasarda unicolor*
11	*Katsuwonus pelamis*
11	*Scomberomorus commerson*
11	*Scomberomorus munroi*
11	*Scomberomorus queenslandicus*
11	*Scomberomorus semifasciatus*
11	*Thunnus albacares*
11	*Thunnus obesus*
11	*Thunnus tonggol*
11	*Coryphaena hippurus*
11	*Elegatis bipunnulata*
12	**Small pelagic piscivores**
12	*Scomber australasicus*
12	*Auxis rochei rochei*
12	*Auxis thazard thazard*
12	*Cybiosarda elegans*
12	*Euthynnus affinis*
12	*Sarda orientalis*
12	*Scomberoides tol*
12	*Ablennes hians*
12	*Chirocentris dorab*
13	**Sawfishes**
13	*Anoxypristis cuspidata*
13	*Pristis pectinata*
13	*Pristis pristis*
13	*Pristis zijsron*
14	**Large teleost benthic piscivores**
Functional group No.	**Weipa Functional Group**
14	*Muraenesox cinereus*
14	*Arius bilineatus*
14	*Arius thalassinus*
14	*Epinephelus areolatus*
14	*Epinephelus malabaricus*
14	*Epinephelus sexfasciatus*
14	Psettodes erumei
15	**Small benthic piscivores**
15	*Saurida longimanus*
15	*Saurida micropectoralis*
15	*Saurida* sp. 2 [Sainsbury et al.,1985]
15	*Saurida* sp. 4 [" " "]
15	*Saurida undosquamis*
15	*Pterois volitans*
15	*Platycephalus arenarius*
15	*Platycephalus endrachtensis*
15	*Platycephalus indicus*
15	*Gazza minuta*
16	**Large Elasmo benthopelagic piscivores**
16	*Carcharhinus amblyrhynchoides*
16	*Carcharhinus amblyrhynchos*
16	*Carcharhinus brevipinna*
16	*Carcharhinus cautus*
16	*Carcharhinus dussumieri*
16	*Carcharhinus fitzroyensis*
16	*Carcharhinus limbatus*
16	*Carcharhinus macloti*
16	*Carcharhinus melanopterus*
16	*Carcharhinus sorrah*
16	*Carcharhinus tilstoni*
16	*Hemipristis elongatus*
16	*Negaprion acutidens*
16	*Rhizoprionodon acutus*
16	*Rhizoprionodon taylori*
16	*Sphyrna lewini*
16	*Sphyrna mokarran*
17	**Large Teleost benthopelagic piscivores**
17	*Caranx bucculentus*
17	*Caranx papuensis*
17	*Scomberoides commersonianus*
17	*Scomberoides tala*
17	*Caranx ignobilis*
17	*Caranx tille*
17	*Scomberoides lysan*
17	*Lutjanus erythropterus*
17	*Lutjanus johnii*
17	*Lutjanus malabaricus*
17	*Lutjanus sebae*
17	*Sphyraena putnamiae*
17	*Sphyraena jello*
18	**Small benthopelagic piscivores**
18	*Priacanthus tayenus*

Functional group No.	Weipa Functional Group
18	*Lactarius lactarius*
18	*Otolithes ruber*
18	*Protonibea diacanthus*
18	*Trichiurus lepturus*
18	*Lutjanus russelli*
18	*Sphyraena forsteri*
18	*Sphyraena obtusata*
19	**Large benthopelagic invert feeders**
19	*Gnathanodon speciousus*
19	*Seriolina nigrofasciata*
19	*Rachycentron canadum*
20	**Small benthopelagic invert feeders**
20	*Plotosus lineatus*
20	*Bregmaceros* sp.
20	*Velifer hypselopterus*
20	*Fistularia commersonii*
20	*Fistularia petimba*
20	*Centriscus scutatus*
20	*Pelates quadrilineatus*
20	*Pelates sexlineatus*
20	*Terapon jarbua*
20	*Terapon puta*
20	*Terapon theraps*
20	*Apogon ellioti*
20	*Apogon hyalosoma*
20	*Apogon poecilopterus*
20	*Apogon quadrifasciatus*
20	*Apogon robustus*
20	*Acropoma japonicum*
20	*Carangoides hedlandensis*
20	*Trachinotus bailloni*
20	*Trachinotus* sp. cf mookalee
20	*Ulua aurochs*
20	*Uraspis uraspis*
20	*Alectis ciliaris*
20	*Apolectus niger*
20	*Mene maculata*
20	*Leiognathus bindus*
20	*Leiognathus decorus*
20	*Leiognathus equulus*
20	*Leiognathus fasciatus*
20	*Leiognathus leuciscus*
20	*Leiognathus moretoniensis*
20	*Leiognathus popei*
20	*Leiognathus smithursti*
20	*Leiognathus* sp. 2 (Jones, 1985)
20	*Leiognathus splendens*

Functional group No.	Weipa Functional Group
20	*Secutor insidiator*
20	*Secutor ruconius*
20	*Lutjanus carponotatus*
20	*Lutjanus lutjanus*
20	*Lutjanus vitta*
20	*Nemipterus celebicus*
20	*Nemipterus furcosus*
20	*Nemipterus hexodon*
20	*Nemipterus nematopus*
20	*Nemipterus peronii*
20	*Nemipterus tambuloides*
20	*Pentapodus porosus*
20	*Scolopsis monogramma*
20	*Scolopsis taeniopterus*
20	*Chaetodontoplus duboulayi*
20	*Chelmon mulleri*
20	*Coradion chrysozonus*
20	*Parachaetodon ocellatus*
20	*Pristotis jerdoni*
20	*Psenopsis humerosus*
20	*Abalistes stellaris*
20	*Alutera monoceros*
20	*Monacanthus chinensis*
20	*Paramonacanthus japonicus*
20	*Paramonacanthus filicauda*
20	*Lagocephalus lunaris*
20	*Lagocephalus sceleratus*
20	*Lagocephalus spadiceus*
21	**Large elasmo benthic invert feeders**
21	*Hemigaleus microstoma*
21	*Nebrius ferrugineus*
21	*Stegostoma fasciatum*
21	*Rhina ancylostoma*
21	*Rhinobatos* sp. 1 [Sainsbury et al. 1985]
21	*Rhynchobatus djiddensis*
21	*Dasyatis annotatus*
21	*Dasyatis kuhlii*
21	*Dasyatis leylandi*
21	*Dasyatis sephen*
21	*Dasyatis thetidis*
21	*Himantura granulata*
21	*Himantura toshi*
21	*Himantura uarnak*
21	*Taeniura lymna*
21	*Gymnura australis*
21	*Aetobatus narinari*
21	*Aetomyleus nichofii*
21	*Rhinoptera* sp. cf adspersa

Functional group No.	Weipa Functional Group
22	**Large teleost benthic invert feeders**
22	*Pomadasys argenteus*
22	*Pomadasys kaakan*
22	*Lethrinus choerorynchus (*Now *L. nebulosus)*
22	*Lethrinus fraenatus* (Now *L. nebulosus*)
22	*Lethrinus lentjan*
22	*Choerodon schoenleinii*
22	*Diagramma pictum*
22	*Gaterin sordidus*
22	*Plectorhinchus gibbosus*
23	**Small benthic invert feeders**
23	*Moringua microchir*
23	*Ophichthus* sp. (of Castle)
23	*Apistus carinatus*
23	*Lepidotrigla spiloptera*
23	*Elates ransonetti*
23	*Suggrundus isacanthus*
23	*Suggrundus japonicus*
23	*Suggrundus macracanthus*
23	*Pseudochromis quinquedentatus*
23	*Sillago maculata*
23	*Sillago sihama*
23	*Sillago lutea*
23	*Pomadasys maculatus*
23	*Pomadasys trifasciatus*
23	*Argyrops spinifer*
23	*Austronibea oedogenys*
23	*Johnieops vogleri*
23	*Johnius amblycephalus*
23	*Parupeneus pleurospilus*
23	*Upeneus asymmetricus*
23	*Upeneus luzonius*
23	*Upeneus sulphureus*
23	*Upeneus sundaicus*
23	*Polynemus multiradiatus*
23	*Choerodon monostigma*
23	*Engyprosopon grandisquama*
23	*Grammatobothus polyophthalmus*
23	*Pseudorhombus argus*
23	*Pseudorhombus arsius*
23	*Pseudorhombus diplospilus*
23	*Pseudorhombus elevatus*
23	*Pseudorhombus spinosis*
23	*Cynoglossus bilineatus*
23	*Dexillichthys muelleri*
23	*Triacanthus biaculeatus*

Functional group No.	Weipa Functional Group
23	*Tripodichthys oxycephalus*
23	*Trixiphichthys weberi*
23	*Rhynchostracion nasus*
23	*Chelonodon patoca*
23	*Torquigener hicksi*
23	*Torquigener whitleyi*
23	*Cyclichthys hardenbergi*
23	*Cyclichthys jaculiferus*
24	**Polychaete feeders (Offshore)**
24	*Gerres filamentosus*
24	*Gerres oyena*
24	*Gerres subfasciatus*
24	*Pentaprion longimanus*
25	**Large pelagic planktivores**
25	*Rastrelliger brachysoma*
25	*Rastrelliger faughni*
25	*Rastrelliger kanagurta*
25	*Megalaspis cordyla*
25	*Absalom radiatus*
25	*Alectis indicus*
25	*Alepes* sp.
25	*Caranx para*
25	*Selar boops*
25	*Selar crumenophthalmus*
25	*Selaroides leptolepis*
26	**Small pelagic planktivores**
26	*Anodontostoma chacunda*
26	*Dussumieria acuta*
26	*Herklotsichthys koningsbergeri*
26	*Herklotsichthys lippa*
26	*Pellona ditchela*
26	*Sardinella albella*
26	*Sardinella gibbosa*
26	*Dussumieria elopsoides*
26	*Stolephorus carpentariae*
26	*Stolephorus indicus*
26	*Thryssa hamiltoni*
26	*Thryssa setirostris*
26	*Parexocoetus mento*
26	*Cypselurus* sp.
26	*Decapterus macrosoma*
26	*Valamugil cunnesius*
27	**Marine benthic herbivores**
27	*Siganus canaliculatus*
27	*Siganus fuscescens*
27	*Drepane punctata*
27	*Platax teira*
27	*Zabidius novaemaculatus*

Functional group No.	Weipa Functional Group
28	**Scavengers**
28	*Echeneis naucrates*
29	**Estuary lg Elasmo benthopelagic pisc/prawn feeders**
29	*Carcharhinus amblyrhynchoides*
29	*Carcharhinus amblyrhynchos*
29	*Carcharhinus brevipinna*
29	*Carcharhinus cautus*
29	*Carcharhinus dussumieri*
29	*Carcharhinus leucas*
29	*Carcharhinus limbatus*
29	*Carcharhinus sorrah*
29	*Negaprion acutidens*
29	*Rhizoprionodon acutus*
30	**Estuary lg teleost benthopelagic pisc/prawn feeders**
30	*Elops machnata*
30	*Megalops cyprinoides*
30	*Lates calcarifer*
30	*Psammoperca waigiensis*
30	*Caranx papuensis*
30	*Caranx sexfasciatus*
30	*Scomberoides commersonianus*
30	*Sphyraena barracuda*
30	*Sphyraena putnamiae*
30	*Sphyraena qenie*
30	*Eleutheronema tetradactylum*
30	*Polynemus sheridani*
30	*Scomberomorus semifasciatus*
30	*Chirocentris nudus*
30	*Lhotskia gavioloides*
30	*Strongylura incisa*
30	*Strongylura leiura*
30	*Strongylura strongylura*
30	*Tylosurus crocodilus*
30	*Tylosurus punctulatus*
31	**Estuary large benthic pisc/prawn feeders**
31	*Arius leptaspis*
31	*Arius mastersi*
31	*Arius proximus*
31	*Arius thalassinus*
31	*Cymbacephalus nematophthalmus*
31	*Platycephalus endrachtensis*
31	*Platycephalus indicus*
31	*Batrachomoeus trispinosus*
31	*Synanceia horrida*

Functional group No.	Weipa Functional Group
31	*Nibea soldado*
31	*Nibea* sp. (of McKay)
31	*Pristis pectinata check*
32	**Estuary large benthopelagic invert feeders**
32	*Centrogenys vaigiensis*
32	*Epinephelus malabaricus*
32	*Epinephelus merra*
32	*Epinephelus suillus*
32	*Gnathanodon speciosus*
32	*Lutjanus argentimaculatus*
32	*Lutjanus johnii*
32	*Lutjanus russelli*
32	*Pomadasys argenteus*
32	*Pomadasys kaakan*
32	*Lethrinus lentjan*
32	*Acanthopagrus berda*
33	**Estuary large benthic invert feeders (Rays)**
33	*Dasyatis annotatus*
33	*Dasyatis leylandi*
33	*Dasyatis sephen*
33	*Himantura granulata*
33	*Himantura uarnak*
33	*Taeniura lymna*
33	*Euristhmus nudiceps*
33	*Rhynchobatus djiddensis*
34	**Estuary polychaete feeders**
34	*Arius graeffei*
34	*Arius* sp. 3 [of Kailola]
34	*Arius* sp. 4 [of Kailola]
34	*Gerres abbreviatus*
34	*Gerres filamentosus*
34	*Gerres oyena*
34	*Gerres poieti*
35	**Estuary small benthic invert feeders**
35	*Apogon ruppelli*
35	*Apogon sangiensis*
35	*Siphamia roseigaster*
35	*Apogon hyalosoma*
35	*Sillago analis*
35	*Sillago ingenuua*
35	*Sillago maculata*
35	*Sillago sihama*
35	*Sillago lutea*
35	*Leiognathus equulus*
35	*Upeneus tragula*
35	*Omobranchus rotundiceps*
35	*Callionymus* sp. (juveniles)

Functional group No.	Weipa Functional Group
35	*Acentrogobius caninus*
35	*Acentrogobius gracilus*
35	*Acentrogobius janthinopterus*
35	*Acentrogobius viridipunctatus*
35	*Amoya* sp. (of Hoese)
35	*Cryptocentrus* sp. (of Hoese)
35	*Drombus globiceps*
35	*Drombus ocyurus*
35	*Drombus palackyi*
35	*Favonigobius melanobranchus*
35	*Glossogobius biocellatus*
35	*Glossogobius celebius*
35	*Glossogobius circumspectus*
35	*Pandaka rouxi*
35	*Pseudogobius* sp. (of Hoese)
35	*Pseudogobius* sp. 5 (of Hoese)
35	*Butis butis*
35	*Ophieleotris aporos*
35	*Ophiocara porocephala*
35	*Oxyeleotris* sp. (of Larson)
35	*Pseudorhombus arsius*
35	*Pseudorhombus elevatus*
35	*Arothron immaculatus*
35	*Marilyna darwinii*
35	*Tetraodon erythrotaenia*
35	*Terapon jarbua*
35	*Pelates quadrilineatus*
35	*Amniataba caudavittatus*
36	**Estuary planktivores**
36	*Herklotsichthys lippa*
36	*Hyperlophus vittatus*
36	*Sardinella albella*
36	*Stolephorus andhraensis*
36	*Stolephorus carpentariae*
36	*Stolephorus indicus*
36	*Thryssa hamiltoni*
36	*Thryssa setirostris*
36	*Atherinomorus duodecimalis*
36	*Atherinomorus endractensis*
36	*Ambassis dussumieri*
36	*Ambassis gymnocephalus*
36	*Ambassis nalua*
36	*Hippichthys heptagonus*
36	*Hippocampus kuda*
36	*Hippocampus whitei*
36	*Monodactylus argenteus*
36	*Pseudomugil gertrudae*
36	*Acreichthys tomentosus*
36	*Pardicula setifer*
36	*Monacanthus chinensis*
37	**Estuary detritivores**
37	*Anodontostoma chacunda*
37	*Nematalosa come*
37	*Nematalosa erebi*
37	*Chanos chanos*
37	*Liza subviridis*
37	*Liza tade*
37	*Liza vaigiensis*
37	*Mugil georgii*
37	*Valamugil buchanani*
38	**Estuary benthic herbivores**
38	*Scatophagus argus*
38	*Selenotoca multifasciatus*
38	*Siganus javus*
38	*Siganus vermiculatus*
38	*Siganus canaliculatus*
39	**Estuary insectivores**
39	*Toxotes chatareus*
40	**Estuary pelagic herbivores**
40	*Arrhamphus sclerolepis*
40	*Hemiramphus far*
40	*Hyporhamphus dussumieri*
40	*Hyporhamphus quoyi*
40	*Zenarchopterus buffonis*
40	*Zenarchopterus dispar*

TROPHOAPPENDIX D. Data pedigree rating scales

Three scales are used in Ecopath to convert qualitative evaluations of data pedigree to quantitative estimates that can be used in probability analyses of to estimate overall data quality of a model. See Christensen et al 2000 for a full explanation of data pedigree methodology.

Biomass

Parameter source	***Index number***	***Index value***	***Default c.i. (+/- %)***
'Missing' parameter (estimated by Ecopath)	1	0.0	n.a.
From other model	2	0.0	80
Guesstimates	3	0.0	80
Approximate or indirect method	4	0.4	60
Sampling based, low precision	5	0.7	30
Sampling based, high precision	6	1.0	10

P/B and Q/B

Parameter source	***Index number***	***Index value***	***Default c.i. (+/- %)***
'Missing' parameter (estimated by Ecopath)	1	0.0	n.a.
Guesstimates	2	0.1	80
From other model	3	0.2	70
Empirical relationships	4	0.5	50
Similar group/species, similar system	5	0.6	40
Similar group/species, same system	6	0.7	30
Same group/species, similar system	7	0.8	20
Same group/species, same system	8	1.0	10

Diets

Parameter source	***Index number***	***Index value***	***Default c.i. (+/- %)***
General knowledge of related group/species	1	0.0	80
From other model	2	0.0	80
General knowledge for same group/species	3	0.2	70
Qualitative diet composition study,	4	0.5	50
Quantitative but limited diet composition study,	5	0.7	40
Quantitative, detailed, diet composition study,	6	1.0	30

Catches

Parameter source	***Index number***	***Index value***	***Default c.i. (+/- %)***
Guesstimates	1	0.0	80
From other model	2	0.0	80
FAO statistics	3	0.2	50
National statistics	4	0.5	40
Local study, low precision/incomplete	5	0.7	30
Local study, high precision/complete	6	1.0	10

References

Christensen, V., C.J. Walters, and D. Pauly. 2000. Ecopath with Ecosim Version 4, Help system©.

TROPHOAPPENDIX E. The Ecopath with Ecosim approach

The Ecopath with Ecosim approach (Christensen and Walters 2004, Christensen *et al.* 2004) consists initially of a static description of the biomass flows through the whole food web (Ecopath proper) in the chosen area and time specified according to standing biomass, production rates, consumption rates, migration and multi-year trends, diet compositions, and fishery information. This information is used as a starting point for dynamic simulations in which fishery and various biophysical changes (environmental data) can be imposed on modelled biomasses to attempt retrospective fitting to particular observed trends with the goal of identifying the relative efficacy of alternative explanations. The three general aspects of the approach are described below.

Ecopath models rely on the truism that *Production = fisheries catch + mortality due to predation + other mortality + biomass accumulation + migration*. This applies to each system as a whole, as well as to any producer (e.g. a given population) and time period (e.g. a year or season). Groups are linked through predators consuming prey, where *Consumption = production + non-assimilated food + respiration*. Mass is accounted for, or ‘conserved’, according to these two relationships. Ecopath models are focal points for ecosystem synthesis, as large amounts of disparate information is standardized, explored for continuity, and rendered mutually compatible.

Ecosim (Walters *et al.* 1997) expresses the Ecopath system of linear equations as differential and delay-difference equations to simulate the whole community effects of changes in any sources of mortality such as fishing, predation, food availability, or environmental. Ecosim therefore indicates the likely directions of biomass change in various groups under different experimental policies aimed at improving overall ecosystem management. Recent developments include: (i) provision for the analysis of the effect of environmental factors in the ecosystem; (ii) analysis of stock-recruitment dynamics; (iii) ‘time-series fitting’ to explore explanations for observed population changes; (iv) a policy-analysis routine for exploring fisheries policies that would optimize an objective function that balances economic, social, and ecological goals; and (v) a routine for comparing Maximum Sustainable Yield (MSY) with Maximum Ecosystem Yield, which is MSY in a whole community context that essentially recognizes allocation of some production of each component to predators.

Ecospace (Walters et al. 1999) is a spatially explicit Ecosim module that allows exploration of spatially explicit policies, such as spatial and temporal closures, in a trophic context. Assumed homogeneous distributions of functional groups redistribute spatially according to specified habitat preference, resulting patterns of trophic interactions and movement rates, distributions of fishing effort (driven by local abundances and fishing costs), and physical factors.

Construction of Ecopath models can be straightforward in well studied systems because the required information is routinely collected by fisheries scientists and marine biologists. The most useful insights from this approach for ecologists and managers result from counter-intuitive simulation results that indicate dynamics that might not have been considered, and for indicating the indirect effects of human actions. The approach is also useful for highlighting knowledge gaps and for science program planning. This aspect of the approach underscores the importance of including all components of the defined ecosystem rather than just the components the researchers set out to focus on. The software and a variety of information on this modelling approach are available at www.Ecopath.org.

The goal for the Weipa region ecological model is to have a preliminary balanced Ecopath model by the second project workshop (May 2005), or soon thereafter. Example Ecosim simulations can be run for demonstration purposes at that time. A subsequent refinement stage will be necessary to make the Weipa region model more useful and robust. Once the Ecopath model is constructed and refined a comparison of the explanations for changes in banana prawn catches can be conducted using methods to fit simulated biomass trajectories to observed time series of changes in biomasses or catches by systematically adding simulated time series of fishery and environmental forces.

References

Christensen, V., and Walters CJ. 2004. Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling* **172**:109-139.

Christensen, V., Walters CJ, and Pauly D. 2004. Ecopath with Ecosim: a user's guide. University of British Columbia Fisheries Centre, Vancouver, Canada.

Walters, C., Christensen V, and Pauly C. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Reviews in Fish Biology and Fisheries* **7**:139-172.

Walters, C., Pauly D, and Christensen V. 1999. Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems* **2**:539-554.

TROPHOAPPENDIX F. Simplified guide to deriving Ecopath model parameters

Step 1: Select a functional group to provide information for based on the group aggregation developed during the workshop. If others have interest / expertise in the same group, consider collaborating.

Step 2: Estimate the basic input parameters for the model (see information below). **Hint:** For fishes, check FishBase at www.fishbase.org; search for a species, go to "key facts," and look for estimates of some of the basic input parameters. You can also refer to the 'help' menu in the Ecopath program, the Ecopath users manual, and the approaches outlined below. It is best to calculate *representative* values (e.g., *weighted* averages) for functional groups containing more than one species.

Step 3: Write a 1-3 page authored "mini-paper" documenting the basic input parameters and the methods you used to derive them. Also include information on 'secondary' input parameters and other relevant information in this section if possible. This additional information includes spatial and temporal distributions, habitat associations, food assimilation efficiencies (unassimilated food / consumption), migration patterns (in and out of nearshore areas), multi-year trends in biomass if applicable, time-series data, and fisheries information (e.g., landings *and* discards).

Basic Ecopath input parameters

B	Biomass	($t{\cdot}km^{-2}$)
P/B	Production / Biomass	($year^{-1}$)
Q/B	Consumption / Biomass	($year^{-1}$)
DC	Diet Composition	(proportions)

Estimating production rate (P/B)

Production refers to the elaboration of tissue (whether it survives or not) by a group over the period considered, expressed in whatever currency has been selected. Total mortality, under the condition assumed for the construction of mass-balance models, equal to production over biomass (Allen 1971). Therefore, one can use estimates of total mortality (Z) as input values for the production over biomass ratio (P/B) in Ecopath models. Check the "key facts" in FishBase for estimates of natural mortality (M) and fishing mortality (F); adding the two will give you total mortality (Z). You can use this for P/B, but keep in mind the assumption of equilibrium that P/B = Z relies on.

Total mortalities can be estimated from catch curves, i.e., from catch composition data, either in terms of age (age-structured catch curves; Robson and Chapman 1961), or of length-converted catch curves (Pauly et al 1995). The estimation can be carried out using appropriate software for analysis, such as the FiSAT package (Gayanilo et al 1995).

Production rate (P/B) is the sum of natural mortality (M = M0 + M2) and fishing mortality (F), i.e., Z = M + F. In the absence of catch-at-age data from an unexploited population, natural mortality for finfish can be estimated from an empirical relationship (Pauly 1980) linking M, two parameters of the von Bertalanffy Growth Function (VBGF) and mean environmental temperature, i.e.,

$$M = K^{0.65} \cdot L_{\infty}^{-0.279} \cdot Tc^{0.463}$$

where:

M is the natural mortality (/year),

K is the curvature parameter of the VBGF (/year),

Loo is the asymptotic length (total length, cm), and

Tc is the mean habitat (water) temperature, in °C .

In equilibrium situations, fishing mortality can be estimated directly from the catch (or more precisely from the ‘yield’, which expresses catches in weight):

Fishing mortality = catch / biomass

where the catch is a rate, (e.g., $t/km^2/year$), the biomass lacks a time dimension, (i.e., is expressed as t/km^2), and thus the fishing mortality is an instantaneous rate, (e.g., per year).

Estimating consumption rate (Q/B)

Consumption is the intake of food by a group over the time period considered. It is entered as the ratio of consumption over biomass (Q/B). Absolute consumption computed by Ecopath is a flow expressed e.g., in t/km^2 /year, while the corresponding Q/B would be /year.

There are various approaches for obtaining estimates of the consumption/ biomass ratio (Q/B). They may be split into (i) analytical methods and (ii) holistic methods:

(i) The analytical methods involve estimation of ration, pertaining to one or several size/age classes, and their subsequent extrapolation to a wide range of size/age classes, representing an age-structured population exposed to a constant or variable mortality;

The required estimates of ration are obtained from laboratory experiments, from studies of the dynamics of stomach contents in nature (Jarre et al. 1991b), or by combining laboratory and field data (Pauly 1986).

(ii) The existing holistic methods for estimation of Q/B are empirical regressions for prediction of Q/B from some easy-to-quantify characteristics of the animals for which the Q/B values are required.

One such model (included in Ecoempire) for finfishes is,

$$Q/B = 3.06 \cdot W_{\infty}^{-0.2018} \cdot Tc^{0.6121} \cdot Ar^{0.5156} \cdot 3.53^{H}{}_{d}$$

derived by Palomares and Pauly (1989) from 33 analytical estimates of Q/B, from data on marine fishes.

Here,Q/B is the annual food consumption/ biomass ratio (in /year, not in % /day as suggested in Palomares and Pauly 1989)

Woo is the asymptotic (or maximum) weight of these same fishes (wet weight, in g),

Tc is the mean habitat temperature for the fishes in question (in °C),

Ar is the aspect ratio of their caudal fin and

Hd is the food type (0 for carnivores and 1 for herbivores and detritivores).

If you are using FishBase to find consumption rate information (Q/B), use the consumption rate calculator (discussed previously), which is found in the ‘life-history’ tool once you have found the species page that you are interested in. The life history tool also contains a natural mortality (M) calculator. Remember that in equilibrium situations P/B = Z (total mortality) = M (natural mortality) + F (fishing mortality). So if you have an idea of F for a species, you can get M and (roughly) estimate P/B. Then you should do some weighted averaging to estimate P/B for your whole group.

Elements of 'mini-papers' for the Albatross Bay Ecopath model

For examples of mini-paper sections, please refer to Okey and Mahmoudi 2002 at J:\WorkGroups\Northern_Fisheries_Ecosystems\Weipa Banana Prawn Variability\References, or contact Steve Edgar steve.edgar@csiro.au or Chris Moeseneder chris.moeseneder@csiro.au) to get that]. Please be sure to include abstracts.

Title (e.g., Amphipods)

Author(s)
Affiliation (s)

Abstract (50-80 words): Describe the parameters for the functional group

Paragraph one:

1. Define the functional group;
2. Provide general information about life habits and diet;
3. Discuss spatial distributions and habitat preferences;
4. Discuss migration patterns, seasonal trends, or multi-year trends in abundance;
5. Discuss the fishery importance of this group, or other special reasons of importance (e.g., discuss the ecological role).

Paragraph two:
State the biomass estimate for this group (in tonnes·km^{-2}). Your overall biomass estimate will be the sum of your biomass estimates for all the species in your group. To estimate biomass, you will need to extrapolate the biomass estimates from the sampled areas to the entire area of focus. State all the assumptions you make. For example, the density of a species will vary among habitat types; consider the relative areas of these different habitat types, and weight the corresponding biomass estimates accordingly. State your calculations explicitly, so that someone can easily repeat your calculations.

Paragraph 3:
State the estimated P/B (production/biomass) for the functional group. Detail how you derived this parameter. Guidelines for P/B are on the 'invitation' sheet and the Ecopath users manual. **Hint:** Refer to 'key facts' in FishBase, www.fishbase.org, to derive P/B estimates (and Q/Bs).

Paragraph 4:
State the estimated Q/B (consumption/biomass) for the functional group. Again, detail how you derived the Q/B. Guidelines are found on the 'invitation' sheet, and in the Ecopath users manual

Paragraph 5:
Provide a diet composition in proportion of biomass (as shown on the invitation sheet). If you are combining the diets of several species, you should calculate averages that are appropriately weighted. You can weight these averages by relative biomass, but the proper (and better) way is to weight them by relative consumption (Q). This information should be presented as a table instead of a paragraph, and you can refer to the table in the paragraph on consumption.

Diet composition table
See example table on following page. Remember that the prey categories should correspond to the functional groups shown in Table 45. Your diet data should be adapted to those groups

Table 45: Diets of green lobsters (*Panulirus gracilis*) red lobsters (*P. pennicillatus*) and slipper lobsters (*Scyllarides astori*) in the Galapagos (adapted from Martínez 2000).

Prey category	**Proportion of diet**			
	Panulirus gracilis	*P. pennicillatus*	*Scyllarides astori*	*Average*
Crabs	0.21	0.30	0.05	0.187
Gastropods	0.22	0.23	0.05	0.167
Bivalves	0.13	0.13	0.28	0.180
Digested material	0.20	0.10	0.35	0.217
Barnacles	0.04	0.06	0.05	0.050
Echinoids	0.07	0.05	0.05	0.056
Polychaetes	0.03	0.02		0.017
Algae	0.04	0.02	0.05	0.037
Fishes	0.03	0.02	0.07	0.040
Chitons	0.03	0.02		0.017
Sponges		0.01		0.003
Asteroids		0.01		0.003
Turbellarians		0.01		0.003
Ophiuroids		0.01	0.05	0.020
Anemones		0.01		0.003
Total	**1.000**	**1.000**	**1.000**	**1.000**

Note: Prey categories must correspond to the list of functional groups. Averages should be *weighted* by either relative biomasses or relative consumption of the predator species in this functional group.

Literature cited (Functional group name)

Cite your references wherever necessary. Indeed, the documentation of your derivations is a central point of this paper. List all of your cited literature here. The other main point is to get credit in the literature for your work, and to establish yourself as a source of information.

Note: Please use tables wherever necessary to clarify or summarize your derivations; be sure to refer to your tables in your text. Examples of 'mini-papers' are found in (Okey and Mahmoudi 2002). Also, refer to the Ecopath users manual (Christensen and Walters 2004)—find this in the Weipa repository, at www.Ecopath.org, or in the Ecopath software help directory. Contact Tom Okey at Tom.Okey@csiro.au with any questions.

References

Okey, T.A. & Mahmoudi, B. (2002). An ecosystem model of the West Florida Shelf for use in fisheries management and ecological research: Volume II: Model construction. Florida Marine Research Institute, Florida Fish and Wildlife Conservation Commission, St. Petersburg.

IV-6. Estimating density of pelagic fishes using gillnet catches: a Bayesian approach (Draft Manuscript)

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Introduction

Pelagic fishes such as tunas, mackerel and billfish support some of the most valuable commercial and recreational fisheries worldwide (FAO, 1994). Moreover, these species are ecologically important as they are often high order or apex predators, which are important structuring agents in pelagic ecosystems (Olson and Boggs, 1986; Maldeniya, 1996). A critical requirement for understanding and managing the dynamics of pelagic fish populations is having knowledge of their density or biomass. Not only is this information important for stock assessment models in order to manage commercially important species, but in recent years with the growing interest in ecosystem-based approaches to fisheries management, this type of information has become increasingly important for ecosystem models such as the trophic mass balance models in the widely used Ecopath software. However, measuring or estimating pelagic fish density has long been problematic for fisheries scientists.

Pelagic fishes are generally fast swimming, wide ranging and vary greatly in size up to hundreds of kilograms, which make them difficult to sample using methods which have generally been used to infer information about density, such as a trawl. In trawl catches fish densities can be estimated since the area covered by the trawl can be calculated from the spread of the net opening, trawl duration, trawl speed, and including a catchability coefficient for each species (Blaber et al. 1990; King, 1995). However, large pelagic fishes can easily avoid the net. Aerial surveys have been used to estimate the biomass of commercially important tunas (Cowling and Polacheck, 1995), since large areas can be covered quickly. However, this method is expensive, fish weights or lengths cannot be measured accurately, species differentiation can be poor (Bell, 1976), and the accuracy of the survey is highly dependent upon a number of factors including the visibility of fish, weather conditions and experience of the spotter censusing the fish (Cowling and Polacheck, 1995).

The most effective methods for capturing pelagic fishes is the use of gillnets and longlines, which are employed by many pelagic fisheries worldwide. Gillnets are effective since they can cover large areas and be set to be selective for particular species by the depth at which they are set and the size and type of mesh used. Gillnets are a highly size- and species-selective passive fishing method whereby the probability of fish being caught depends upon their mobility, body shape and size, particularly body girth since capture generally depends on a fish wedging its head into a mesh to a point past the operculum. Unfortunately for scientists, gillnets are not particularly useful for estimating fish density in many situations for a variety of reasons. The main reasons being that many fish are able to swim backward when encountering the net, or swim slowly enough to be able to detect and avoid the net altogether. Furthermore, many fish species are able to remain fairly stationary in the water column meaning that a fish’s probability of capture in a gillnet set nearby may have no relationship to the nets soak time. As a result, it is difficult to determine the effective area that is fished by a gillnet in order to be able to estimate the density or biomass of a species in a given area.

In contrast, fast-moving oceanic pelagic fishes may be one of the few fish groups where density may be reasonably estimated from gillnet catches. Many pelagic fishes, namely scombrids and istiophorids, are obligate ram ventilators (Brown and Muir, 1970), requiring fish to move forward constantly to maintain oxygen supply to the gills to facilitate their high metabolic rates (Korsmeyer and Dewar, 2001), as well as maintaining buoyancy, particularly in species lacking a swim bladder. Consequently, most pelagic fish have little capability of swimming backwards if it encounters a net. Most scombrids and istiophorids are capable of swimming at very high speeds in order to catch prey and are generally visual predators and so most feeding activity is restricted to daytime (Kobayashi and Yamaguchi, 1971; Roger, 1994; Buckley and Miller, 1994; Maldeniya, 1996; Menard et al. 2000; Itoh et al. 2003). However, during the night when these fish do not actively feed, they probably swim at a more constant rate to maintain their metabolic requirements and buoyancy. Therefore, by having some idea of the cruising speed of a fish species it may be possible to calculate the maximum distance from which a fish can interact with a gillnet set at night in a given period. By incorporating information of the size selectivity of the fishing method to determine the proportion of the population susceptible to capture, an estimate of fish density is possible.

We were specifically interested in estimating the density of many high trophic-level pelagic fishes associated with Australia's second most valuable fishery, the Northern Prawn Fishery (NPF). With knowledge of fish size, density can be used to estimate biomass density, which is a key parameter of an Ecopath model being developed to facilitate ecosystem based management of the NPF (Okey et al. 2005). Because most pelagic fish species in this region are not fished commercially, our only source of information on pelagic fishes was gillnet catch data from fishery dependent and scientific surveys. With the growing importance of pelagic fish density information for Ecopath models being developed for many fisheries, we developed a new method that can be used to estimate the density of pelagic fishes from gillnet catches based on fish swimming speeds. In this paper we provide density estimates for six pelagic scombrid and two istiophorid species common to the waters of northern Australia.

Materials and methods

Collection of catch data

Data for this study were collected by scientific observers derived from shark gillnet catches in the Queensland N9 offshore gillnet fishery in the Gulf of Carpentaria, Australia and the Taiwanese Gillnet operation which operated in Australia's Northern Prawn Fishery from 1979-1986 (see Stevens and Davenport 1991). Data were collected between March 2001-April 2005 by scientific observers from CSIRO Marine and Atmospheric research and Queensland Department of Primary Industries and Fisheries independently monitoring catches in this fishery for different purposes. For example, QDPI monitored the catch and bycatch in this fishery whereas CSIRO collected pelagic fishes for biological and dietary analyses (Griffiths et al. 2005). A total of 268 shots were monitored in which observers recorded net length and drop, mesh size and type (in this case 6.5 inch monofilament), set type (surface or bottom set), deployment and winching time, total soak time, number and fork length of each species. The length of the net used in each shot ranged between 300 m and 10000 m and soak times ranged between 1.3 to 9.7 hours.

We only included the 208 shots taken during the night when pelagic fishes do not generally actively feed (Kobayashi and Yamaguchi 1971; Menard et al. 2000) and so they are more likely to swim at a more constant speed and their spatial distribution less biased by the presence of prey aggregations. To account for possible differences in susceptibility of each species to capture by the fishing gear due to diel vertical migrations (Brill et al. 1999; Pepperell and Davis 1999; Schaefer and Fuller 2002), we only included surface set shots where the net covers approximately the top 10 m of the water column.

For the purposes of this paper we restricted our analyses to six scombrid and two istiophorid species that are common in northern Australia and were caught in reasonable numbers in our samples. These species include: grey mackerel (*Scomberomorus semifasciatus*), Spanish mackerel (*S. commerson*), spotted mackerel (*S. munroi*), longtail tuna (*Thunnus tonggol*), mackerel tuna (*Euthynnus affinis*), leaping bonito (*Cybiosarda elegans*), Indo-Pacific sailfish (*Istiophorus platypterus*) and black marlin (*Makaira indica*). Only common names are used in this paper.

Size selectivity function

For calculations of size selectivity of the gillnet we employed the methods of Milton et al. (1998).

2.1 Model assumptions

The method is based on a number of simplifying assumptions which we now outline. Later we will discuss the unrealistic aspects of these assumptions and their possible effect.

Suppose a gillnet of length h , indicated by the central horizontal line in Figure 69 below, is set for a known period of time. Since the target species are mainly scombrids we may assume that they are continuously swimming, and we assume further that they swim *in straight lines*, at a *constant known speed* and in a *random direction* uniformly distributed over the compass directions. We also assume that the fish are distributed within the drop of the net (in this case within 10 m of the surface) and do not undertake diel vertical migrations since there is no evidence of this occurring in the shallow waters of the Gulf of Carpentaria. However, this may be added to the model should this need to be employed in other regions.

If d is the maximum distance an animal can swim while the net is set, the domain of attraction consists of a rectangular region with sides parallel to the net at a distance *d* away from it, together with two semi-circular regions at each end of radius *d*, as in Figure 69. Under the assumptions, when the net is set, no animal outside the domain of attraction can reach the net in time to be caught.

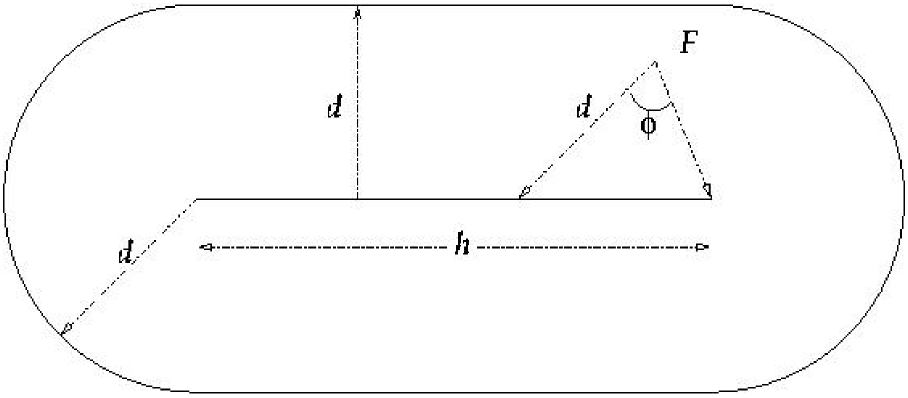


Figure 69: A set gillnet and its domain of attraction.

An animal at some position *F* within the domain of attraction swims in a random direction and may reach any point on a circle of radius *d* centred on the initial point *F*. This circle will intersect the net at one or two points, and the angle at F defined by the section of the net within this circle, denoted by f in Figure 69, specifies the range of directions the animal may take to reach the net.

If we further assume that any animal reaching the net is caught, the probability that an animal initially located at the point *F* is caught by the net is clearly

$$\Pr(\text{Capture} \mid F) = \frac{f}{2p}$$

We may think of f as a function of geographical coordinates, $f = f(x,y)$. If we further assume that fish are uniformly distributed within the domain of attraction at the time the net is set, the average proportion of fish caught within the domain of attraction is then the average of this conditional probability over the region:

$$p = \frac{\underset{D}{\text{òò}} f(x,y)dxdy}{2p(2dh + pd^2)}$$

where the integral is over the domain of attraction, say D , whose area is $2hd + pd^2$.

From geometric considerations it is apparent that this average proportion will be a function only of the ratio $r = d / h$. It is not possible to evaluate this integral in closed form, but it is possible to get a good approximation to it by numerical quadrature. Figure 70(a) shows a plot of this function. We see from this figure that as d / h approaches infinity, the probability of capture tends to zero. It is also clear from this figure that *p* lies between 0 and 0.5. An image plot showing how the local probability of capture is distributed over the domain of attraction is shown in Figure 71.

An alternative approach to evaluating $p(r)$ is through a piecewise cubic spline approximation developed to explain the relationship between $\mathrm{logit}(p)$ and $\log(r)$. This approximation is shown in Figure 70(b). In this figure, the red points are the result of numerical quadrature, while the solid line represents the piecewise cubic spline approximation. We used the `splines` library in R (Ihaka and Gentleman 1996) to construct this relationship. Table 46 contains information about the parameters used in the approximation. Each row represents a cubic function constructed over an interval *a:b* (on the log scale), centred around the lower boundary of that interval. For example, for the interval $\log(r) \le -10$, we use the constant -0.7626896 to approximate logit(p). If $-10 < \log(r) \le -7.78$ we use the following approximation:

$$\mathrm{logit}(p) = -0.7626896 + 0.007790967 \times (\log(r) + 10) - 0.001570167 \times (\log(r) + 10)^3$$

Table 46: Coefficients used in the piece-wise cubic spline approximation for specified intervals.

Interval	constant	linear	quadratic	cubic
$\mathrm{logit}(r) \le -10$	-0.7626896	0	0	0
$-10 < \mathrm{logit}(r) \le -7.78$	-0.7626896	0.007790967	0	-0.001570167
$-7.78 < \mathrm{logit}(r) \le -5.56$	-0.7626073	-0.015470773	-0.010467783	0.004025204
$-5.56 < \mathrm{logit}(r) \le -3.33$	-0.8045072	-0.002361607	0.016366908	-0.009485520
$-3.33 < \mathrm{logit}(r) \le -1.11$	-0.8330245	-0.070146021	-0.046869894	-0.011011937
$-1.11 < \mathrm{logit}(r) \le 1.11$	-1.3412051	-0.441596465	-0.120282805	0.007879952
$1.11 < \mathrm{logit}(r) \le 3.33$	-2.8300457	-0.859446684	-0.067749794	0.011076719
$3.33 < \mathrm{logit}(r) \le 5.56$	-4.9529388	-0.996457336	0.00609500	-0.001245409
$5.56 < \mathrm{logit}(r) \le 7.78$	-7.1508567	-0.987818946	-0.002207725	-0.001408638
$7.78 < \mathrm{logit}(r) \le 10$	-0.3723706	-1.018499767	-0.011598645	0.001739797
$\mathrm{logit}(r) > 10$	-11.673888	-1.044274533	0	0

2.2 Statistical Models and Estimation

Let g be the *average relative abundance,* which represents the average number of animals per unit area. If Y is the number caught in the gillnet, then the mean of Y is clearly

$$m = E[Y] = g\{p(d/h)(2hd + pd^2)\} = g\left\{\frac{1}{2p}\iint_D f(x,y)dxdy\right\} = gA(h,d)$$

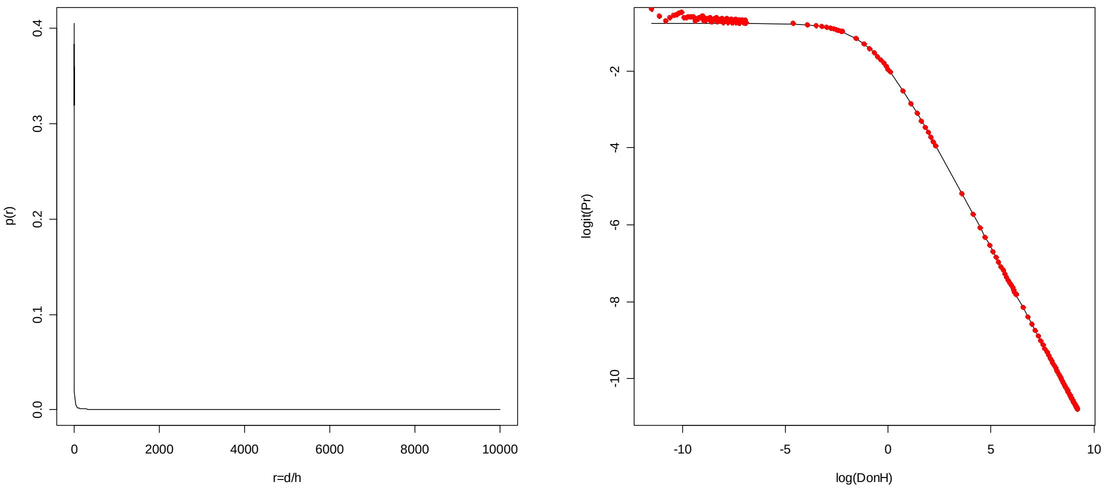


Figure 70: Plots showing (a) the average probability of capture in the domain of attraction and (b) the cubic spline approximation of the transformed probability.

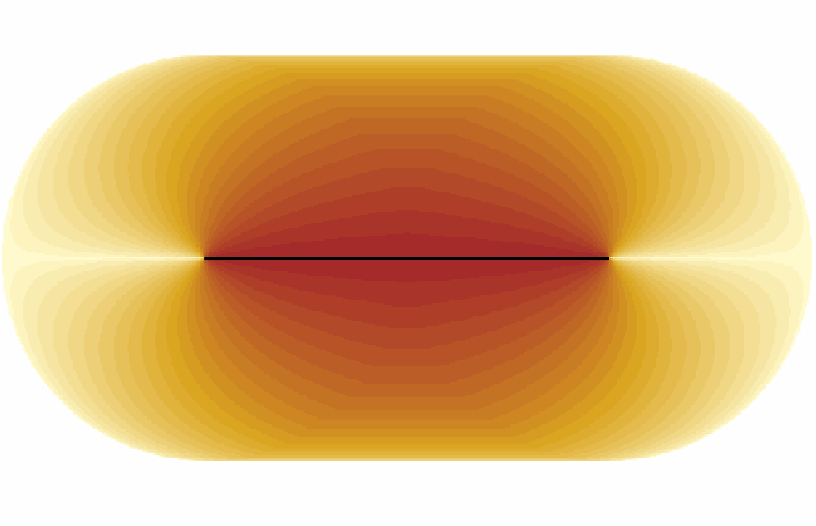


Figure 71: Image plot of probabilities in the domain of attraction. Darker colours indicate higher probabilities.

where we may think of $A(h,d)$ as the "equivalent area" of the domain of attraction, that is, the area of a region in which the mean number of fish equals the average number caught in the gillnet.

The distribution of Y is clearly discrete, and for animals which occur only sparsely within the domain of attraction a natural model is to assume that Y has a Poisson distribution, with an obvious notation

$$Y \sim \mathrm{Po}\left[m = gA(h,d)\right]$$

This will be a credible model if the animals occur at random within the domain of attraction. If there is some clumping of animals, the Poisson model may be replaced by the negative binomial,

$$Y \sim \mathrm{NB}\left[m = gA(h,d), q\right]$$

where q is the negative binomial parameter defined by $\mathrm{Var}[Y] = m + m^2 / q$.

If there are very few captures resulting in a large number of zeros, a zero-inflated mixture model such as a zero-inflated Poisson (ZIP) or zero-inflated negative binomial (ZInb) model may need to be considered:

$$Y \sim \mathrm{ZI}(m = gA(h,d); q, q)$$

The mixture model assumes that counts arise from a mixture of a point mass at zero and a discrete distribution (either Poisson or Negative Binomial) with an unknown probability, q assigned to each component. These distributions are most useful when there is some information about the source of the zero inflation that can be input into the model. For more information about models for count data see McCullagh & Nelder (1989). Information about models for zero-inflated models can be found in the following references (Lambert 1992, Welsh 1996, 2000, Kuhnert et al. 2005).

2.3 A Prior for Random Swimming Speeds

The assumption of a constant swimming speed for all animals is unrealistic, but probably reasonable in this modelling context. We used published swimming speeds for the same or similar-sized scombrid and istiophorid species used in the present study including yellowfin tuna (*Thunnus alabacares*) (Sambilay, 1990), bigeye tuna (*Thunnus obesus*) (Sambilay 1990; Block et al. 1997; Schaefer and Fuller 2002), southern bluefin tuna (*Thunnus maccoyii*) (Davis and Stanley 2001), spotted mackerel (*Scomberomorus munroi*) (Block et al. 1992) Pacific bonito (*Sarda chiliensis*) (Dowis et al. 2003), skipjack (*Katsuwonus pelamis*) (Sambilay 1990), black marlin (*Makaira indica*) (Pepperell and Davis 1999) and blue marlin (*Makaira nigricans*) (Yuen 1974; Holland et al. 1990; Block et al. 1992; Graves et al. 2002) (Table 47). This information was used to develop three informative priors for the following pelagic groups: tunas and mackerels, billfish including sailfish and marlin, and cobia.

To reflect uncertainty in the swimming speed, we considered an informative prior of the form

$$(s-c) \sim \mathrm{Ga}(\alpha, \beta)$$

where c is a constant that shifts the distribution of s to the lowest possible swimming speed for scombrids ($c = 23$) and α and β represent respectively, the shape and scale parameters for the gamma distribution. The parameters α and β were determined from the published swimming speeds and were then used to construct a prior with density similar to that displayed in Figure 72(a)-5(c). Table 47 lists the mean, standard deviation and corresponding distribution parameters used to develop the prior distributions shown in Figures 5(a)-5(c) for the three pelagic groups. Of the three groups, cobia represents the slowest moving fish (6.62 m/min), followed by the tunas and mackerels (15.5 m/min) and lastly, the billfish (25.96 m/min).

Table 47: Summary statistics and parameters used to define the prior swimming speeds (metres per minute) for the three pelagic groups.

Fish Groups	Mean	Standard Deviation	Parameters for Prior α	β
Cobia	6.62	4.08	2.5893	0.3971
Tunas & Mackerel	15.50	10.66	2.1062	0.1363
Billfish	25.96	12.06	5.0136	0.1918

2.4 Estimation

We consider a Bayesian hierarchical model which incorporates the prior information for swimming speeds. The model can be formulated generally as shown in Equation 1, where $f(y_i; \mu_i, \theta, q)$ represents one of the four models proposed in Section 2.2. More explicitly,

$$f(y_i; \mu_i, \theta, q) = \begin{cases} \dfrac{e^{\mu} \mu_i^{y_i}}{y_i!} & \text{Poisson} \\[2ex] \dfrac{\Gamma(\theta + y_i)}{\Gamma(\theta) y_i!} \dfrac{\theta^{\theta} \mu_i^{y_i}}{(\theta + \mu)^{\theta + y_i}} & \text{Negative Binomial} \\[2ex] (1\text{-}q) I_0(y_i) + q \times f(y_i; \mu_i) & \text{ZIP} \\ (1-q) I_0(y) + q \times f(y_i; \mu_i, \theta) & \text{ZInb} \end{cases}$$

In Equation 1, the mean, μ is modelled on the log scale and p_i represents the probability of fish, *i* residing in the domain of capture as determined by the cubic spline (CS) approximation, h_i represents the net length and d_i represents the maximum distance that fish *i* can swim to the net, which is comprised of the duration, t_i and swimming speed, s_i. Note, we define area in square kilometres so the estimate of abundance is number of fish per one square kilometre.

$$\Pr(Y_i = y_i) = f(y_i; \mu, \theta, q)$$

where

$$\log(\mu_i) = \log(\lambda) + \log[A(h_i, d_i)]$$

and

$$\log[A(h_i, d_i)] = \log[p(d_i / h_i)] + \log(\text{Area}_i)$$

$$\log(\text{Area}_i) = \log(t_i) + \log(2h_i + \pi d_i) - \log(10^6) \qquad (1)$$

$$d_i = t_i s$$

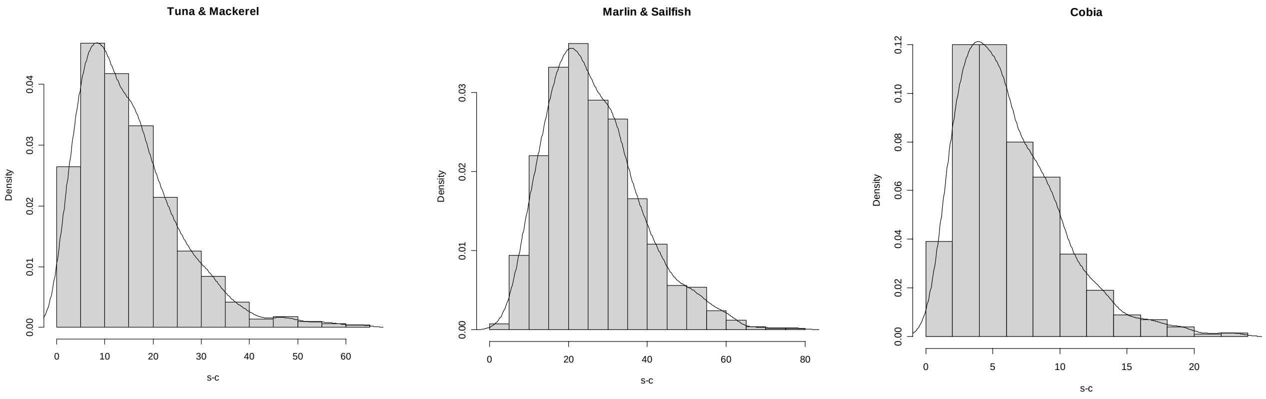
$$\text{logit}[p(d_i / h_i)] = \text{CS}(d_i / h_i)$$

and

$$\log(\lambda) \sim \text{N}(0, 0.1)$$

$$(s - 23) \sim \text{Ga}(\alpha, \beta)$$

We originally considered a non-informative prior for the relative abundance parameter, γ described in Section 2.2. However, as γ and the parameter for swimming speed, *s* are related, (i.e. to estimate abundance we need to know something about the speed at which the fish swims), we placed a prior on their joint distribution, $\lambda = f(\gamma, s)$. This improved convergence considerably, allowing adequate estimation of parameters in the model. The prior chosen for $\log(\lambda)$ therefore was a Normal distribution with a mean of zero and precision, 0.1 representing a fairly non-informative prior but one that was sensible with regards to the range of values λ would likely take. The term precision, represents the inverse of the variance and it is typically represented by the parameter, τ. The estimate of abundance, γ can then be found through the ratio of the posterior distributions of λ and the swimming speed of the fish.



(a) (b) (c)

Figure 72: Informative prior distribution for the shifted swimming speed, s-c for (a) tunas and mackerels, (b) sailfish and marlins and (c) cobia. Speeds are recorded in metres per minute.

For the Negative Binomial model, we introduced an additional overdispersion parameter, θ. We place a fairly non-informative Gamma prior on this parameter, selecting parameters for this distribution that were sensible for the application at hand. In the case of the zero inflated models, the mixing parameter, q also has a non-informative prior distribution attached to it. In this case, $\mathrm{logit}(q) = \alpha$, where α was assigned a non-informative Normal distribution.

Initially, we coded up the problem in WinBUGS (Speigelhalter et al. 2003) and compared models using the deviance information criterion (DIC) (Spiegelhalter et al, 2002) to determine the most appropriate model for each type of fish. However, due to the computational nature of the problem, in particular, the evaluation of the spline approximation, we coded up the problem in C using the Metropolis-Hastings algorithm (Gilks et al. 1996, Gelman et al. 2004) to generate samples from the respective posterior distributions and ran the model on a Windows machine running cygwin. In addition, we appropriately scaled the input variables to encourage adequate mixing of the Markov chains. Estimates were obtained from 10,000 iterations after an initial burn-in of 10,000 iterations. Convergence was assessed using the CODA package in R (Celeux et al. 2003). Computing time took approximately two minutes to perform 20,000 iterations based on a Windows machine running XP with a 2 GHz processor and 1GB of RAM.

Data used for this analysis was collected by scientific observers from the Queensland N9 offshore gillnet fishery. Information collected consisted of counts and fork lengths of each pelagic species caught in each gillnet shot, the length of the net in metres and the shot duration in minutes. Net lengths ranged from 300m to 2200m, with the average net length being approximately 1400 metres in length. Each shot lasted on average, 267 minutes. The minimum shot duration was just over an hour, while the maximum was nearly ten hours.

Out of the four models explored, we found the best model by far was the Negative Binomial as it has the capacity to take into account large counts due to schooling fish as well as the zero inflation, which was evident in many of the datasets.

2.5 Adjusting for Size Selectivity

The methodology described in Section 2.4 for estimating the density of fish does not take into account size selection, which relates to a net's capacity to target a particular size of fish. In this report, we examine catches from gillnets whose mesh size is approximately 6 1/2 inches and develop methodology that incorporates this information into the model to provide an adjusted density estimate.

If we knew the probability of capture, p_c for a given net size, we could adjust for size selection in the model as follows

$$\Pr(Y_i = y_i) = f(y_i; \psi_i = p_c \mu_i, \theta, q)$$

where

$p_c =$ prior distribution for the probability of capture

$\psi_i =$ observed mean density for the i-th shot

$\mu_i =$ true mean density for the i-th shot

In the above expression, p_c can represent a Uniform prior of probabilities between an elicited lower and upper interval having support between 0 and 1. Alternatively, we can find a mathematical expression for p_c with additional input from an expert about the population and captured fork lengths for each fish and input this information into the model. The term "fork length" refers to the length of the fish from the tip of its snout to the fork in its tail. This is considered a more robust measure of fish length than total length of the fish as the size of the tails may vary considerably within a species sometimes due to damage during capture. We explore the latter approach in this report for estimating p_c, which will be used to adjust the density estimates for size selection accordingly.

Consider the population density of fork lengths $\phi(l)$ for a fish with an average fork length $\bar{l}$. Data on most pelagic species in northern Australia is quite sparse and therefore information on the population fork length is poorly documented. We also consider the probability of capture of a fish given its fork length, $\Pr(c\,|\,l)$. An expression for the density of observed fork lengths of a pelagic species given that it is captured in the gillnet can be written as

$$f(l\,|\,c) = \frac{\Pr(c\,|\,l)\phi(l)}{\int_0^\infty \Pr(c\,|\,l)\phi(l)dl} = \frac{\Pr(c\,|\,l)\phi(l)}{p_c} \qquad (2)$$

The expression for p_c in Equation 2 can be thought of as the area under the population density, $\phi(l)$ weighted by the probability of capture for a given fork length. So if $\Pr(c\,|\,l) = 1$, then we capture everything in the population. If $\Pr(c\,|\,l) < 1$, we only capture a proportion, $\Pr(c\,|\,l)$ of the population. Rearranging Equation 2 to provide an expression for the probability of capture given fork length gives the following

$$\Pr(c\,|\,l) = p_c \times \frac{f(l\,|\,c)}{\phi(l)} \quad (3)$$

From the above expression, we know that $\Pr(c\,|\,l)$ is equal to one when the ratio of the observed fork lengths given capture and the population density is at its maximum. If we assume that $f(l\,|\,c)$ and $\phi(l)$ are both Normal densities, (based on empirical data for pelagic species in the NPF) we can write down the following expression for this ratio.

$$\text{Ratio} = \frac{f(l\,|\,c)}{\phi(l)} = \frac{\frac{1}{\sqrt{2\pi}\sigma_f}\exp(-0.5(l-\mu_f)^2/\sigma_f^2)}{\frac{1}{\sqrt{2\pi}\sigma_\phi}\exp(-0.5(l-\mu_\phi)^2/\sigma_\phi^2)}$$

Taking logs of this expression gives

$$-\log(\sigma_f) - \frac{0.5(l-\mu_f)^2}{\sigma_f^2} + \log(\sigma_\phi) + \frac{0.5(l-\mu_\phi)^2}{\sigma_\phi^2}$$

and differentiating with respect to *l* and setting the expression to zero to solve for $\tilde{l}$ provides an expression for the estimated fork length at the maximum.

$$\tilde{l}\left(\frac{1}{\sigma_\phi^2} - \frac{1}{\sigma_f^2}\right) + \frac{\mu_f}{\sigma_f^2} - \frac{\mu_\phi}{\sigma_\phi^2} = 0$$

$$\tilde{l} = \frac{\mu_\phi\sigma_f^2 - \mu_f\sigma_\phi^2}{\sigma_f^2 - \sigma_\phi^2}$$

Substituting $\tilde{l}$ into the expression for the ratio and rearranging gives

$$\text{Ratio} = \frac{f(\tilde{l}\,|\,c)}{\phi(\tilde{l})} \text{ and } p_c = 1/\text{Ratio}, \qquad (4)$$

An expression for the probability of capture, p_c. In Equation 4 however, only one of the terms, $f(\tilde{l}\,|\,c)$ is known with some degree of certainty. To evaluate this expression, we need to elicit information about the population density, $\phi(l)$ for the species of interest. Section 2.6 outlines the elicitation process undertaken to evaluate a prior density for $\phi(l)$.

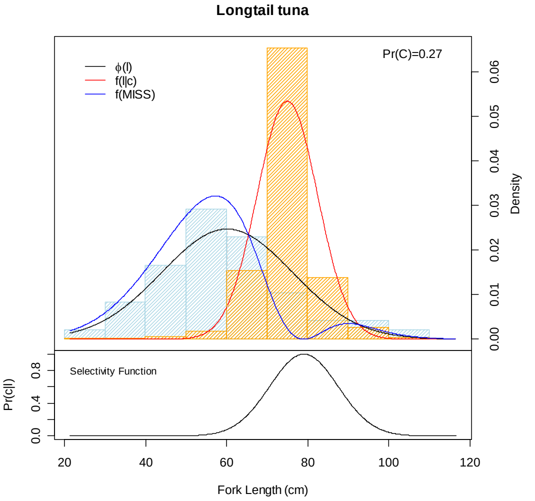
2.6 Elicitation of $\phi(l)$

The elicitation of information regarding the fork length distributions for each pelagic species was a three stage process.

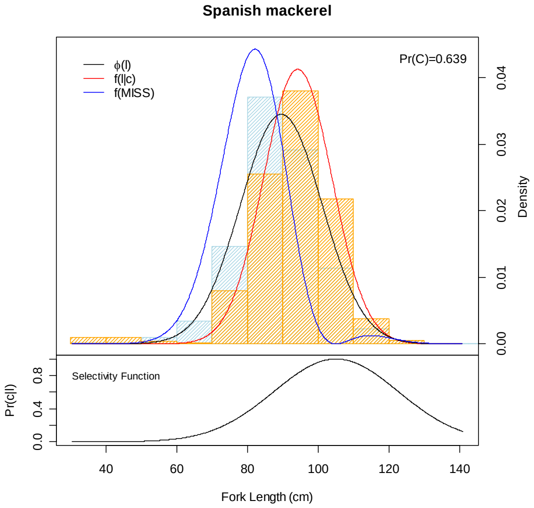
The first stage involved extracting relevant data for the distribution of fork lengths for each pelagic species in the N9 fishery and developing an appropriate prior distribution for $\phi(l)$ which also incorporated expert information about the region and likely catches for each pelagic species. To complete this first stage of the elicitation process, we used catch data from a Taiwanese gillnet operation which operated in Australia's NPF from 1979-1986, long-line fishing and N9 catch records to provide a baseline from which a population density could be extracted. Input from a fish biologist was required here to determine the shape and structure of the prior distribution, which in this case was a Normal distribution. This became an iterative process and involved a lot of fine tuning to capture what had been observed in the NPF.

The second stage involved building a relevant prior distribution for the observed catches in the N9 region, $f(l \mid c)$. This again was based on fork length data collected in the N9 fishery. However, for some fish, where the data was scarce, we relied on experts to provide information about the shape, centre and extreme values of this distribution. In situations where the expert did not feel confident reporting about the density of observed catches, no distribution was constructed. This meant that an estimate for the probability of capture could not be formed for that pelagic species. This was the case for spotted mackerel, a species for which density estimates could not be determined with high precision.

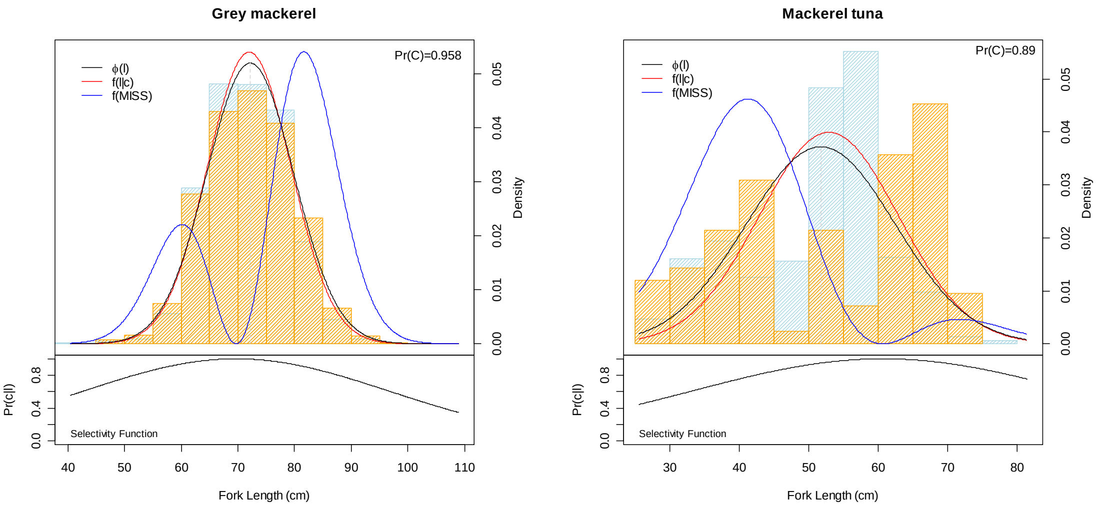
The final stage of the elicitation process involved using a graphical aid to visualise the elicited distributions and confirm their validity through the construction of the selectivity function using the expression shown in Equation 3. We found this graphical aid useful for confirming the expert's prior judgement in situations where not much data had been collected for a fish.



(a)



(b)



(c) (d)

Figure 73: Prior distributions for the population fork length (black curve) and observed fork length distribution (red) curve in the N9 fishery for (a) longtail tuna, (b) Spanish mackerel, (c) grey mackerel and (d) mackerel tuna. Components of the population that are missed are represented by the blue density. The selectivity function is shown beneath each plot and represents the probability of capture, *Pr(C)*. Data used to define each density is shown as a histogram. The orange histogram represents observed catches in the N9 fishery while the blue histogram represents "population" data.

Figure 73 and Figure 74 summarise the results of the elicitation process for the eight pelagic species investigated. The top plot of each figure shows the prior distribution elicited for that population, $\phi(l)$ (black line), the prior distribution elicited for the observed fork lengths in the N9 fishery, $f(l \mid c)$ (red line), and the density corresponding to the portion of the population that is missed from gillnet fishing, $f(\text{MISS})$ (blue line). The latter density was derived from the expression

$$f(\text{MISS}) = \frac{(1 - \Pr(c \mid l))\phi(l)}{1 - p_c}$$

Observed data are also shown on this plot using histograms. Data used to derive the population distribution is shown in blue, while data collected from the N9 fishery is shown in orange. Beneath each figure is a second plot showing the probability of capture or selectivity given a specific fork length of the fish, $\Pr(c \mid l)$.

For the majority of the pelagic species, the observed fork length distribution in the N9 fishery captures the majority of the population reasonable well. Grey mackerel for example, matches the population quite closely, missing only a small proportion of the larger fish as indicated by the selectivity function. Black marlin presents a similar scenario as the selectivity function also indicates that some of the larger sized marlin are not being captured by the gillnet in the N9 fishery. The selectivity curve of mackerel tuna however indicates that a small proportion of smaller fish, between 28cm and 45cm are not adequately captured by the gillnet. This is also somewhat true of cobia. Sailfish, Spanish mackerel and leaping bonito all show a bell shaped selectivity function, indicating that the highest proportion of fish caught are mid ranged in terms of size.

In determining the population distribution of fork lengths for each species, catches from a Taiwanese expedition were used. These gave a reasonable baseline from which to elicit the distribution for all fish with the exception to longtail tuna. We found that the distributions based on the Taiwanese catches were quite different to what was observed in the N9 fishery, resulting in a probability of capture of approximately 0.004. It was evident that smaller sized longtail tunas were being caught in the Taiwanese gillnet operation compared to catches in the N9 fishery. This prompted further investigation into the biology and ecology of the fish to determine why such marked differences in distributions would be observed. One possible conclusion is that juveniles appear in the north-western region of the NPF where the Taiwanese operation took place and then migrate to the N9 fishery in the eastern Gulf of Carpentaria, where typically larger individuals are observed.

To justify this theory, we extracted some additional information from two independent surveys conducted within the N9 fishery and compared this information with data collected from the Taiwanese fishing operation and catches recorded in the N9 fishery. We found that the independent surveys were similar to the N9 catches and therefore we were able to derive a more plausible population distribution using this data in conjunction with expert opinion about the fishery and longtail tuna. The resulting prior distributions for $f(l \mid c)$ and $\phi(l)$ from this elicitation exercise are displayed in Figure 73(a) (red and black lines respectively) and show a smaller proportion of the juveniles being missed compared to previous calculations (blue line), resulting in a probability of capture of 0.27. Although this result seems plausible, it would be worthwhile investigating the migratory patterns of longtail tuna in northern Australia more closely.

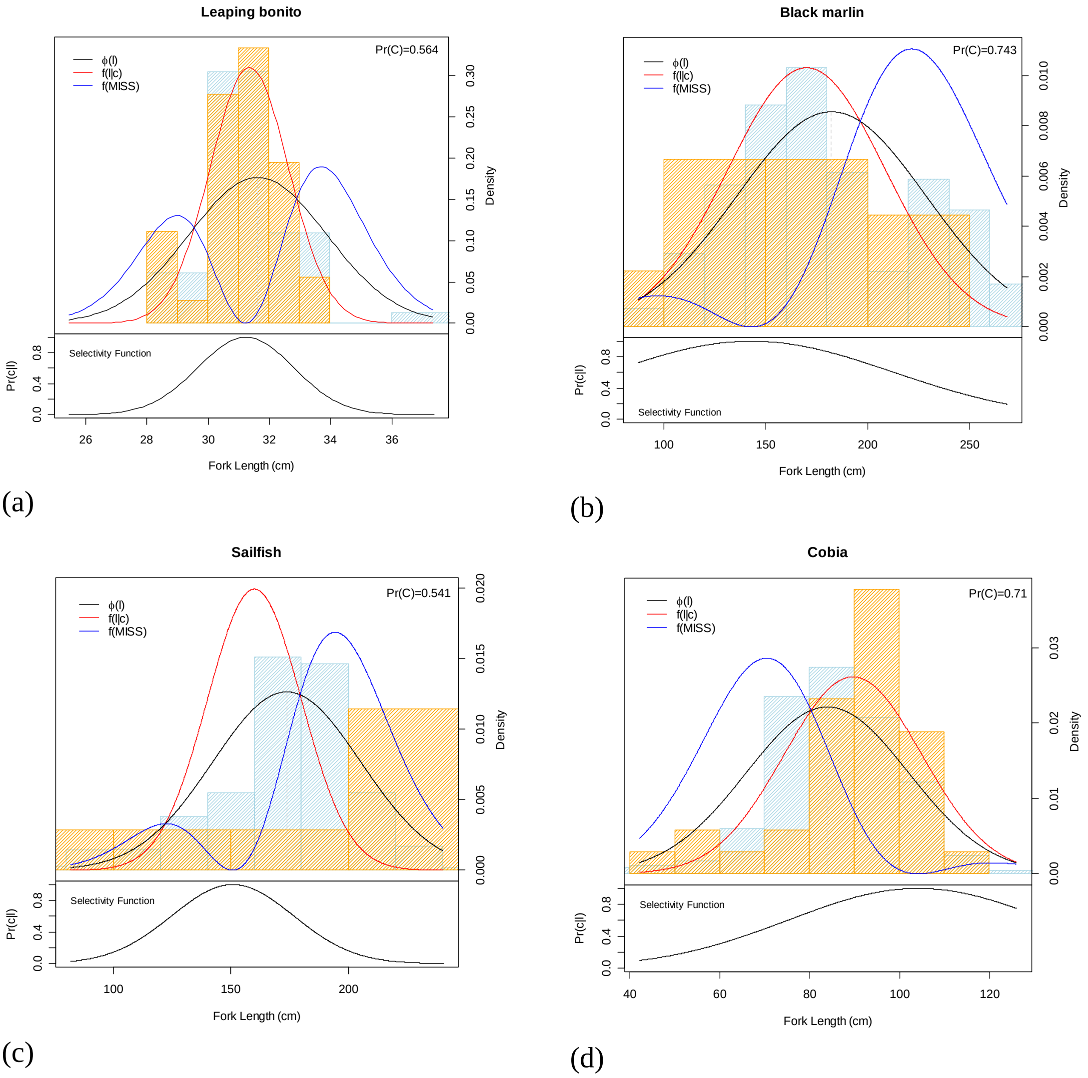


Figure 74: Prior distributions for the population fork length (black curve) and observed fork length distribution (red) curve in the N9 fishery for (a) leaping bonito, (b) black marlin, (c) sailfish and (d) cobia. Components of the population that are missed are represented by the blue density. The selectivity function is shown beneath each plot and represents the probability of capture, *Pr(C)*. Data used to define each density is shown as a histogram. The orange histogram represents observed catches in the N9 fishery while the blue histogram represents "population" data.

Results

Results from fitting the gillnet model to eight pelagic species are shown in Table 48 and Table 49. Estimates shown are based on 10,000 iterations after an initial burn-in of 10,000 iterations for the Negative Binomial model only. (Note, we examined the fit of all four models explored in the previous section and found that the Negative Binomial provided the best fit in terms of the Deviance information Criterion. We also examined each model for adequate mixing of the Markov chains and also for convergence using CODA and concluded that a burn-in of 10,000 iterations was sufficient.)

Results presented in Table 48 consist of the posterior mean, standard deviation and 95% credible interval for the swimming speed (s) of each fish and the overdispersion parameter (θ) resulting from the Negative Binomial model. It is clear from this table that the swimming speed posterior mean summaries reflect the informative prior chosen for each fish. Overdispersion was evident in all eight models as it took into account large counts due to schooling fish (grey mackerel) as well as low counts for species such as the billfish, where many zeros were recorded.

Table 48: Results from fitting the Negative binomial model to the pelagic fish dataset. Posterior mean estimates, standard errors and 95% credible intervals are shown for the swimming speed (s) and overdispersion parameter (θ).

Fish	**Swimming Speed *(s)***			**Overdispersion** (θ)		
	Estimate	**SD**	**95% CI**	**Estimate**	**SD**	**95% CI**
Longtail Tuna	39.101	11.054	(25.09,67.15)	0.2779	0.035	(0.21,0.35)
Spanish Mackerel	38.567	10.769	(25.04,65.86)	0.4103	0.056	(0.32,0.53)
Grey Mackerel	39.026	10.748	(25.16,65.36)	0.2740	0.028	(0.22,0.33)
Mackerel Tuna	38.009	10.626	(25.02,64.55)	0.0406	0.019	(0.02,0.08)
Leaping Bonito	37.996	10.229	(25.15,63.58)	0.0590	0.024	(0.03,0.12)
Black Marlin	48.870	11.337	(31.79,75.32)	3.8100	6.046	(0.03,20.27)
Sailfish	48.622	11.329	(31.66,75.78)	3.7557	5.902	(0.03,20.27)
Cobia	29.563	4.280	(24.03,40.92)	0.2654	0.083	(0.15,0.47)

Table 49 presents the density estimates from the eight models before and after adjusting for size selection using the methods developed in Sections 2.5 and 2.6. Note that the posterior estimates for swimming speed and overdispersion did not change once the adjustment for size selection was incorporated into the model.

Table 49: Results from fitting the Negative binomial model to the pelagic fish dataset. Posterior mean estimates, standard errors and 95% credible intervals are shown for the density (γ) and adjusted density (γ^*), which takes into account size selection. Density estimates are highlighted in bold font

Fish	**Density** (γ)				**Adjusted Density** (γ^*)		
	Estimate	**SD**	**95% CI**	p_c	**Estimate**	**SD**	**95% CI**
Longtail Tuna	0.4915	0.139	(0.257,0.780)	**0.2705**	1.8099	0.499	(0.965,2.874)
Spanish Mackerel	0.3986	0.106	(0.206,0.616)	**0.6388**	0.6210	0.166	(0.324,0.963)
Grey Mackerel	3.9754	1.087	(2.090,6.208)	**0.9582**	4.1737	1.167	(2.173,6.641)
Mackerel Tuna	0.0207	0.013	(0.007,0.053)	**0.8905**	0.0228	0.015	(0.008,0.056)
Leaping Bonito	0.0244	0.012	(0.009,0.053)	**0.5643**	0.0438	0.021	(0.017,0.096)
Black Marlin	0.0032	0.002	(0.001,0.007)	**0.7434**	0.0042	0.002	(0.001,0.009)
Sailfish	0.0027	0.001	(0.001,0.006)	**0.5408**	0.0050	0.003	(0.002,0.012)
Cobia	0.0573	0.013	(0.034,0.086)	**0.7101**	0.0806	0.018	(0.050,0.120)

Density estimates did not change substantially after size selection for most pelagic fish investigated, with the exception to longtail tuna. The density estimate for this species jumped from 0.49 fish per square kilometre to 1.81 fish per square kilometre.

The largest density estimate was obtained for grey mackerel, where the number of fish per square kilometre was estimated to be 4.17 (2.17, 6.64) after adjusting for size selection. Smaller density estimates were obtained for the billfish (sailfish and marlin), cobia, leaping bonito and mackerel tuna, where between 0.004 and 0.08 fish per square kilometre was estimated. The density of Spanish mackerel in the NPF is somewhat higher, an estimate of 0.621 fish per square kilometre, with confidence intervals ranging between 0.32 and 0.96 fish per square kilometre.

Discussion

Estimating the density or biomass of pelagic species is a difficult and complex problem, especially for species having little economic importance for which little data is generally available. However, it is the low value species that are becoming increasingly important for scientists to determining their role in ecosystems in which fisheries interact. In northern Australia, many species of scombrids and istiophorids are not harvested commercially, but are ecologically important as they occupy high trophic levels or are even apex predators. As a result, it is important to obtain reasonable estimates of their biomass to include in ecosystem models to more closely reflect the real world in order for is application to ecosystem-based fisheries management to be successful.

We recognise that our model for gillnet catches has a number of assumptions which may not be entirely realistic in the real world, such as fish swimming in straight lines and in random directions. As individuals, fish are not constrained to swim in such a manner, and their swimming behaviour and probability of capture in a gillnet, is likely to be influenced by numerous factors including strength and direction of prevailing currents and wind (Sugimoto and Tameishi 1992); proximity of fish to reefs, seamounts, landmasses, or FADs (Itano and Holland 2000; Klimley et al. 2003; Musyl et al. 2003; Ohta and Kakuma 2005); water temperature and the depth of the thermocline (Itoh et al. 2003; Schick et al. 2004), and the presence of prey or predators (Chase 2002; Musyl et al. 2003). However, there are great difficulties in quantifying the behaviour of pelagic fish in the open ocean to warrant inclusion in our model. With the advances in satellite tag technology such behaviour has only recently being started to be understood in some economically important species.

Nonetheless, we feel that our model is robust enough to provide reasonable first order estimates of pelagic fish densities, which may be modified to become increasingly sophisticated depending on the data available for particular species. It has been widely shown that many pelagic fishes including bigeye tuna (Schaefer and Fuller 2002), yellowfin tuna (Brill et al. 1999), Pacific bluefin tuna (Kitagawa et al. 2000), blue marlin (Holland et al. 1990), black marlin (Pepperell and Davis 1999) and striped marlin (Domeier and Dewar 2003) undertake strong diel vertical migrations where most they generally migrate to surface waters during the night. This would result in fish being less susceptible to capture by surface set gillnets during the day, leading to underestimates of density using our model.

We did not incorporate a diel vertical migration function in our model for a number of reasons. First, there is no available data on the diel movements of pelagic fishes in the Gulf of Carpentaria. Pepperell and Davis (1999) studied the diel vertical migrations of black marlin at similar latitude as the present study off the Great Barrier Reef, Australia and showed fish regularly dived deeper than 60 m when in water depths of 200 m, but did not show any significant diel vertical movement when in shallower depths of less than 100 m. Because the maximum water depth in our study was 32 m we presumed that the diel vertical movement of fish was probably minimal, or at least not significant enough to exclude fish from the path of the 10 m drop of the gillnet. However, our model may be modified to incorporating data on the diel vertical movements of individual species where available, which would improve the probability estimate of interactions with fishing gear.

Acknowledgements

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IV-7. Environmental predictors of Banana Prawn abundance

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Environmental predictors of Banana Prawn abundance

In this chapter we consider part of the role of environmental drivers in the life cycle of the common banana prawn, *Penaeus merguiensis*. We will be concerned with environmental correlates with catch, or CPUE, using both as possible indices of abundance. We will mostly be concerned with the evidence as presented by the experience in the Weipa region, initially and with the Mitchell and Karumba regions, also in the Eastern Gulf Of Carpentaria for comparative purposes.

Introduction

The following Figure 75 shows a schematic representation of the life cycle of the common banana prawn, involving a short offshore migration between adolescence and spawning. Catch takes place generally in the months of April and May when the individuals are generally at their largest size. The timing of the catch is generally an economic compromise between loss of value due to the animals being too small and loss of product due to natural mortality.

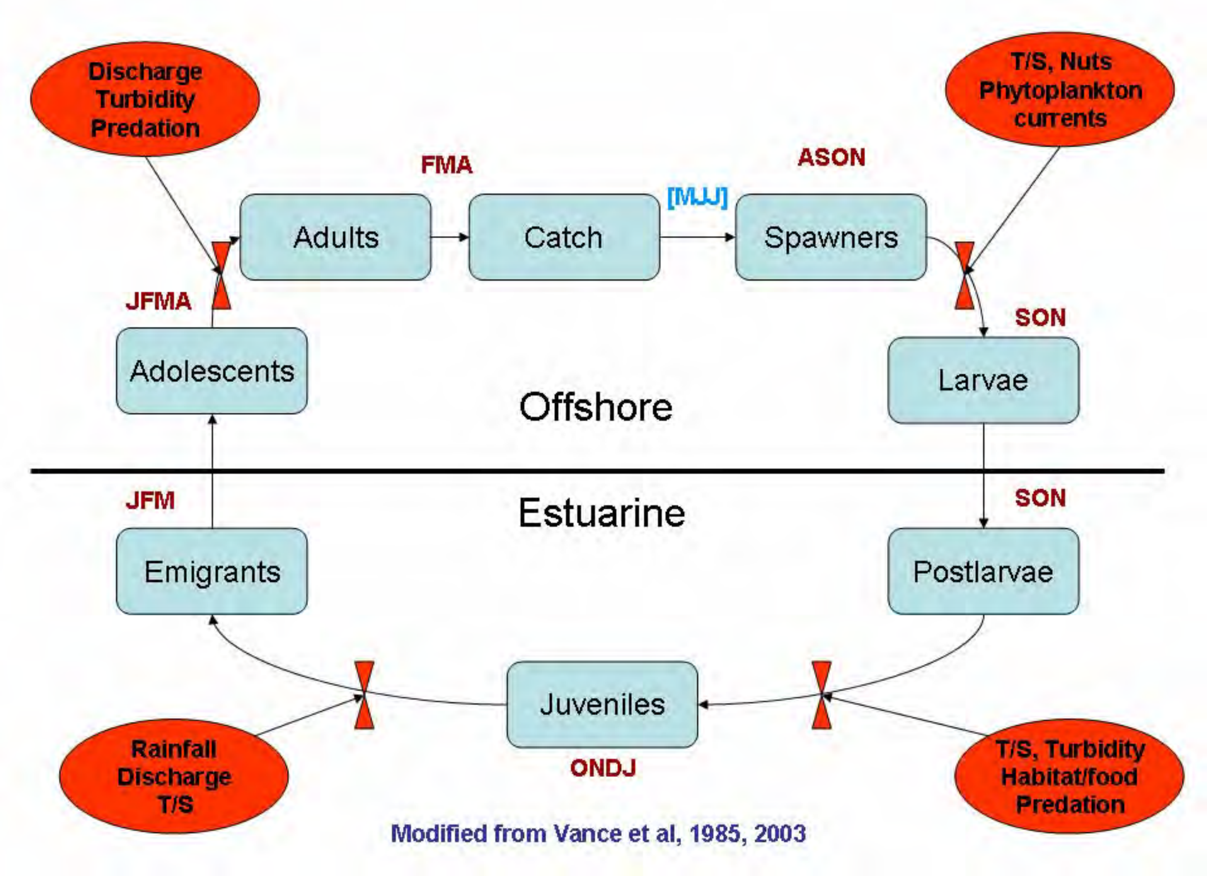

Figure 75: Schematic diagram of the life stages of *P. merguiensis*. The animal is spawned in the near offshore by the survivors of the commercial catch and natural mortality. As larvae the animals then migrate to the estuarine areas where they mature. Later in the life cycle they migrate to the offshore areas again where they develop into adults. Environmental influences are seen to be important in at least four stages, as indicated by the red ellipses.

As we will be relying on catch data for evidence of abundance, of the four stages identified on Figure 75 as being times when environmental influences may play a large role in determining abundance, we will be mostly concerned with the lower left and upper left stages, that is, those which have the most direct effect on catch. Since catch largely takes place at Weipa in April, the environmental predictors will largely be focused on events in the preceding months from about October to February. This is not to discount the potential influence of environmental predictors at earlier life stages, but merely to focus on those which *prima facie* might be considered to have the more direct effect for the immediate purposes of this study.

Previous studies have focused on the environmental predictors which might conceivably be associated with the egress of the animals from the estuary, chiefly rainfall events (Staples *et al.* 1982). We consider a range of predictors that might explain the apparent major change in abundance in Banana prawns in recent years, but mostly concentrate on functions of annual rainfall. This is partly because of the findings of previous studies cited, but also because other potential predictors from the area are simply unavailable, at least to the extent that would be useful for this study.(Vance *et al.* 1983a;Vance *et al.* 1983b;Staples *et al.* 1984;Vance *et al.* 1985)

This makes a study of the Gulf of Carpentaria catchments a natural first step and we return to this question in the next section.

Most previous studies have used point sources of data to define the predictors. This has the advantage, where such a data set is available, of immediacy with the system under study. We consider some data of this kind, but or main focus will be data pertaining to an entire catchment, as provided by the 'SILO' data sets (see, for example http://silo.eoc.csiro.au/html/grids/griddata.htm/). This has the advantage of integrating all available data on the indicator of interest, hopefully in a useful and reliable way. We return to this question in a later section.

Abundance indices

The banana prawn catch in the Gulf of Carpentaria is exclusively of *P. merguiensis* and typically relies on the fishers locating large aggregations of animals known as 'boils', when catchability is at its peak. Harvest typically takes place in a relatively short space of time and when the aggregations become fragmentary, fishing generally focuses on other targets, usually tiger prawns. The main banana fishing period is usually over by mid to late May, but may be much quicker than this. Nevertheless a small part of the banana prawn catch can occur at any time of the fishing year.

Since the catch of banana prawns is such a well-defined annual event, we consider the annual catch within a specific stock region as a single event and base indicators of annual abundance on it alone. There is a question whether the index of abundance should be the catch itself or the more usual catch per unit effort (CPUE). It could be argued that since the animals are generally located in 'boils' (though not always as such in Weipa, it has been reported) a very productive year would generally quickly become obvious to the fleet, thus attracting effort to the harvest. Conversely a very unproductive year would also become quickly obvious as well, and would have the effect of turning the fleet to tiger prawn fishing earlier than usual. In this sense, it may be argued, that 'catch attracts effort', making the catch alone an appropriate indicator of annual abundance. Against this is the argument put forward by some commentators that, particularly at Weipa, 'boils' are not as common or as easy to spot because of local conditions; that locating the stock of banana prawns requires a certain minimum preliminary search effort, which may not take place in recent times for several reasons, including the shortened fishing season, the reduced fleet and the relative ease of locating boils elsewhere, notably at Karumba or Groote. This would argue in favour of the more customary CPUE indicator of abundance.

In this study we adopt a very pragmatic empirical approach and consider both possibilities. This study of environmental predictors should be considered only as an investigative study for the purpose of hypothesis generation as much as for answering those key questions. Since essentially all the catch data we have is observational, and hence unplanned, this stance is almost unavoidable.

Banana prawn stock regions in the NPF

The NPF has been partitioned into (putative) stock regions for *P. merguiensis*, based on expert opinion and to some extent confirmed by fishing practice by the industry. These regions are shown in Figure 76. For our purposes the key stock region is **11**, centred on the Weipa region and informally named 'Weipa'. For comparative purposes we will also study regions **09**, 'Karumba' and **10**, 'Mitchell'. Catchment regions in the Gulf of Carpentaria are to be described next, but notice that these three focus regions, Karumba, Mitchell and Weipa, or at least the heavily fished areas within these regions, are spatially concentrated near the mouths of the Norman, Mitchell and Embley rivers, respectively. Other rivers may well exert an influence on these stocks, but we will use these three catchments as the primary drivers. If there is an environmental connexion it should be possible to show it using these three rivers alone. This is also supported by the evidence we present below (see Figure 78) that the catchments may be grouped into similarly behaving clusters with respect to their rainfall characteristics, suggesting a strong surrogacy relationship between rivers within a cluster as regards their predictive capacity for the kinds of models we construct below.

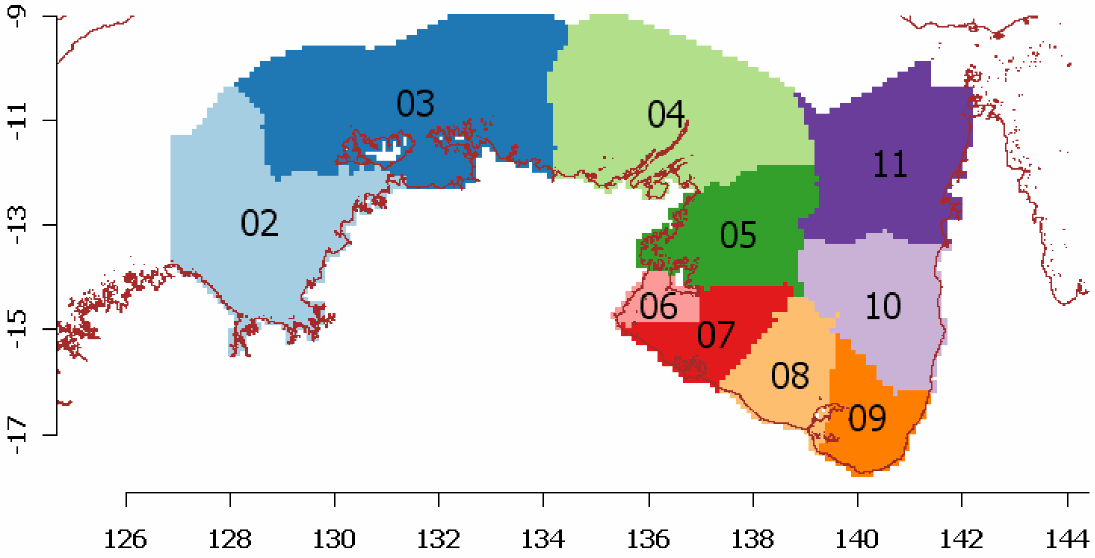

Figure 76: Common banana prawn (*P. merguiensis*) stock regions used in the NPF. These are based on expert opinion and are used mainly for stock assessment purposes. The regions of most concern in this study are **09**, 'Karumba', **10**, 'Mitchell' and **11**, 'Weipa'. (Note that region **01,** 'Kimberley'**,** is no longer included in the NPF.)

Gulf of Carpentaria catchments

The following

Figure 77 shows the principal river catchments draining in to the Gulf of Carpentaria. Our interest will shortly focus on a much smaller subset of these, namely those determining the Weipa, Mitchell and Karumba banana prawn stock regions, but we begin by looking at them as a group.

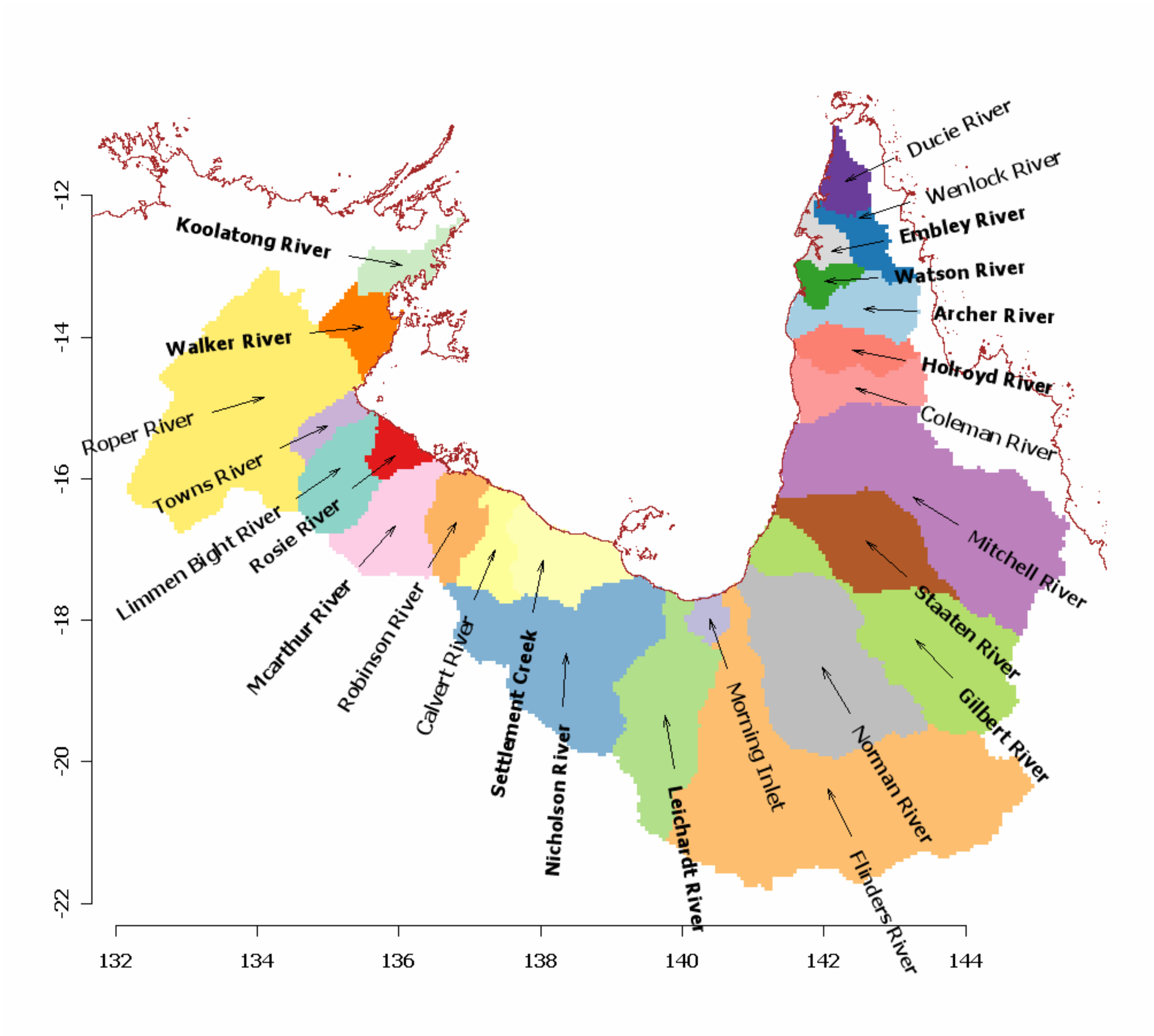

Figure 77: Principal catchments of the Gulf of Carpentaria.

We use the SILO data to generate ***daily averages over a catchment*** for the years 1969 to 2004 of the four parameters ***Rainfall***, ***Evaporation***, ***Maximum Temperature*** and ***Minimum Temperature*** as raw material from which specific predictors will ultimately be constructed. It is useful initially to consider the way in which these catchments differ in their rainfall characteristics.

Table 50 below shows the monthly mean rainfall profiles. It is clear even from this simple overview that the rainfall is strongly monsoonal with highest rainfall in the early and late months of the year and a prolonged dry period in the middle. It is also clear that the strongest wet seasons occur in the northern regions, particularly the north-east, and the southern regions are much dryer. The tentative division into three groups by dashed lines shown on Table 50 is based not only on the mean profile, but on covariance properties of the rain record as well. We turn to this in the next section.

Classification of gulf catchments by their rainfall records

The previous Table 50 merely looked at the mean monthly rainfall profile for different catchments. There are also strong correlations between daily rainfall patterns for different catchments as well, with adjacent catchments generally the most highly correlated. Some of this correlation is clearly caused by a shared strong monsoonal seasonal pattern, but even if the series are de-trended and de-seasonalised (by a method to be outlined in the next section), the resulting series are still are still quite highly correlated, suggesting that the catchments not only share a seasonal pattern, but variations to the underlying mean pattern are also shared between catchments as well, at least to a fairly high degree.

Tables on the following two (landscape) pages show these correlation matrices the uncorrected version first followed by the corrected version. See Table 49 and Table 50 on pages following.

Some care needs to be taken in considering these correlation matrices as the raw data from which they are formed are not really statistical samples but averages of data that has already been extrapolated from a much smaller number of genuine data sources. At best this is a pseudo-analysis, but adequate for comparative and exploratory purposes, we contend.

The covariance matrix of the daily rainfalls can be used to define a natural metric on the stations. This is done by finding the eigenvectors of the variance matrix, scaling each column by the square root of the eigenvalues (or principal variance) and using the rows of the resulting matrix as a Euclidean coordinate system. Using the "distances" between coordinates so defined we can either use multi-dimensional scaling to find a lower dimensional coordinate system that preserves most of the relativities, (in this case the simplest method would be simply to choose the first two columns as a two-dimensional representation, which is identical to using the first two principal components for variance reduction) or clustering the stations using some clustering method. We choose the latter and use a hierarchical clustering using "Wards method" a well-known criterion.

This leads to the following representation of the stations themselves, shown in Figure 78.

Figure 78: Hierarchical clustering of Gulf of Carpentaria catchments based on covariances between de-seasonalised, de-trended time series of daily rainfall.

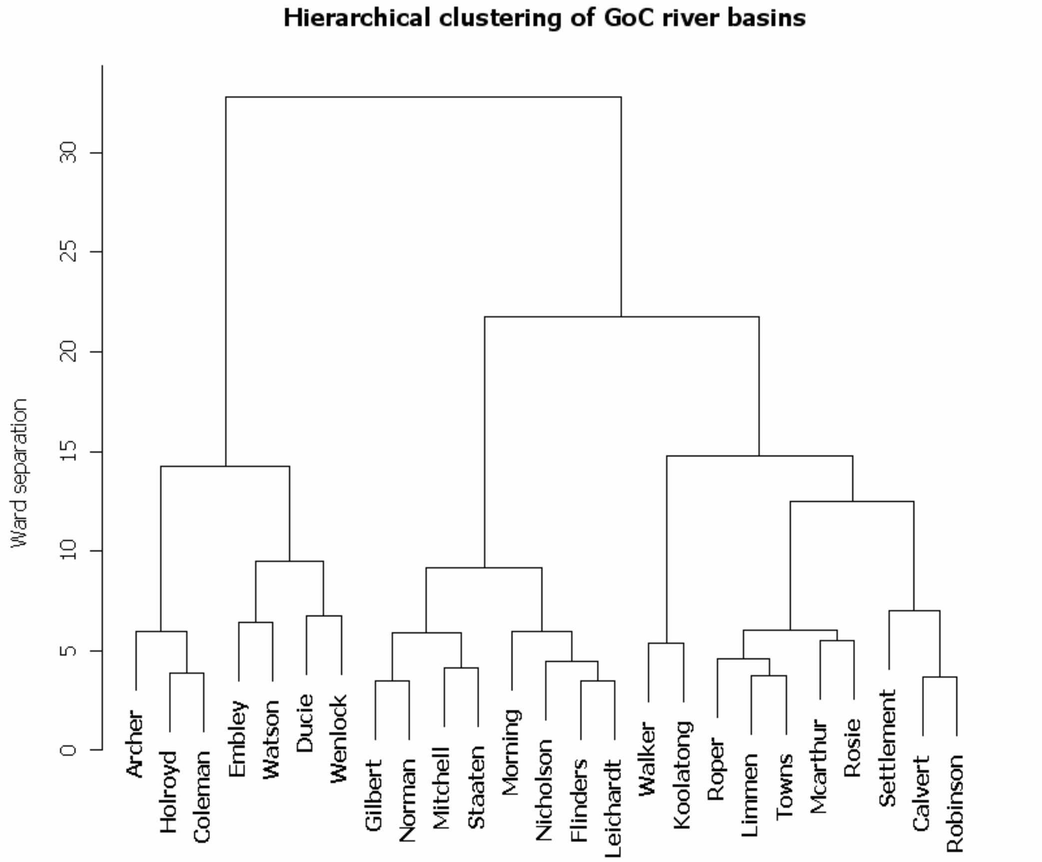

Table 50: Correlations between raw daily rainfall measurements for 25 gulf catchments

	Ducie	Wenlock	Embley	Watson	Archer	Holroyd	Coleman	Mitchell	Staaten	Gilbert	Norman	Flinders	Morning	Leichardt	Nicholson	Settlement	Calvert	Robinson	Mcarthur	Rosie	Limmen	Towns	Roper	Walker	Koolatong
Ducie	1.000	0.775	0.756	0.602	0.578	0.494	0.452	0.383	0.299	0.258	0.233	0.184	0.208	0.185	0.234	0.253	0.241	0.248	0.255	0.275	0.285	0.311	0.356	0.314	0.363
Wenlock	0.775	1.000	0.835	0.753	0.771	0.589	0.522	0.434	0.337	0.291	0.263	0.206	0.236	0.209	0.259	0.286	0.266	0.263	0.264	0.274	0.286	0.304	0.359	0.307	0.347
Embley	0.756	0.835	1.000	0.856	0.712	0.606	0.544	0.451	0.355	0.311	0.278	0.211	0.245	0.215	0.261	0.270	0.252	0.247	0.258	0.255	0.284	0.295	0.352	0.288	0.311
Watson	0.602	0.753	0.856	1.000	0.847	0.742	0.628	0.495	0.404	0.352	0.317	0.233	0.262	0.234	0.266	0.278	0.258	0.249	0.259	0.255	0.283	0.300	0.363	0.288	0.315
Archer	0.578	0.771	0.712	0.847	1.000	0.883	0.724	0.538	0.430	0.362	0.324	0.245	0.279	0.251	0.293	0.314	0.290	0.282	0.280	0.278	0.292	0.313	0.378	0.310	0.335
Holroyd	0.494	0.589	0.606	0.742	0.883	1.000	0.902	0.615	0.490	0.406	0.358	0.267	0.298	0.271	0.302	0.306	0.288	0.280	0.279	0.272	0.292	0.308	0.370	0.293	0.313
Coleman	0.452	0.522	0.544	0.628	0.724	0.902	1.000	0.723	0.563	0.461	0.406	0.296	0.336	0.303	0.332	0.326	0.305	0.292	0.291	0.284	0.304	0.318	0.379	0.294	0.312
Mitchell	0.383	0.434	0.451	0.495	0.538	0.615	0.723	1.000	0.803	0.708	0.577	0.439	0.426	0.397	0.399	0.355	0.324	0.306	0.318	0.284	0.321	0.313	0.388	0.270	0.280
Staaten	0.299	0.337	0.355	0.404	0.430	0.490	0.563	0.803	1.000	0.758	0.653	0.457	0.468	0.436	0.414	0.361	0.311	0.297	0.306	0.276	0.300	0.299	0.348	0.247	0.253
Gilbert	0.258	0.291	0.311	0.352	0.362	0.406	0.461	0.708	0.758	1.000	0.815	0.670	0.522	0.517	0.444	0.349	0.304	0.275	0.297	0.252	0.282	0.273	0.322	0.207	0.213
Norman	0.233	0.263	0.278	0.317	0.324	0.358	0.406	0.577	0.653	0.815	1.000	0.757	0.627	0.642	0.515	0.382	0.321	0.287	0.300	0.246	0.267	0.254	0.294	0.203	0.204
Flinders	0.184	0.206	0.211	0.233	0.245	0.267	0.296	0.439	0.457	0.670	0.757	1.000	0.598	0.753	0.526	0.331	0.284	0.254	0.283	0.209	0.235	0.219	0.254	0.169	0.155
Morning	0.208	0.236	0.245	0.262	0.279	0.298	0.336	0.426	0.468	0.522	0.627	0.598	1.000	0.749	0.622	0.486	0.371	0.324	0.338	0.276	0.299	0.276	0.302	0.215	0.203
Leichardt	0.185	0.209	0.215	0.234	0.251	0.271	0.303	0.397	0.436	0.517	0.642	0.753	0.749	1.000	0.740	0.465	0.372	0.329	0.357	0.264	0.288	0.261	0.290	0.200	0.183
Nicholson	0.234	0.259	0.261	0.266	0.293	0.302	0.332	0.399	0.414	0.444	0.515	0.526	0.622	0.740	1.000	0.736	0.624	0.523	0.534	0.379	0.420	0.358	0.378	0.236	0.217
Settlement	0.253	0.286	0.270	0.278	0.314	0.306	0.326	0.355	0.361	0.349	0.382	0.331	0.486	0.465	0.736	1.000	0.789	0.661	0.582	0.477	0.479	0.423	0.416	0.276	0.262
Calvert	0.241	0.266	0.252	0.258	0.290	0.288	0.305	0.324	0.311	0.304	0.321	0.284	0.371	0.372	0.624	0.789	1.000	0.890	0.694	0.565	0.550	0.484	0.458	0.310	0.275
Robinson	0.248	0.263	0.247	0.249	0.282	0.280	0.292	0.306	0.297	0.275	0.287	0.254	0.324	0.329	0.523	0.661	0.890	1.000	0.820	0.686	0.633	0.554	0.512	0.344	0.301
Mcarthur	0.255	0.264	0.258	0.259	0.280	0.279	0.291	0.318	0.306	0.297	0.300	0.283	0.338	0.357	0.534	0.582	0.694	0.820	1.000	0.741	0.780	0.615	0.579	0.331	0.291
Rosie	0.275	0.274	0.255	0.255	0.278	0.272	0.284	0.284	0.276	0.252	0.246	0.209	0.276	0.264	0.379	0.477	0.565	0.686	0.741	1.000	0.823	0.802	0.636	0.493	0.396
Limmen	0.285	0.286	0.284	0.283	0.292	0.292	0.304	0.321	0.300	0.282	0.267	0.235	0.299	0.288	0.420	0.479	0.550	0.633	0.780	0.823	1.000	0.845	0.705	0.407	0.334
Towns	0.311	0.304	0.295	0.300	0.313	0.308	0.318	0.313	0.299	0.273	0.254	0.219	0.276	0.261	0.358	0.423	0.484	0.554	0.615	0.802	0.845	1.000	0.815	0.592	0.432
Roper	0.356	0.359	0.352	0.363	0.378	0.370	0.379	0.388	0.348	0.322	0.294	0.254	0.302	0.290	0.378	0.416	0.458	0.512	0.579	0.636	0.705	0.815	1.000	0.589	0.488
Walker	0.314	0.307	0.288	0.288	0.310	0.293	0.294	0.270	0.247	0.207	0.203	0.169	0.215	0.200	0.236	0.276	0.310	0.344	0.331	0.493	0.407	0.592	0.589	1.000	0.790
Koolatong	0.363	0.347	0.311	0.315	0.335	0.313	0.312	0.280	0.253	0.213	0.204	0.155	0.203	0.183	0.217	0.262	0.275	0.301	0.291	0.396	0.334	0.432	0.488	0.790	1.000

Table 51: Correlations between de-seasonalised, de-trended daily rainfalls for 25 Gulf of Carpentaria catchments.

	Ducie	Wenlock	Embley	Watson	Archer	Holroyd	Coleman	Mitchell	Staaten	Gilbert	Norman	Flinders	Morning	Leichardt	Nicholson	Settlement	Calvert	Robinson	Mcarthur	Rosie	Limmen	Towns	Roper	Walker	Koolatong
Ducie	1.000	0.692	0.675	0.470	0.425	0.320	0.260	0.149	0.079	0.045	0.038	0.017	0.041	0.022	0.059	0.094	0.078	0.087	0.084	0.122	0.116	0.143	0.144	0.152	0.192
Wenlock	0.692	1.000	0.778	0.669	0.686	0.444	0.349	0.212	0.123	0.082	0.072	0.039	0.072	0.047	0.086	0.131	0.106	0.103	0.091	0.118	0.113	0.131	0.141	0.141	0.169
Embley	0.675	0.778	1.000	0.809	0.611	0.475	0.389	0.249	0.159	0.119	0.099	0.053	0.090	0.062	0.096	0.120	0.097	0.091	0.093	0.104	0.120	0.130	0.145	0.131	0.138
Watson	0.470	0.669	0.809	1.000	0.795	0.656	0.503	0.311	0.223	0.172	0.148	0.081	0.111	0.085	0.103	0.130	0.104	0.094	0.095	0.105	0.120	0.137	0.160	0.132	0.146
Archer	0.425	0.686	0.611	0.795	1.000	0.841	0.624	0.357	0.246	0.174	0.148	0.086	0.124	0.097	0.127	0.166	0.135	0.127	0.110	0.123	0.120	0.143	0.166	0.149	0.158
Holroyd	0.320	0.444	0.475	0.656	0.841	1.000	0.868	0.472	0.332	0.236	0.196	0.118	0.152	0.127	0.143	0.161	0.138	0.129	0.115	0.121	0.126	0.141	0.164	0.134	0.140
Coleman	0.260	0.349	0.389	0.503	0.624	0.868	1.000	0.619	0.426	0.304	0.254	0.151	0.196	0.163	0.177	0.182	0.155	0.140	0.127	0.134	0.138	0.151	0.171	0.133	0.135
Mitchell	0.149	0.212	0.249	0.311	0.357	0.472	0.619	1.000	0.734	0.615	0.459	0.313	0.294	0.264	0.246	0.205	0.165	0.143	0.145	0.122	0.145	0.131	0.161	0.093	0.082
Staaten	0.079	0.123	0.159	0.223	0.246	0.332	0.426	0.734	1.000	0.690	0.567	0.349	0.361	0.328	0.285	0.234	0.172	0.157	0.156	0.138	0.146	0.142	0.149	0.095	0.083
Gilbert	0.045	0.082	0.119	0.172	0.174	0.236	0.304	0.615	0.690	1.000	0.772	0.609	0.431	0.431	0.329	0.228	0.173	0.139	0.155	0.119	0.134	0.122	0.132	0.060	0.050
Norman	0.038	0.072	0.099	0.148	0.148	0.196	0.254	0.459	0.567	0.772	1.000	0.716	0.563	0.585	0.425	0.280	0.207	0.169	0.175	0.127	0.133	0.116	0.120	0.073	0.058
Flinders	0.017	0.039	0.053	0.081	0.086	0.118	0.151	0.313	0.349	0.609	0.716	1.000	0.540	0.719	0.454	0.238	0.185	0.152	0.177	0.106	0.121	0.101	0.105	0.058	0.028
Morning	0.041	0.072	0.090	0.111	0.124	0.152	0.196	0.294	0.361	0.431	0.563	0.540	1.000	0.714	0.563	0.414	0.282	0.229	0.238	0.179	0.190	0.163	0.159	0.105	0.080
Leichardt	0.022	0.047	0.062	0.085	0.097	0.127	0.163	0.264	0.328	0.431	0.585	0.719	0.714	1.000	0.701	0.392	0.287	0.238	0.264	0.170	0.183	0.151	0.151	0.094	0.062
Nicholson	0.059	0.086	0.096	0.103	0.127	0.143	0.177	0.246	0.285	0.329	0.425	0.454	0.563	0.701	1.000	0.696	0.566	0.450	0.456	0.288	0.321	0.248	0.238	0.119	0.084
Settlement	0.094	0.131	0.120	0.130	0.166	0.161	0.182	0.205	0.234	0.228	0.280	0.238	0.414	0.392	0.696	1.000	0.759	0.612	0.517	0.405	0.397	0.332	0.296	0.171	0.143
Calvert	0.078	0.106	0.097	0.104	0.135	0.138	0.155	0.165	0.172	0.173	0.207	0.185	0.282	0.287	0.566	0.759	1.000	0.875	0.646	0.505	0.479	0.402	0.347	0.210	0.157
Robinson	0.087	0.103	0.091	0.094	0.127	0.129	0.140	0.143	0.157	0.139	0.169	0.152	0.229	0.238	0.450	0.612	0.875	1.000	0.793	0.643	0.576	0.483	0.415	0.248	0.187
Mcarthur	0.084	0.091	0.093	0.095	0.110	0.115	0.127	0.145	0.156	0.155	0.175	0.177	0.238	0.264	0.456	0.517	0.646	0.793	1.000	0.704	0.743	0.549	0.488	0.228	0.169
Rosie	0.122	0.118	0.104	0.105	0.123	0.121	0.134	0.122	0.138	0.119	0.127	0.106	0.179	0.170	0.288	0.405	0.505	0.643	0.704	1.000	0.797	0.773	0.571	0.421	0.299
Limmen	0.116	0.113	0.120	0.120	0.120	0.126	0.138	0.145	0.146	0.134	0.133	0.121	0.190	0.183	0.321	0.397	0.479	0.576	0.743	0.797	1.000	0.818	0.642	0.314	0.217
Towns	0.143	0.131	0.130	0.137	0.143	0.141	0.151	0.131	0.142	0.122	0.116	0.101	0.163	0.151	0.248	0.332	0.402	0.483	0.549	0.773	0.818	1.000	0.779	0.527	0.329
Roper	0.144	0.141	0.145	0.160	0.166	0.164	0.171	0.161	0.149	0.132	0.120	0.105	0.159	0.151	0.238	0.296	0.347	0.415	0.488	0.571	0.642	0.779	1.000	0.510	0.369
Walker	0.152	0.141	0.131	0.132	0.149	0.134	0.133	0.093	0.095	0.060	0.073	0.058	0.105	0.094	0.119	0.171	0.210	0.248	0.228	0.421	0.314	0.527	0.510	1.000	0.752
Koolatong	0.192	0.169	0.138	0.146	0.158	0.140	0.135	0.082	0.083	0.050	0.058	0.028	0.080	0.062	0.084	0.143	0.157	0.187	0.169	0.299	0.217	0.329	0.369	0.752	1.000

The classification shown in Figure 78 shows three clear groups of stations, namely

1. The north-eastern group, from the Ducie to the Coleman,
2. The south-eastern group, from the Mitchell to the Nicholson,
3. The western group, from the Settlement creek to the Koolatong.

This classification strongly suggests that the predictive capacity of rainfall figures for responses such as banana prawn catch is likely to be very similar for adjacent or close catchments. We will use this contention to reduce the number of possible predictors in our search for links with banana prawn catch.

Although we have focused upon rainfall, it is important to notice that the other possible predictors: Evaporation rate, Maximum daily temperature and Minimum daily temperature also show very similar intercorrelation patterns both between catchments within parameter and between parameters themselves. Essentially all four parameters appear to be largely driven by a common underlying latent climate variable, which they all display to a different degree. It is beyond the scope of this report to go into any more detail as it is not particularly relevant to the subject of the study, other than to explain why the search for environmental predictors can be safely confined to a relatively few functions of those available.

Has there been a change in rainfall patterns?

One clear question to address is “Has there been any progressive change in the rainfall pattern in the gulf catchments that might explain a change in the catch, assuming a link can be established?” Although this question logically might be consider to arise after the question of a link has been settled, it is convenient from a presentation point of view to consider it slightly out of sequence at this point here.

Table 52: Mean daily rainfall pattern, per month, for the principal catchments draining into the Gulf of Carpentaria, over the years 1969-2004. The figures are obtained by taking daily averages over all points in the catchment and then averaging these daily measurements over the month (and year). The catchments are arranged in a clockwise manner starting in the North-East of the gulf.

Catchment	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Ducie	12.93	14.72	11.24	4.76	1.11	0.38	0.24	0.15	0.14	0.53	2.48	7.34
Wenlock	12.14	13.82	10.68	4.09	0.81	0.26	0.19	0.20	0.12	0.70	3.05	7.05
Embley	14.24	16.98	11.68	3.30	0.50	0.11	0.05	0.09	0.07	0.72	3.56	8.72
Watson	13.58	16.18	10.67	2.61	0.33	0.05	0.01	0.05	0.04	0.71	3.44	7.91
Archer	11.04	13.46	9.26	2.46	0.39	0.11	0.06	0.06	0.05	0.60	2.85	6.38
Holroyd	10.73	12.99	8.47	1.85	0.24	0.08	0.03	0.02	0.03	0.55	2.52	6.02
Coleman	10.30	12.45	8.07	1.80	0.28	0.09	0.03	0.03	0.05	0.52	2.18	6.08
Mitchell	8.05	9.49	5.13	1.22	0.41	0.18	0.08	0.13	0.11	0.59	2.29	5.31
Staaten	8.57	9.43	4.56	0.94	0.22	0.12	0.04	0.04	0.06	0.57	2.09	4.91
Gilbert	7.29	7.32	3.43	0.74	0.38	0.24	0.14	0.10	0.14	0.62	1.95	4.07
Norman	6.63	6.27	3.07	0.49	0.23	0.21	0.08	0.04	0.11	0.48	1.53	3.79
Flinders	4.49	4.14	1.95	0.49	0.37	0.24	0.22	0.11	0.16	0.59	1.25	2.64
Morning inlet	6.35	6.87	3.73	0.30	0.14	0.11	0.07	0.01	0.05	0.35	1.45	4.27
Leichardt	4.72	5.03	2.50	0.35	0.25	0.12	0.13	0.05	0.18	0.60	1.39	3.25
Nicholson	4.85	5.86	2.89	0.42	0.17	0.14	0.08	0.02	0.13	0.71	1.49	3.36
Settlement creek	7.19	8.95	5.57	0.93	0.14	0.15	0.06	0.01	0.10	0.80	1.99	4.96
Calvert	6.54	7.89	4.88	1.05	0.14	0.11	0.06	0.01	0.13	0.83	1.88	4.35
Robinson	6.60	8.10	5.06	1.34	0.12	0.19	0.05	0.01	0.15	0.69	1.84	4.22

Catchment	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Mcarthur	5.78	7.06	4.26	0.78	0.12	0.19	0.06	0.02	0.19	0.69	1.68	3.66
Rosie	6.56	8.16	5.57	1.54	0.16	0.20	0.05	0.02	0.10	0.38	1.48	4.20
Limmen bight	5.96	7.48	4.26	0.77	0.10	0.16	0.06	0.03	0.14	0.63	1.47	3.75
Towns	6.37	7.86	4.88	1.20	0.15	0.14	0.06	0.03	0.07	0.44	1.48	3.77
Roper	6.50	7.98	5.15	1.13	0.13	0.13	0.07	0.02	0.12	0.65	2.24	4.65
Walker	6.69	7.99	7.38	4.27	0.53	0.20	0.05	0.01	0.08	0.41	1.73	4.30
Koolatong	8.07	8.88	8.15	5.95	1.09	0.34	0.13	0.03	0.07	0.36	1.93	5.31

Detecting a change in a relatively short time series is always difficult, but one way to investigate this is to look at a smoothed version of the series and check for change graphically. In a sense the question of the existence of a change is less important than whether a change of sufficient magnitude has occurred to make material difference to the prawn abundance.

The smoothing device we use is to fit a two-stage generalized additive model to the data. We use the model fitting process in two ways, firstly to view the components of the model most relevant to the question of change and secondly to produce a smoothed series, which is also available for graphical inspection.

The data sets we use for this are genuine daily time rainfall time series from stations:

a) In East Avenue, Weipa, where the record we have runs from 1969-01-01 to 2005-02-28, with a few minor gaps, and

b) In Normanton. In this case the series comes from the Normanton Post Office from 1969-01-01 to 2001-07-31 when it ceases, but a second series resumes from Normanton Aerodrome from 2001-04-11 to 2005-03-16. We regard these as comparable series and in the modelling we make a simple allowance for the possible effect of a small change in location after the hiatus. The series also has other small gaps.

Two stage models are needed to accommodate the presence of a large number of zeros in the data. The model takes the following form:

1. On any day, the probability of a non-zero rainfall is given by a logistic generalized additive model of the form

$$\log\frac{p}{1-p} = b_1 + h_1(\mathrm{Day}) + s_1(\mathrm{Time}) + q_1(s)$$

   where $h_j(\mathrm{Day})$ is a periodic term in 'day of the year' to allow for the seasonal component, $s_j(\mathrm{Time})$ is a smooth flexible term in the elapsed time since 1970-01-01, to allow for the possibility of a long-term time trend and $q_j(s)$ is zero for the start of the series, or a constant if that part of the series has had a location shift relative to the earlier part.

2. Conditional on a positive rainfall reading, the actual rainfall record is modelled as having a log-normal distribution, with similar smooth components to those used for the first stage. That is, using an obvious notation:

$$m = E\left[\log(\mathrm{Rain}) \mid \mathrm{Rain} > 0\right] = b_2 + h_2(\mathrm{Day}) + s_2(\mathrm{Time}) + q_2(s)$$

   where the individual terms are similar in form to, but different in detail from, those of the first stage.

3. In the first stage the observations are binary and have a Bernoulli distribution $B(1, p)$, and in the second stage the observations are non-negative rainfall figures, modelled as $\log(\mathrm{Rain}) \sim N(m, s^2)$, in both case with (conditional) independence between days.

We estimate the terms in both components of the model using penalised spline estimation, in one case with a periodic basis and in the other, without. We have used the software supplied in the mgcv package of the R statistical environment, due to Simon Wood. (Wood 2004) (Wood 2001).

When the components in the model have been estimated, the mean daily rainfall is then estimated using

$$\hat{E}[\mathrm{Rain}] = \hat{p}\ ´\ \exp(\hat{m}) G_n\left(\hat{s}^2/2\right)$$

where $G_n(z)$ is Finney's G-function (where n is the degrees of freedom), used to define the minimum variance unbiased estimator of the lognormal mean (Finney 1941).

The smooth terms $h(\ldots)$ and $s(\ldots)$ are of interest in themselves, though not on a natural scale, in graphically detecting changes within and between years. We looked at these initially.

The results are shown in Figure 79 for Weipa and in Figure 80, for Normanton. In both cases a strong within season periodic oscillation is apparent with a peak in the early months of the year and for the trend components, in both probability of non-zero rain and conditional mean log-rain given non-zero there is some evidence of local variations in the rainfall level, but no clear evidence of the kind of dramatic change we might expect to result in a collapse of the banana prawn catch at Weipa. Another way of looking at this is to notice that even though these figures are on a logistic or log scale, it is clear that recent variations in the long term trends are entirely comparable with previous possible variations, appear not to have affected the banana prawn stocks appreciably.

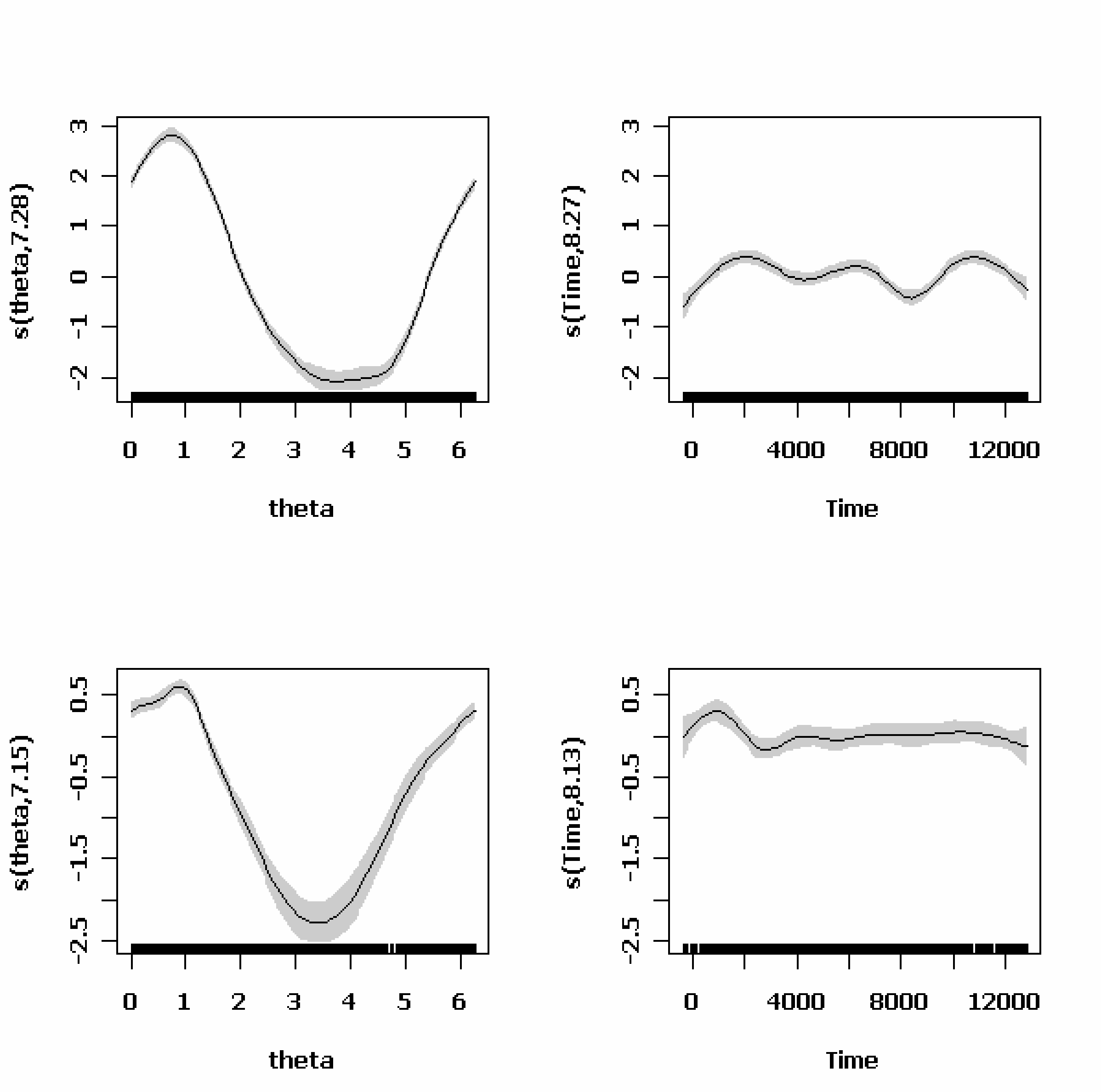

Figure 79: Additive components of the two-stage generalized additive model for the rainfall at Weipa station, The top two figures show the periodic component (left) and trend component (right) and the bottom two figures show the same components for the conditional lognormal regression. The horizontal axis for the periodic terms correspond to the time of year and for the trend terms, to the number of elapsed days since 1970-01-01. Note that the vertical axes are the same for components in the same model to aid comparability.

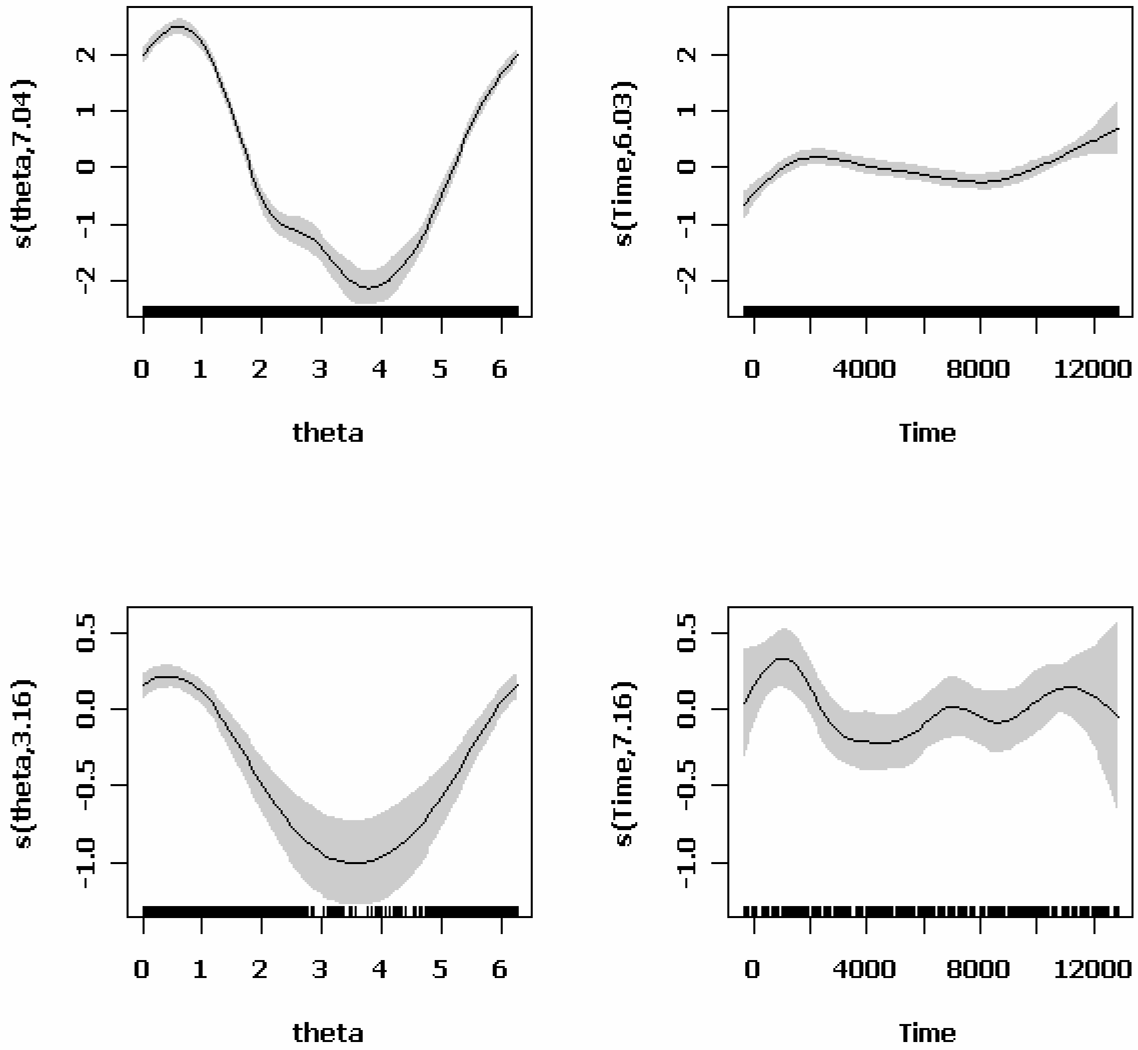

Figure 80: Additive components of the two-stage generalized additive model for the rainfall at Normanton, The top two figures show the periodic component (left) and trend component (right) and the bottom two figures show the same components for the conditional lognormal regression. The horizontal axis for the periodic terms correspond to the time of year and for the trend terms, to the number of elapsed days since 1970-01-01.s Note that the vertical axes are the same for components in the same model to aid comparability.

Combining the two components of the model then leads to estimates of the daily mean, allowing for the possibility of zero rainfall. These are plotted in Figure 81 for East Avenue, Weipa (on the Embley river) and in Figure 82 for the Normanton Post Office (close to the Norman river). The correction for the location shift at Normanton to the Aerodrome was significant statistically, but not large in either probability or condition log-mean components.

Notice that Figure 81 and Figure 82 share the same scales, making it very clear how the Norman catchment has a much lower average rainfall than the Embley.

Superimposing the actual data on these diagrams confirms that the mean figures capture the major signal in the data, but with a very considerable noise level particularly evident in the ‘wet’ season (Figure 83 and Figure 84 respectively). It is somewhat unclear how a multiple correlation figure could be meaningfully given for these two-stage models, since it is not clear how ‘variability’ itself should be measured, but for the second stage components of the model for each catchment the multiple correlation was only about 20%, indicating this high noise level.

Similar patterns emerge using similar pseudo-analyses of the catchment average figures from the SILO data source rather than the genuine statistical data from essentially a single recording station, leading us to feel confident enough to use the averaged catchment figures in the search for potential predictors. This then provides (what appears to be) a fairly consistent data basis in which to investigate the three main stock areas with which we will be concerned: the Weipa region and two 'control' regions to the south, namely Mitchell and Karumba.

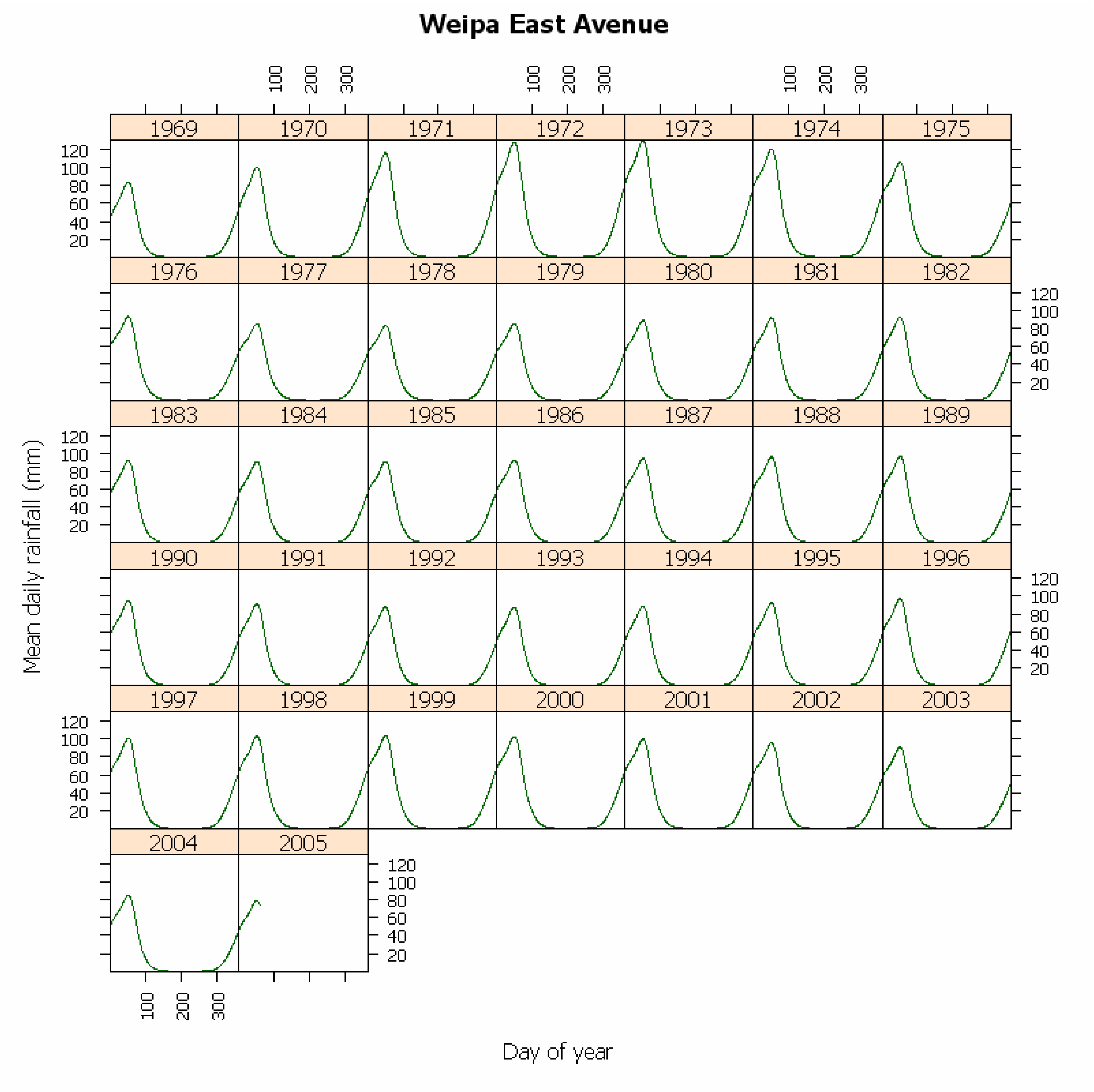

Figure 81: Daily (smoothed) mean rainfall estimates for the recording station in East Avenue, Weipa.

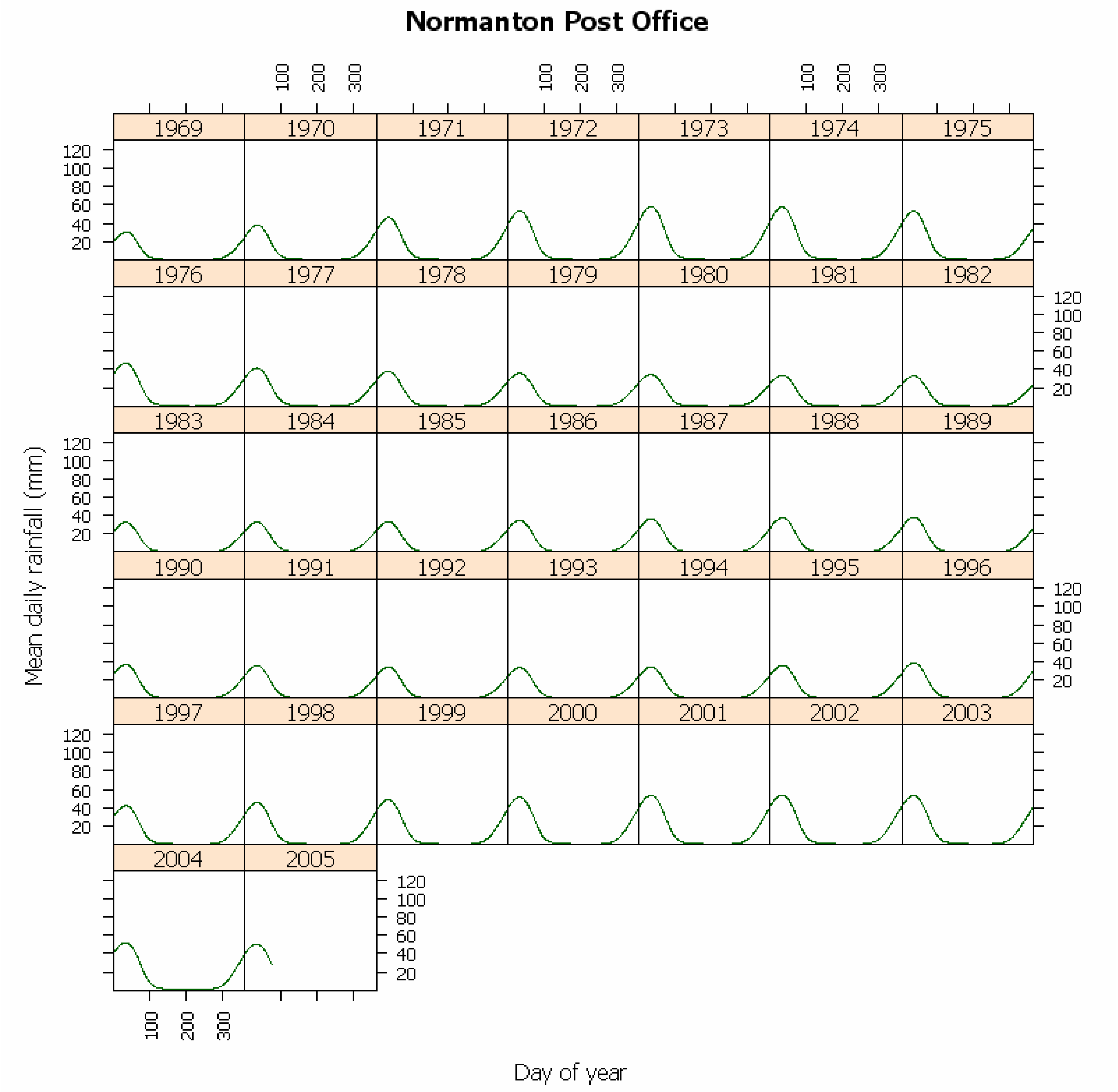

Figure 82: Daily (smoothed) estimates of mean rainfall for the recording station at Normanton Post Office.

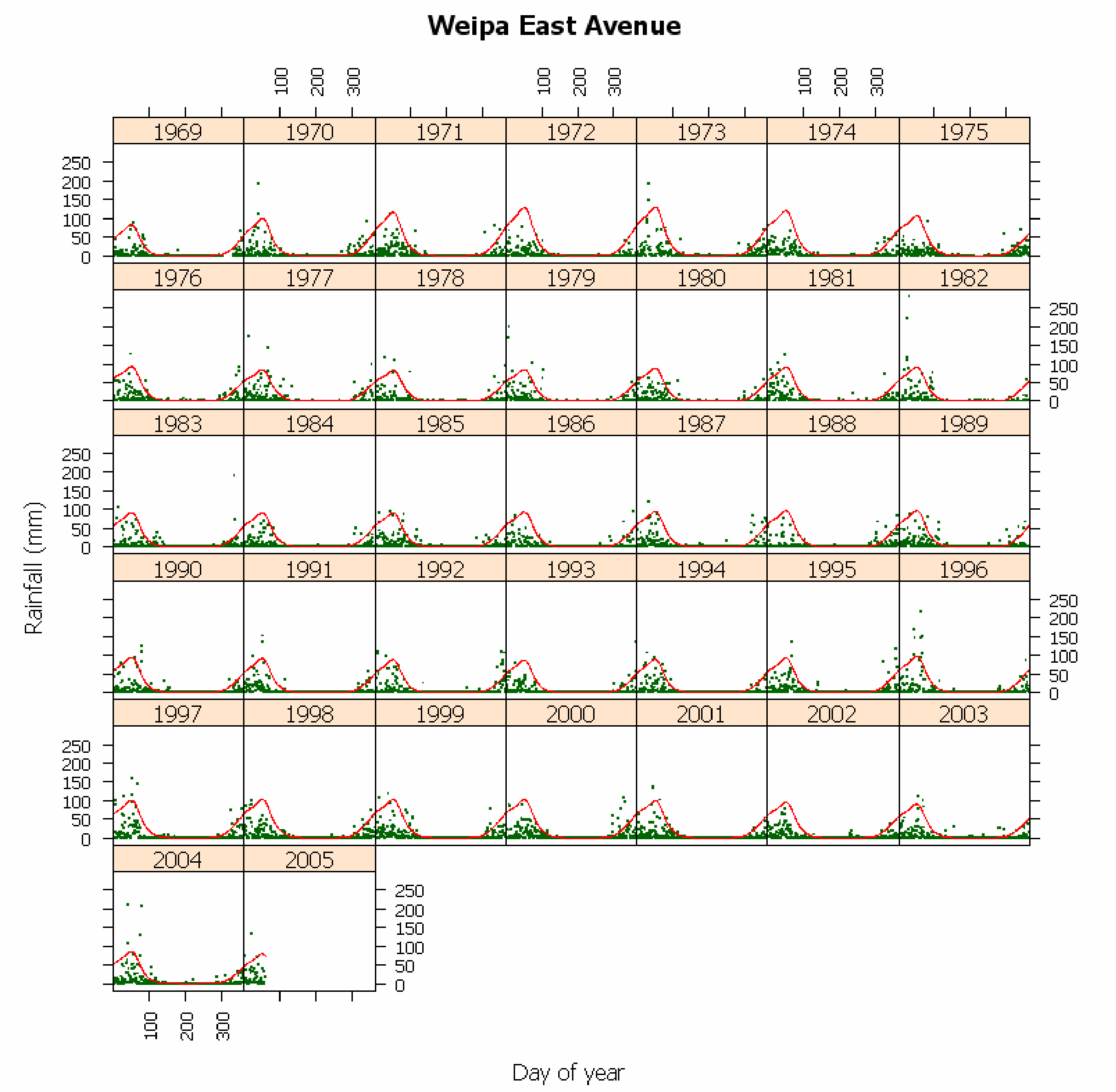

Figure 83: Estimated mean rain profile for Weipa for the Weipa recording station with daily measurements superimposed.

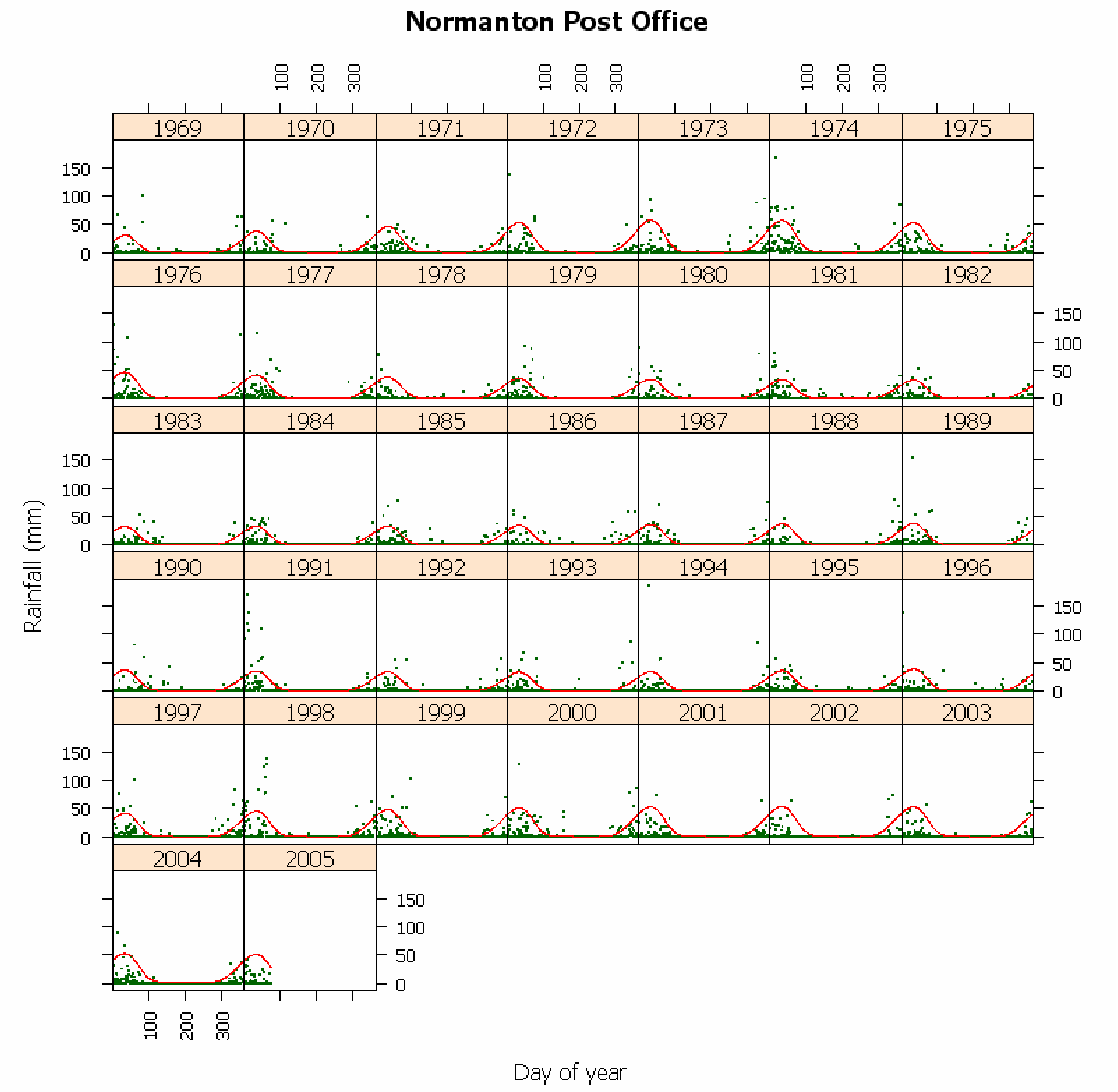

Figure 84: Normanton Post Office estimated mean rainfall with daily measurements superimposed.

Environmental predictors of catch and CPUE

Connections between apparent banana prawn abundance and weather events, principally related to rainfall, have long been noticed in the Gulf of Carpentaria (Vance, Staples, and Kerr 1983b), there is as yet no complete consensus as to the mechanism by which this happens. One likely possibility from various laboratory studies (Vance, personal communication; see also (Staples *et al.* 1995)) is that the banana prawn migration offshore may be triggered by a change in salinity in the estuaries of an appropriate magnitude and at the right time of year, but this is still conjectural. In this study we adopt an empirical approach and investigate possible predictors without too much recourse to underlying theory, simply because not much is yet available. This should therefore be considered more of an investigative, hypothesis-generating study, with confirmation (or rejection) to follow. As we have noted before, since it relies entirely on observational data – mostly logbook data, which has its own sampling difficulties – not much else is possible.

Response measures: catch and CPUE

Banana prawn fishing, particularly in stock regions **09**, **10** and **11**, is largely confined to a narrow time window at the beginning of the first season. The percentage of the annual banana catch caught between mid-March and mid-June (day 73 to day 134 of the year) is shown in Figure 85. The corresponding information for effort is shown in Figure 86. In other stock regions the banana catch is less temporally concentrated.

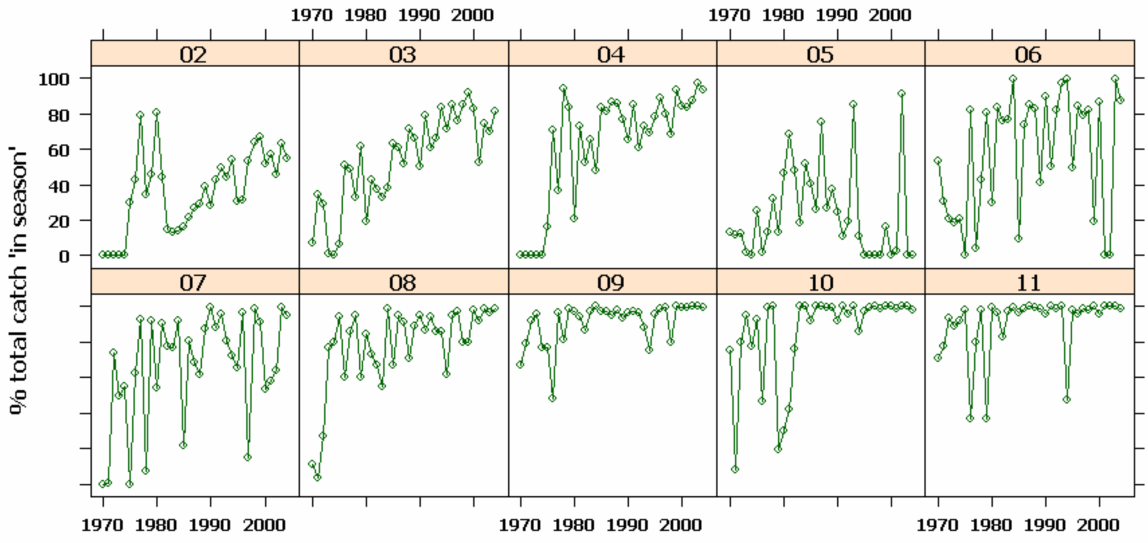

Figure 85: Percentages of the total *P. merguiensis* catch caught 'in season', i.e. between mid-March and mid-June, by stock region, for the years 1970-2004.

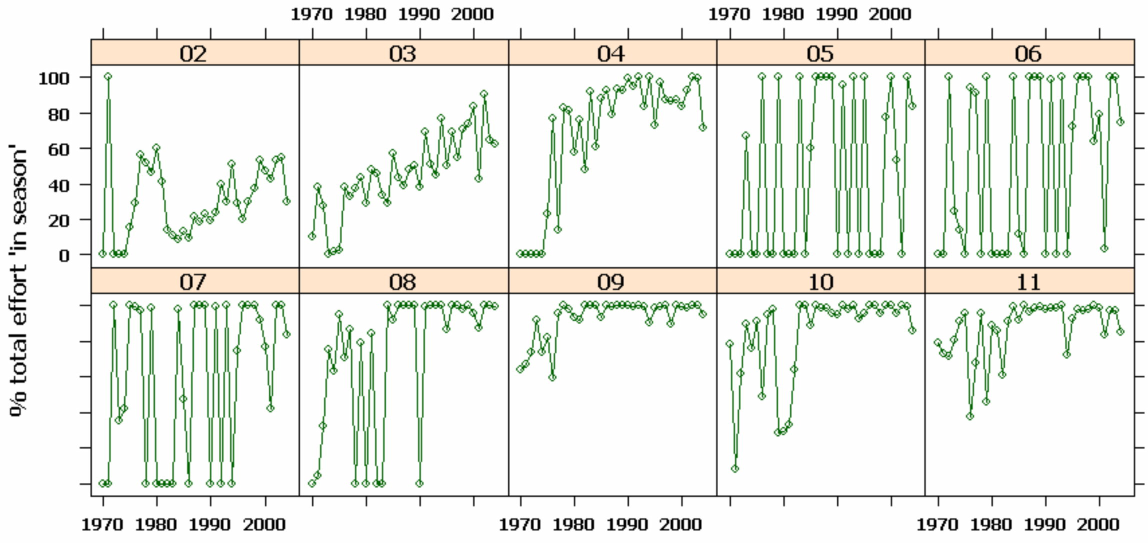

Figure 86: Percentages of the total *P. merguiensis* effort expended 'in season', i.e. between mid-March and mid-June, by stock region, for the years 1970-2004.

To establish any link between environmental predictors and banana catch within a stock region, we will use the *total annual banana prawn catch* as the primary response. Alternatively we could limit the response to the banana prawn catch 'in season', but for the three focus stock areas this makes very little difference to the outcome. We choose total annual catch for continuity with the prior work of Vance (e.g. (Vance, Staples, and Kerr 1983a)).

In fact we consider models both for *total catch* and for *annual CPUE*. The first is relevant if we assume that catch is the appropriate index of abundance, which would be appropriate if effort were largely determined by factors independent of abundance. Annual CPUE is the more conventional index of abundance, but for an annual species largely caught in a very short time window and in relatively limited spatial locations, it is not clear which assumption, if either, is entirely appropriate. The mere fact that Effort emerges as a strong predictor of catch is no evidence for (or against) a causal link, as this is an observational study, with the industry free to fish or refrain from fishing in an area.

As most of the influences on catch are likely to act multiplicatively rather than additively, i.e. changing by a percentage rather than adding or subtracting an increment, we use $\log(\mathrm{Catch})$ as the response, with the log transformation both simplifying the predictor structure and (hopefully) providing a response scale in which the variance is approximately constant. For CPUE we could use $\log(\mathrm{CPUE})$ as the response, but we will generally use $\log(\mathrm{Effort})$ as a predictor as well. This caters for an intermediate possibility where some power of Effort is the appropriate denominator to use in forming an abundance index. This would correspond, for example, to a situation where Catch was only partly influenced by effort – or where effort were to some extent determined by (news of) the prevailing catch rates. Note that using $\log(\mathrm{Effort})$ as a predictor for $\log(\mathrm{Catch})$ is equivalent to using $\log(\mathrm{CPUE})$ as the response, provided $\log(\mathrm{Effort})$ is included within the predictors.

Environmental predictors

Choosing annual catch as the primary response, as is appropriate for a 'pulse' activity such as this, severely limits our capacity to investigate predictive models, as it limits the sample size to just 35 values (at present), as we have data only for the seasons 1970 – 2004. Moreover our environmental predictors must be similarly 'aggregated' to match the scale of the response. We consider a wide range of possibilities for environmental predictors, and use variable selection methods to check for those which appear to be effective.

The environmental predictors will be built from information pertaining to the six months prior to a season opening on 1 April in any one year, i.e. for the preceding October to March. For definiteness consider Rainfall. From the SILO data putative daily measures are available for all pixels in the catchment. This is clearly interpolated data, but the first step is to average over the catchment for each day, which will go some way to offsetting the artificial effects of this interpolation. We also form further aggregate measures in other ways, namely

- The monthly average precipitation provides six possible predictors, labelled Rain.MMean.Oct, …, Rain.MMean.Mar. These measure the crude amount of precipitation by month.
- The standard deviations of precipitation provide six more possible predictors, labelled Rain.MStdev.Oct, …, Rain.MStdev.Mar. These reflect the variability of precipitation, across days, within each monthly period. Low variability should reflect relatively consistent rainfall over the month, whereas high variability would reflect occasional heavy showers with intervening dry days. The effect on salinity for these two cases may be different, even under constant monthly precipitation, because of potentially different runoff patterns.
- Two more measures are the mean precipitation and daily standard deviation for the entire six month period, Rain.Mean and Rain.Stdev. The first of these is linearly dependent on the monthly means, but may still be used as a possible predictor of course.
- To describe two more aggregate measures for the system we need to define the 'time deviation' within the six month period as, for any days, the number of days from an arbitrary origin taken to be 1 January. This may be positive or negative. The first aggregate measure is the weighted mean time deviation, where the weights are given by the daily precipitations. The second is the weighted standard deviation of the time deviation, again with the weights given by the daily precipitations. These measures provide a convenient measure of the 'location' and 'spread' of the rainfall events relative to the start of the season. These two variables will be labelled Rain.MDev and Rain.SDev respectively.

This gives a list of 16 possible predictors based on the SILO rainfall data for the catchment.

- We obtain a further 16 using the SILO 'Evaporation' data in precisely the same way. These variables have prefix 'Evap'.

- We also used Maximum and Minimum daily temperatures over the catchment in an analogous way, but without the two ‘time deviation’ variables in each case. This gives a further 28 possible predictors, 14 of which have the prefix ‘MaxT’ and 14 ‘MinT’.
- The year itself was also considered as a possible predictor, Year, to allow for a linear change in the log scale of the catch (i.e. a proportional change in the untransformed scale).
- Finally, we have also considered the monthly average SOI for each of the 9 months prior to the opening of the season as possible predictors, SOI_Jul, SOI_Aug, … , SOI_Mar. These values were obtained from the Australian Bureau of Meteorology and given on the web site: http://www.bom.gov.au/climate/current/soihtm1.shtml.

This makes a total of up to 71 possible predictors, namely

- 16 Rainfall measures,
- 16 Evaporation measures,
- 14 Maximum temperature measures,
- 14 Minimum temperature measures,
- 9 SOI monthly averages,
- 1 time variable, ‘Year’ and
- 1 effort variable, $\log(\mathrm{Effort})$, where appropriate.

As it happens this is over twice the number of points we have to calibrate our models, so fitting all possible predictors and using backward elimination is not an option. We can fit at most 34 predictor variables, bur realistically far fewer, with 6 variables perhaps the realistic maximum.

Model fitting strategy: exhaustive search

Our purpose in constructing a predictive model for catch is mainly to identify any effective variables for so doing, with the hope that this will elucidate connections between environmental variables and abundance indicators. The intercept term will be included in all regression models considered, and this constant term is not considered as a predictor in the description that follows here.

Rather than use a stepwise selection method, we prefer to consider all possible regressions and pick the best three of sizes 1, 2, …, 6. The computational method is based on an algorithm described in (Miller 2002) using the contributed R package, leaps.

The two cases we consider are:

- Excluding $\log(\mathrm{Effort})$ as a predictor, and hence predicting $\log(\mathrm{Catch})$, and
- Fixing $\log(\mathrm{Effort})$ as a predictor, and hence (effectively) using $\log(\mathrm{CPUE})$ as the response.

In the latter case we consider up to five *further* predictors from the field of candidates.
In the search for optimal regressions we have found, and report below, the three ‘best’ regressions (in the sense of yielding the three lowest residual sums of squares) for each number of variables. However where $\log(\mathrm{Effort})$ is fixed in the equation as a predictor, there is only one possible regression with one predictor.

The coefficients and their significances in the fitted models are shown inTable 53, Table 54 and Table 55 below. The estimated multiple correlation is also shown for each fitted model.

Table 53: Optimal regression coefficient estimates for the Weipa stock area, including multiple correlation coefficients. The left hand panel shows the details for when log(Effort) is excluded as a predictor and the right hand panel those for when it is forced into the regresson.

	Estimate	**Std. Error**	**t value**	***R*²**		**Estimate**	**Std. Error**	**t value**	***R*²**
(Intercept)	5.694	0.178	32.056	**0.359**	(Intercept)	-2.280	0.656	-3.476	**0.828**
Year	-0.072	0.017	-4.298		log(EffortY)	1.320	0.105	12.601	
(Intercept)	39.458	14.147	2.789	**0.146**					
MinT.MMean.Feb	-1.393	0.587	-2.371						
(Intercept)	36.739	14.860	2.472	**0.115**					
MaxT.Mean	-0.940	0.453	-2.075						
(Intercept)	6.946	0.426	16.296	**0.511**	(Intercept)	-4.250	0.927	-4.584	**0.861**
Year	-0.082	0.015	-5.359		Year	0.036	0.013	2.780	
Evap.MStdev.Feb	-0.875	0.277	-3.159		log(EffortY)	1.655	0.154	10.771	
(Intercept)	3.883	0.924	4.203	**0.430**	(Intercept)	-17.609	5.621	-3.133	**0.861**
Year	-0.079	0.016	-4.800		MaxT.MMean.Oct	0.425	0.155	2.743	
Rain.Mean	0.193	0.097	1.995		log(EffortY)	1.442	0.106	13.665	
(Intercept)	4.950	0.416	11.891	**0.428**	(Intercept)	-22.868	7.576	-3.018	**0.860**
Year	-0.070	0.016	-4.290		MinT.Mean	0.850	0.312	2.726	
Rain.MStdev.Dec	0.064	0.032	1.961		log(EffortY)	1.418	0.102	13.858	
(Intercept)	4.911	0.822	5.973	**0.610**	(Intercept)	-3.780	0.801	-4.718	**0.896**
Year	-0.090	0.014	-6.381		Evap.MMean.Oct	0.282	0.072	3.903	
Rain.Mean	0.230	0.082	2.804		Evap.MStdev.Feb	-0.597	0.151	-3.954	
Evap.MStdev.Feb	-0.959	0.253	-3.787		log(EffortY)	1.350	0.086	15.628	
(Intercept)	6.359	0.450	14.135	**0.601**	(Intercept)	-4.321	0.850	-5.085	**0.887**
Year	-0.085	0.014	-6.062		Year	0.039	0.012	3.281	
Rain.MMean.Mar	0.063	0.024	2.643		Rain.MStdev.Jan	-0.027	0.010	-2.669	
Evap.MStdev.Feb	-0.995	0.258	-3.853		log(EffortY)	1.742	0.145	12.055	
(Intercept)	4.947	0.984	5.026	**0.579**	(Intercept)	10.685	5.741	1.861	**0.887**
Year	-0.091	0.015	-6.074		Year	0.041	0.012	3.414	
Evap.MMean.Oct	0.331	0.149	2.225		MinT.MMean.Feb	-0.614	0.233	-2.630	
Evap.MStdev.Feb	-1.283	0.319	-4.019		log(EffortY)	1.633	0.141	11.551	
(Intercept)	18.403	5.751	3.200	**0.672**	(Intercept)	-32.682	6.588	-4.961	**0.920**
Year	-0.086	0.013	-6.441		Evap.MStdev.Feb	-0.469	0.127	-3.709	
Rain.Mean	0.264	0.078	3.394		Evap.Mean	0.425	0.101	4.228	
Evap.MStdev.Feb	-1.174	0.253	-4.638		MinT.Mean	1.166	0.260	4.482	
Evap.SDev	-0.258	0.109	-2.367		log(EffortY)	1.505	0.086	17.514	
(Intercept)	2.849	1.219	2.337	**0.664**	(Intercept)	-16.670	4.422	-3.770	**0.919**
Year	-0.095	0.014	-7.032		Evap.MMean.Oct	0.258	0.065	3.958	
Rain.Mean	0.272	0.080	3.410		Evap.MStdev.Feb	-0.568	0.135	-4.198	
Evap.MMean.Dec	0.342	0.156	2.193		MaxT.MMean.Oct	0.362	0.123	2.954	
Evap.MStdev.Feb	-1.265	0.277	-4.571		log(EffortY)	1.449	0.084	17.205	
(Intercept)	5.626	0.533	10.546	**0.659**	(Intercept)	-33.852	6.779	-4.994	**0.919**
Year	-0.086	0.013	-6.480		Evap.MMean.Dec	0.335	0.081	4.141	
Rain.MMean.Dec	0.075	0.033	2.255		Evap.MStdev.Feb	-0.497	0.131	-3.803	

	Estimate	Std. Error	t value	R^2		Estimate	Std. Error	t value	R^2
Rain.MMean.Mar	0.067	0.022	2.985		MinT.Mean	1.249	0.270	4.624	
Evap.MStdev.Feb	-0.961	0.243	-3.950		log(EffortY)	1.461	0.084	17.437	
(Intercept)	23.317	5.917	3.941	**0.716**	(Intercept)	-30.477	5.995	-5.084	**0.941**
Year	-0.082	0.013	-6.379		Rain.MMean.Dec	0.049	0.015	3.248	
Rain.MMean.Dec	0.078	0.037	2.119		Evap.MMean.Dec	0.389	0.072	5.371	
Rain.Mean	0.201	0.079	2.529		Evap.MStdev.Feb	-0.525	0.114	-4.598	
Evap.MStdev.Feb	-1.182	0.240	-4.933		MinT.Mean	1.084	0.241	4.507	
Evap.SDev	-0.352	0.112	-3.138		log(EffortY)	1.427	0.074	19.334	
(Intercept)	2.261	1.199	1.886	**0.705**	(Intercept)	-24.313	7.311	-3.325	**0.934**
Year	-0.099	0.013	-7.583		Evap.MMean.Dec	0.397	0.079	5.055	
Rain.Mean	0.350	0.085	4.097		Evap.MStdev.Feb	-0.544	0.122	-4.462	
Evap.MMean.Dec	0.410	0.152	2.690		MaxT.MMean.Dec	-0.191	0.076	-2.513	
Evap.MStdev.Nov	-0.688	0.344	-2.001		MinT.Mean	1.109	0.255	4.350	
Evap.MStdev.Feb	-1.005	0.294	-3.416		log(EffortY)	1.422	0.079	18.039	
(Intercept)	16.535	5.656	2.924	**0.704**	(Intercept)	-33.040	6.267	-5.272	**0.933**
Year	-0.087	0.013	-6.745		Rain.MStdev.Jan	-0.020	0.008	-2.491	
Rain.Mean	0.304	0.078	3.871		Evap.MMean.Dec	0.306	0.076	4.044	
Evap.MStdev.Feb	-1.197	0.245	-4.887		Evap.MStdev.Feb	-0.483	0.121	-4.000	
Evap.SDev	-0.246	0.105	-2.332		MinT.Mean	1.226	0.249	4.913	
MinT.MStdev.Feb	1.296	0.732	1.771		log(EffortY)	1.500	0.079	19.012	
(Intercept)	21.595	5.674	3.806	**0.753**	(Intercept)	-30.428	5.739	-5.302	**0.948**
Year	-0.083	0.012	-6.799		Rain.MMean.Dec	0.041	0.015	2.747	
Rain.MMean.Dec	0.082	0.035	2.365		Rain.MStdev.Jan	-0.015	0.008	-1.908	
Rain.Mean	0.240	0.078	3.087		Evap.MMean.Dec	0.359	0.071	5.058	
Evap.MStdev.Feb	-1.207	0.228	-5.304		Evap.MStdev.Feb	-0.510	0.110	-4.660	
Evap.SDev	-0.345	0.107	-3.241		MinT.Mean	1.094	0.230	4.747	
MinT.MStdev.Feb	1.403	0.681	2.058		log(EffortY)	1.460	0.073	20.068	
(Intercept)	15.868	5.397	2.940	**0.750**	(Intercept)	-30.072	6.548	-4.593	**0.947**
Year	-0.097	0.013	-7.627		Evap.MStdev.Feb	-0.399	0.110	-3.619	
Rain.Mean	0.295	0.079	3.747		Evap.Mean	0.519	0.092	5.652	
Evap.MMean.Oct	0.333	0.142	2.352		MaxT.MMean.Feb	-0.203	0.068	-2.968	
Evap.MStdev.Nov	-0.904	0.347	-2.605		MaxT.MStdev.Feb	-0.473	0.168	-2.816	
Evap.MStdev.Feb	-1.126	0.281	-4.002		MinT.Mean	1.320	0.239	5.531	
Evap.SDev	-0.242	0.100	-2.426		log(EffortY)	1.535	0.074	20.690	
(Intercept)	2.482	1.144	2.170	**0.743**	(Intercept)	-29.298	5.797	-5.054	**0.947**
Year	-0.103	0.013	-8.202		Rain.MMean.Dec	0.080	0.022	3.611	
Rain.MMean.Jan	-0.052	0.025	-2.043		Rain.MStdev.Dec	-0.031	0.017	-1.841	
Rain.Mean	0.437	0.092	4.770		Evap.MMean.Dec	0.410	0.071	5.817	
Evap.MMean.Dec	0.398	0.145	2.747		Evap.MStdev.Feb	-0.593	0.116	-5.121	
Evap.MStdev.Nov	-0.974	0.355	-2.743		MinT.Mean	1.031	0.233	4.425	
Evap.MStdev.Feb	-0.882	0.286	-3.087		log(EffortY)	1.450	0.072	20.119	

Table 54: Optimal regression coefficient estimates for the Mitchell stock area, including multiple correlation coefficients. The left hand panel shows the details for when log(Effort) is excluded as a predictor and the right hand panel those for when it is forced into the regresson.

	Estimate	Std. Error	t value	R^2		Estimate	Std. Error	t value	R^2
(Intercept)	4.953	0.554	8.946	**0.184**	(Intercept)	-0.353	0.981	-0.360	**0.593**
Evap.MDev	-0.134	0.049	-2.728		log(EffortY)	1.022	0.147	6.938	
(Intercept)	4.405	0.765	5.758	**0.178**					
Evap.Stdev	1.156	0.432	2.676						
(Intercept)	5.112	0.545	9.385	**0.157**					
Rain.Stdev	0.183	0.074	2.478						
(Intercept)	-4.591	4.285	-1.072	**0.295**	(Intercept)	-1.277	0.956	-1.335	**0.671**
Evap.MDev	-0.123	0.047	-2.635		Evap.MStdev.Feb	0.830	0.301	2.754	
MaxT.MMean.Oct	0.283	0.126	2.244		log(EffortY)	1.027	0.135	7.634	
(Intercept)	-5.281	4.301	-1.228	**0.293**	(Intercept)	-0.177	0.915	-0.193	**0.659**
Evap.Stdev	1.070	0.408	2.620		SOI_Nov	0.017	0.007	2.477	
MaxT.MMean.Oct	0.288	0.126	2.284		log(EffortY)	0.993	0.138	7.219	
(Intercept)	-5.186	4.324	-1.200	**0.285**	(Intercept)	-6.561	3.062	-2.143	**0.644**
Rain.Stdev	0.175	0.069	2.534		MaxT.MMean.Oct	0.194	0.091	2.129	
MaxT.MMean.Oct	0.303	0.126	2.399		log(EffortY)	0.960	0.143	6.713	
(Intercept)	-7.709	4.072	-1.893	**0.419**	(Intercept)	-1.611	0.886	-1.820	**0.732**
Rain.Stdev	0.244	0.068	3.564		Rain.Mean	0.128	0.048	2.661	
MaxT.MMean.Oct	0.311	0.116	2.691		Evap.MStdev.Feb	0.951	0.280	3.397	
MinT.MStdev.Jan	2.148	0.804	2.671		log(EffortY)	0.959	0.126	7.612	
(Intercept)	-8.098	4.187	-1.934	**0.393**	(Intercept)	-1.019	0.906	-1.124	**0.718**
Rain.Mean	0.248	0.075	3.293		Evap.MStdev.Feb	0.734	0.286	2.564	
MaxT.MMean.Oct	0.339	0.118	2.864		SOI_Nov	0.015	0.006	2.281	
MinT.MStdev.Jan	2.059	0.819	2.515		log(EffortY)	1.001	0.127	7.887	
(Intercept)	-24.396	9.954	-2.451	**0.390**	(Intercept)	-2.314	1.041	-2.222	**0.717**
Rain.Mean	0.516	0.123	4.186		MaxT.MStdev.Jan	-0.574	0.180	-3.193	
MaxT.Mean	0.791	0.280	2.826		MaxT.Stdev	1.000	0.338	2.960	
MinT.MStdev.Jan	2.296	0.830	2.767		log(EffortY)	1.141	0.137	8.298	
(Intercept)	-38.695	9.845	-3.930	**0.543**	(Intercept)	-2.040	0.941	-2.168	**0.778**
Rain.Mean	0.634	0.115	5.532		MaxT.MStdev.Jan	-0.584	0.162	-3.612	
MaxT.MStdev.Mar	-0.838	0.264	-3.175		MaxT.Stdev	0.936	0.305	3.074	
MaxT.Mean	1.230	0.282	4.356		SOI_Nov	0.017	0.006	2.885	
MinT.MStdev.Jan	2.549	0.734	3.472		log(EffortY)	1.120	0.124	9.041	
(Intercept)	-12.006	4.165	-2.883	**0.541**	(Intercept)	-1.750	0.822	-2.129	**0.778**
Rain.Stdev	0.268	0.068	3.932		Rain.Mean	0.144	0.045	3.184	
MaxT.MMean.Dec	0.411	0.111	3.707		Evap.MStdev.Feb	0.891	0.260	3.422	
MinT.MStdev.Jan	2.997	0.760	3.944		MaxT.MStdev.Jan	-0.372	0.150	-2.475	
SOI_Nov	0.039	0.011	3.534		log(EffortY)	1.070	0.125	8.559	
(Intercept)	-9.637	3.876	-2.486	**0.513**	(Intercept)	-7.990	2.614	-3.056	**0.778**
Rain.Stdev	0.234	0.064	3.675		MaxT.MMean.Nov	0.215	0.071	3.054	
MaxT.MMean.Oct	0.390	0.113	3.462		MaxT.MStdev.Jan	-0.433	0.149	-2.907	
MaxT.MStdev.Mar	-0.591	0.246	-2.398		SOI_Nov	0.025	0.006	3.989	
MinT.MStdev.Jan	2.263	0.750	3.015		log(EffortY)	1.146	0.124	9.209	

	Estimate	**Std. Error**	**t value**	***R*²**		**Estimate**	**Std. Error**	**t value**	***R*²**
(Intercept)	-15.499	4.072	-3.806	**0.624**	(Intercept)	6.354	3.240	1.961	**0.819**
Rain.Stdev	0.313	0.065	4.805		Rain.Mean	0.157	0.042	3.763	
Evap.MStdev.Mar	-1.079	0.425	-2.537		Evap.MStdev.Feb	1.091	0.251	4.342	
MaxT.MMean.Dec	0.516	0.110	4.686		MaxT.MStdev.Jan	-0.425	0.139	-3.050	
MinT.MStdev.Jan	3.749	0.759	4.937		MinT.MMean.Mar	-0.373	0.145	-2.572	
SOI_Nov	0.043	0.010	4.211		log(EffortY)	1.060	0.115	9.232	
(Intercept)	-12.361	3.973	-3.111	**0.597**	(Intercept)	-8.531	2.862	-2.981	**0.816**
Rain.Stdev	0.294	0.066	4.443		Rain.Mean	0.146	0.042	3.496	
MaxT.MMean.Dec	0.387	0.106	3.631		Evap.MStdev.Feb	0.996	0.245	4.071	
MinT.MStdev.Nov	0.669	0.334	2.006		MaxT.MStdev.Jan	-0.350	0.139	-2.514	
MinT.MStdev.Jan	3.253	0.735	4.424		MinT.MMean.Dec	0.282	0.115	2.458	
SOI_Nov	0.043	0.011	3.996		log(EffortY)	1.100	0.116	9.454	
(Intercept)	-26.734	9.098	-2.939	**0.587**	(Intercept)	-7.460	2.670	-2.794	**0.810**
Rain.Stdev	0.316	0.071	4.457		Rain.Mean	0.185	0.046	4.001	
MaxT.MMean.Dec	0.501	0.118	4.246		Evap.MStdev.Feb	0.676	0.263	2.572	
MaxT.MMean.Mar	0.340	0.188	1.804		MaxT.MMean.Nov	0.164	0.073	2.234	
MinT.MStdev.Jan	3.681	0.825	4.462		MaxT.MStdev.Jan	-0.438	0.144	-3.039	
SOI_Nov	0.054	0.013	4.009		log(EffortY)	1.088	0.118	9.240	
(Intercept)	-32.372	7.149	-4.528	**0.681**	(Intercept)	7.403	3.176	2.331	**0.838**
Rain.Stdev	0.313	0.072	4.346		Rain.MStdev.Oct	0.069	0.039	1.798	
Evap.MDev	-0.120	0.040	-2.997		Rain.Mean	0.153	0.040	3.802	
MaxT.MStdev.Mar	-0.743	0.224	-3.312		Evap.MStdev.Feb	1.213	0.252	4.823	
MaxT.Mean	1.026	0.206	4.983		MaxT.MStdev.Jan	-0.380	0.137	-2.781	
MinT.MStdev.Jan	2.562	0.638	4.016		MinT.MMean.Mar	-0.425	0.143	-2.979	
SOI_Nov	0.030	0.009	3.397		log(EffortY)	1.034	0.112	9.274	
(Intercept)	-43.759	10.344	-4.230	**0.673**	(Intercept)	8.804	3.458	2.546	**0.836**
Rain.Stdev	0.321	0.064	5.001		Rain.MMean.Mar	0.047	0.028	1.693	
Evap.MMean.Mar	-0.715	0.263	-2.720		Rain.Mean	0.117	0.047	2.500	
MaxT.MMean.Dec	0.651	0.120	5.416		Evap.MStdev.Feb	1.042	0.245	4.246	
MaxT.MMean.Mar	0.824	0.246	3.343		MaxT.MStdev.Jan	-0.439	0.135	-3.242	
MinT.MStdev.Jan	3.980	0.755	5.273		MinT.MMean.Mar	-0.472	0.152	-3.100	
SOI_Nov	0.061	0.012	4.919		log(EffortY)	1.025	0.113	9.062	
(Intercept)	-29.211	7.312	-3.995	**0.668**	(Intercept)	9.130	3.451	2.646	**0.835**
Rain.MStdev.Feb	0.101	0.029	3.556		Rain.MMean.Mar	0.069	0.024	2.814	
Evap.MMean.Jan	-0.459	0.118	-3.883		Rain.Stdev	0.096	0.039	2.468	
Evap.Stdev	1.128	0.315	3.585		Evap.MStdev.Feb	0.972	0.242	4.022	
MaxT.Mean	0.977	0.222	4.394		MaxT.MStdev.Jan	-0.448	0.136	-3.291	
MinT.MStdev.Jan	3.807	0.774	4.921		MinT.MMean.Mar	-0.479	0.152	-3.145	
SOI_Nov	0.039	0.010	4.037		log(EffortY)	0.983	0.115	8.532	

Table 55: Optimal regression coefficient estimates for the Karumba stock area, including multiple correlation coefficients. The left hand panel shows the details for when log(Effort) is excluded as a predictor and the right hand panel those for when it is forced into the regresson.

	Estimate	**Std. Error**	**t value**		***R^2***		**Estimate**	**Std. Error**	**t value**		***R^2***
(Intercept)	19.188	2.561	7.492		**0.428**	(Intercept)	1.726	0.48	3.597		**0.754**
MaxT.MMean.Feb	-0.368	0.074	-4.965			log(EffortY)	0.758	0.075	10.046		
(Intercept)	5.204	0.291	17.915		**0.413**						
Rain.Mean	0.354	0.073	4.822								
(Intercept)	16.351	2.089	7.826		**0.404**						
MaxT.MMean.Jan	-0.278	0.059	-4.729								
(Intercept)	6.628	0.370	17.928		**0.661**	(Intercept)	1.949	0.441	4.425		**0.805**
Rain.Mean	0.383	0.057	6.727			Rain.Mean	0.146	0.05	2.897		
MaxT.MStdev.Nov	-0.843	0.174	-4.841			log(EffortY)	0.639	0.08	8.01		
(Intercept)	5.211	0.239	21.787		**0.614**	(Intercept)	1.906	0.449	4.243		**0.796**
Rain.MMean.Nov	-0.328	0.080	-4.085			Rain.Stdev	0.076	0.029	2.566		
Rain.Mean	0.490	0.069	7.100			log(EffortY)	0.646	0.082	7.855		
(Intercept)	6.455	0.422	15.287		**0.602**	(Intercept)	2.055	0.471	4.365		**0.79**
Rain.Stdev	0.203	0.035	5.810			Rain.MMean.Jan	0.033	0.014	2.363		
MaxT.MStdev.Nov	-0.754	0.188	-4.015			log(EffortY)	0.671	0.08	8.409		
(Intercept)	6.379	0.367	17.403		**0.708**	(Intercept)	0.552	0.609	0.907		**0.849**
Rain.Mean	0.422	0.057	7.460			Rain.Mean	0.187	0.047	3.98		
MaxT.MStdev.Nov	-0.802	0.166	-4.848			MinT.Stdev	0.537	0.179	3.009		
SOI_Jul	-0.020	0.009	-2.214			log(EffortY)	0.667	0.072	9.276		
(Intercept)	3.315	3.574	0.928		**0.703**	(Intercept)	4.886	1.186	4.121		**0.84**
Rain.Stdev	0.127	0.036	3.514			Rain.Mean	0.169	0.047	3.599		
MaxT.MMean.Feb	-0.448	0.081	-5.530			MinT.MMean.Oct	-0.136	0.052	-2.635		
MinT.MMean.Feb	0.733	0.179	4.090			log(EffortY)	0.622	0.073	8.472		
(Intercept)	6.675	0.354	18.865		**0.701**	(Intercept)	4.535	1.226	3.699		**0.825**
Rain.MStdev.Mar	-0.050	0.025	-2.020			Rain.Stdev	0.084	0.028	3.013		
Rain.Mean	0.433	0.060	7.252			MinT.MMean.Oct	-0.122	0.054	-2.284		
MaxT.MStdev.Nov	-0.828	0.167	-4.969			log(EffortY)	0.637	0.077	8.217		
(Intercept)	5.307	0.214	24.856		**0.790**	(Intercept)	0.946	0.64	1.477		**0.861**
Rain.MMean.Nov	-0.413	0.065	-6.356			Rain.Mean	0.205	0.047	4.357		
Rain.Mean	0.474	0.058	8.160			Evap.MStdev.Mar	-0.268	0.165	-1.631		
SOI_Jul	-0.038	0.008	-4.503			MinT.Stdev	0.568	0.175	3.248		
SOI_Nov	0.032	0.008	3.753			log(EffortY)	0.637	0.072	8.812		
(Intercept)	19.931	4.157	4.795		**0.787**	(Intercept)	1.46	0.834	1.751		**0.86**
MaxT.MMean.Nov	0.519	0.085	6.090			Rain.Mean	0.227	0.053	4.311		
MaxT.Mean	-0.917	0.111	-8.246			MaxT.MStdev.Nov	-0.242	0.155	-1.555		
SOI_Sep	-0.046	0.010	-4.793			MinT.Stdev	0.535	0.175	3.067		
SOI_Nov	0.043	0.009	4.539			log(EffortY)	0.569	0.094	6.047		
(Intercept)	5.786	0.296	19.530		**0.785**	(Intercept)	0.555	0.596	0.931		**0.86**
Rain.MMean.Nov	-0.315	0.062	-5.076			Rain.Mean	0.17	0.047	3.601		
Rain.Mean	0.569	0.056	10.152			MinT.Stdev	0.642	0.188	3.413		
Evap.MStdev.Mar	-0.746	0.205	-3.633			SOI_Feb	0.01	0.006	1.514		
SOI_Jul	-0.034	0.008	-4.158			log(EffortY)	0.643	0.072	8.92		
(Intercept)	6.078	0.235	25.882	0.000	**0.879**	(Intercept)	-2.745	3.001	-0.915	0.368	**0.877**
Rain.MMean.Nov	-0.396	0.050	-7.850	0.000		Rain.Mean	0.271	0.055	4.906	0	
Rain.Mean	0.501	0.045	11.082	0.000		MaxT.MMean.Nov	0.223	0.08	2.791	0.009	

	Estimate	Std. Error	t value		R^2		Estimate	Std. Error	t value		R^2
Evap.MStdev.Mar	-0.724	0.157	-4.613	0.000		MaxT.MStdev.Jan	-0.257	0.119	-2.152	0.04	
SOI_Jul	-0.046	0.007	-6.802	0.000		MinT.MMean.Oct	-0.141	0.047	-2.999	0.006	
SOI_Nov	0.031	0.007	4.724	0.000		log(EffortY)	0.565	0.074	7.664	0	
(Intercept)	7.195	0.575	12.505	0.000	**0.851**	(Intercept)	1.917	0.834	2.299	0.029	**0.876**
Rain.MMean.Nov	-0.415	0.056	-7.464	0.000		Rain.Mean	0.266	0.054	4.89	0	
Rain.Mean	0.337	0.063	5.308	0.000		MaxT.MStdev.Nov	-0.353	0.16	-2.211	0.035	
Evap.MMean.Jan	-0.187	0.054	-3.460	0.002		MaxT.MStdev.Jan	-0.215	0.112	-1.919	0.065	
SOI_Jul	-0.047	0.008	-6.133	0.000		MinT.Stdev	0.601	0.171	3.522	0.001	
SOI_Nov	0.042	0.008	5.366	0.000		log(EffortY)	0.565	0.09	6.262	0	
(Intercept)	6.091	0.262	23.265	0.000	**0.849**	(Intercept)	-5.518	2.846	-1.939	0.062	**0.876**
Rain.MStdev.Nov	-0.245	0.037	-6.632	0.000		Rain.Mean	0.269	0.055	4.85	0	
Rain.Mean	0.512	0.051	9.995	0.000		MaxT.MMean.Nov	0.178	0.081	2.185	0.037	
Evap.MStdev.Mar	-0.757	0.175	-4.333	0.000		MaxT.MStdev.Jan	-0.253	0.12	-2.109	0.044	
SOI_Jul	-0.047	0.008	-6.252	0.000		MinT.Stdev	0.51	0.173	2.94	0.006	
SOI_Nov	0.025	0.007	3.571	0.001		log(EffortY)	0.628	0.076	8.275	0	
(Intercept)	10.310	1.967	5.243	0.000	**0.896**	(Intercept)	-10.799	2.882	-3.747	0.001	**0.905**
Rain.MMean.Nov	-0.386	0.048	-8.100	0.000		Rain.MStdev.Jan	-0.072	0.019	-3.872	0.001	
Rain.Mean	0.486	0.043	11.243	0.000		Rain.Mean	0.588	0.096	6.107	0	
Evap.MStdev.Mar	-0.691	0.149	-4.648	0.000		MaxT.MMean.Nov	0.382	0.083	4.593	0	
MaxT.MMean.Oct	-0.117	0.054	-2.166	0.039		MaxT.MStdev.Mar	-0.447	0.115	-3.886	0.001	
SOI_Jul	-0.047	0.006	-7.356	0.000		SOI_Jul	-0.028	0.007	-4.192	0	
SOI_Nov	0.033	0.006	5.311	0.000		log(EffortY)	0.345	0.082	4.22	0	
(Intercept)	6.169	0.226	27.289	0.000	**0.895**	(Intercept)	-6.32	2.576	-2.453	0.021	**0.901**
Rain.MMean.Nov	-0.430	0.050	-8.542	0.000		Rain.MStdev.Jan	-0.044	0.015	-2.865	0.008	
Rain.Mean	0.726	0.115	6.336	0.000		Rain.Mean	0.415	0.076	5.473	0	
Rain.Stdev	-0.122	0.058	-2.112	0.044		Evap.MStdev.Mar	-0.415	0.151	-2.756	0.01	
Evap.MStdev.Mar	-0.733	0.148	-4.938	0.000		MaxT.MMean.Nov	0.205	0.073	2.824	0.009	
SOI_Jul	-0.049	0.006	-7.486	0.000		MinT.Stdev	0.589	0.16	3.682	0.001	
SOI_Nov	0.030	0.006	4.845	0.000		log(EffortY)	0.533	0.074	7.251	0	
(Intercept)	6.045	0.226	26.704	0.000	**0.892**	(Intercept)	-6.757	2.627	-2.572	0.016	**0.897**
Rain.MMean.Nov	-0.410	0.049	-8.358	0.000		Rain.MStdev.Jan	-0.041	0.016	-2.658	0.013	
Rain.MStdev.Jan	-0.028	0.015	-1.846	0.075		Rain.Mean	0.457	0.081	5.631	0	
Rain.Mean	0.600	0.069	8.697	0.000		Evap.MStdev.Mar	-0.573	0.165	-3.471	0.002	
Evap.MStdev.Mar	-0.771	0.153	-5.040	0.000		MaxT.MMean.Nov	0.27	0.074	3.651	0.001	
SOI_Jul	-0.045	0.006	-7.021	0.000		SOI_Jul	-0.022	0.006	-3.486	0.002	
SOI_Nov	0.027	0.007	4.163	0.000		log(EffortY)	0.402	0.079	5.122	0	

Patterns in the coefficient for the optimal regressions

The message to take from these copious regression estimates is somewhat difficult to comprehend. First, however, note that the significances shown for the regression coefficients are severely compromised by the selection effect that is the fact that the regression models are not prescribed in advance but chosen in an optimal way. See, for example, (Miller 2002). The fact that a coefficient appears highly significant is not particularly remarkable, however if a coefficient fails to reach conventional significance levels it is a clear indication that it is probably not at all effective as a predictor.

We address the question of significance in a different way in Section 0 on page 266ff where we use cross-validation as a tool to check if the regressions are detecting a real signal or are reproducing randomness in the training data.

In Table 49, Table 50 and Table 50, the left hand columns show the coefficients for the cases where $\log(\text{Effort})$ has been excluded as a predictor and the right hand columns show the corresponding cases where it is fixed into the regression as a predictor. There are some general comments that can be made with respect to all stock areas, namely

- Rainfall means are very often chosen as predictors, with the clear majority having positive coefficients. In general the more rainfall the higher the catch of banana prawns.
- Evaporation and Minimum Temperature means, where selected, also generally show positive coefficients but Maximum Temperature means are often given a negative coefficient.
- In some cases standard deviation measures are chosen, and in these cases Rainfall, Evaporation and Minimum Temperature measures are usually given a negative coefficient, but Maximum Temperature standard deviation measures are often given a positive coefficient.
- The year itself (or more precisely, ‘Year – 1970’, the elapsed time since the start of the fishery) is allowed as a predictor along with the true environmental predictors, but only in one stock area was it selected with any regularity.
- SOI measures were not often selected as useful predictors, but where they were the SOI for a month early in the period, say for the preceding July, usually attracted a negative index, whereas SOI measures for months closer to the start of the season generally had a positive index.

Allowing for the strong correlations between predictors and the consequential partial surrogacy effect, it is only possible to conclude at this stage that, in general, higher banana catch is associated with higher pre-season precipitation (or its partial surrogates).

We now consider the three regions in some further detail.

Weipa. Where $\log(\text{Effort})$ is excluded as a predictor, the ‘Year’ predictor is by far the most commonly selected predictor, and it generally has a negative coefficient. One explanation of this is that environmental predictors play little part in determining the Weipa catch, but ‘Year’ is strongly correlated with ‘Effort’ over the latter part of the period, particularly, and ‘Year’ is therefore acting as a partial surrogate for Effort. Note that there has been a strong decline in the absolute level of effort in Weipa over a considerable time period. See Figure 87 below. The other predictors chosen along with ‘Year’ are generally rainfall or evaporation measures, with coefficient signs adhering closely to the general patterns noted above. Where $\log(\text{Effort})$ is fixed in the regression, ‘Year’ is not as often selected as a predictor, but when it is it usually has a slightly *positive* coefficient, suggesting somewhat paradoxically that after allowing for Effort, the catch rate in Weipa is actually *improving*, if only slightly! One consistent and very interesting feature of the Weipa results is that where $\log(\text{Effort})$ is included it usually has a coefficient of about 1.4 to 1.5. This suggests that catch is ‘over responsive’ to effort, that is, to the extent that the model represents a causal relationship, the marginal effect of an increase in effort actually rises with the total effort. This is clearly not entirely a correct implication, but does suggest that Catch and Effort are in some kind of feedback loop – an initially promising CPUE seems to result in a persistence of effort but an initially unpromising CPUE rapidly results in a cessation of effort, or rather a transfer of effort to other stock regions. The multiple correlations, which will be strongly biased upwards because of the selection effect, only rise to 0.75 if $\log(\text{Effort})$ is not included and to 0.94 when it is. In the first case even discounting the selection effect, this relationship would not be considered useful enough for effective prediction. This indicates that links between total catch and environmental variables (or at least those which might be used prior to the opening of the season for catch prediction) are very weak.

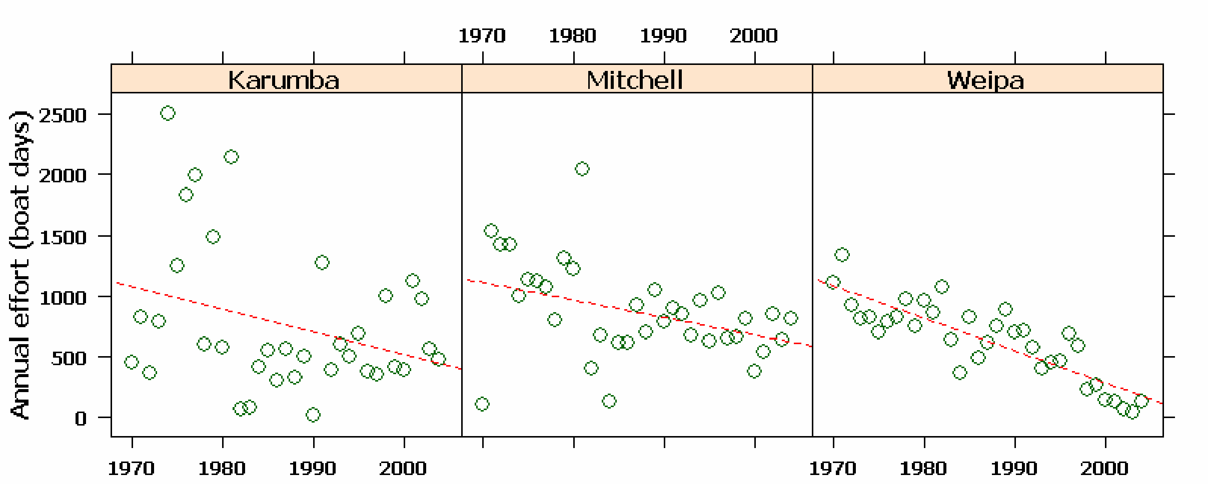

Figure 87: Absolute banana effort at Karumba, Mitchell and Weipa with year of the fishery, with simple least squares line.

Mitchell. When $\log(\text{Effort})$ is excluded, the catch is even less predictable than in Weipa. The 'Year' predictor is not selected at all, possibly due to the weaker connexion between effort levels and year. See Figure 87 although there is some evidence of a decline in recent years, it is by no means as consistently tight a relationship as with Weipa. The environmental variables that are selected are again either rainfall mean measures or putative surrogates of them, and have the pattern of signs in their coefficients outlined in general above. Without $\log(\text{Effort})$ allowed as a predictor the multiple correlation coefficient remains less than 0.7, indicating a relationship probably not useful for prediction and hence somewhat uncertain for interpretation purposes as well. When $\log(\text{Effort})$ is fixed in the regression, predictability increases considerably, as would be expected, but even then the multiple correlation coefficient remains below 0.9. The coefficients of $\log(\text{Effort})$ are now very close to 1 in all cases, indicating a close proportionality relationship between catch and effort for Mitchell. Any interpretation of this feature would be somewhat speculative, but clearly the "over proportional" aspect of the Weipa stock area is not replicated in Mitchell.

Karumba. The catch in the Karumba, by contrast, appears to be well predictable by environmental variates, and annual pre-season mean rainfall appears to be the dominant environmental predictor both when $\log(\text{Effort})$ is excluded and when it is included. Other environmental predictors tend to be either rainfall measures or partial surrogates. The 'Year' predictor is not selected, as in the case of Mitchell. When $\log(\text{Effort})$ is excluded, there appears to be some evidence of a slight relationship with SOI, particularly the contrast between the previous July and November mean values. This may be spurious in the sense that it could be accidentally correlated with other predictors. In the case of Karumba, the coefficient of $\log(\text{Effort})$ is nearly always in the range 0.3-0.5, which suggests that the dependency of catch on effort is much weaker than in the other two regions. This is underscored by the fact that the multiple correlation coefficients start from quite high levels even for just one predictor, and approach 0.9 in both cases.

The three stock areas provide an interesting contrast in the way that the show different patterns of dependency on environmental predictors and Effort. In the case of Weipa, a simplistic interpretation of this is that it is a local fishery that requires more searching time and hence has a stronger dependence on effort than either of the other two.

Mitchell is intermediate and Karumba has the weakest dependence on Effort and a stronger environmental signal than the others. This dependence on environmental variables may imply that

Karumba is the more attractive fishing area, particularly if the industry can have a higher confidence level in knowing what stock might be available prior to the start of fishing than the other two.

Cross validated regression models

We have stated that with the optimally chosen regressions, significance levels and multiple correlation coefficients will be biased upwards because of the strong selection effect. In order to get an objective assessment of what predictive power there is in these relationships, one simple technique to use is cross-validation. This is really a family of techniques, but the version we find most appropriate here is the following.

'Leave-3-out' cross validation

The idea behind cross-validation in general is to build up a picture of how well a *model-building technique* is performing using internal evidence from the training sample. At each stage a section of the training sample is omitted, usually about 10%, and the model, or sequence of models, is built up in the nominated way from the remainder. The models are then used to predict for the omitted set of data and a measure of the effectiveness is constructed by comparing the predictions with the observed values. This is repeated usually for a rotating set of omitted values, so that at the end of the sequence a prediction, or set of predictions, is obtained for each value, where no datum is involved in training the models from which its predictions for it are obtained.

'Leave-*v*-out' cross-validation is a comprehensive version of this scheme, where each possible subset of *v* data is excluded in turn. Hence if there are n observations, there will be $\binom{n}{v}$ sets of data on which the sequence of models is fitted. For n = 35 observations as we have her, a prudent choice seems to be *v* = 3, which requires models to be build on an interlocking series of 6545 data sets. Unlike simple cross-validation, the result is not subject to random fluctuations, but for larger samples the computations rapidly become prohibitive. Note that in our case leave-4-out CV would require 52360 data sets.

We concentrate on the cross-validated multiple regression coefficients. The usual estimate in regression is

$$R^2 = 1 - \frac{\mathrm{ESS}}{\mathrm{TSS}}$$

where ESS and TSS are the "Error" and "Corrected Total" sums of squares respectively. The cross-validated analogue of this is

$$\dot{R}^2_{\mathrm{CV}} =^{\mathrm{def.}} 1 - \frac{\mathrm{ESS}_{\mathrm{CV}}}{\mathrm{TSS}}$$

where the "Error" sum of squares is now the sum of squared differences between observations and cross-validated predictions, averaged over cross-validation runs.

With the standard definition of the multiple correlation coefficient is always non-negative and must increase as the regression involves more predictors. This is not the case with its cross-validated analogue. Generally the coefficient initially rises as the number of predictor variables increases, but as the model becomes too complicated predictive power is lost, noise in the training set is not separated from reliable signal and is transferred through to predictions, thus increasing the cross-validated Error sum of squares and reducing the coefficient. If the model is highly ineffective pure noise is transferred as signal and the error sum of squares can easily exceed the total, giving a negative cross-validated estimate. The suggestion often used in practice is that while the multiple correlation continues to increase the predictive capacity (and to a lesser extent the interpretative utility) of the model is generally maintained.

Figure 88 gives a graphical comparison of the cross-validated multiple regression estimates with their standard counterparts, as reported in Table 53, and Table 54 and Table 55 above.

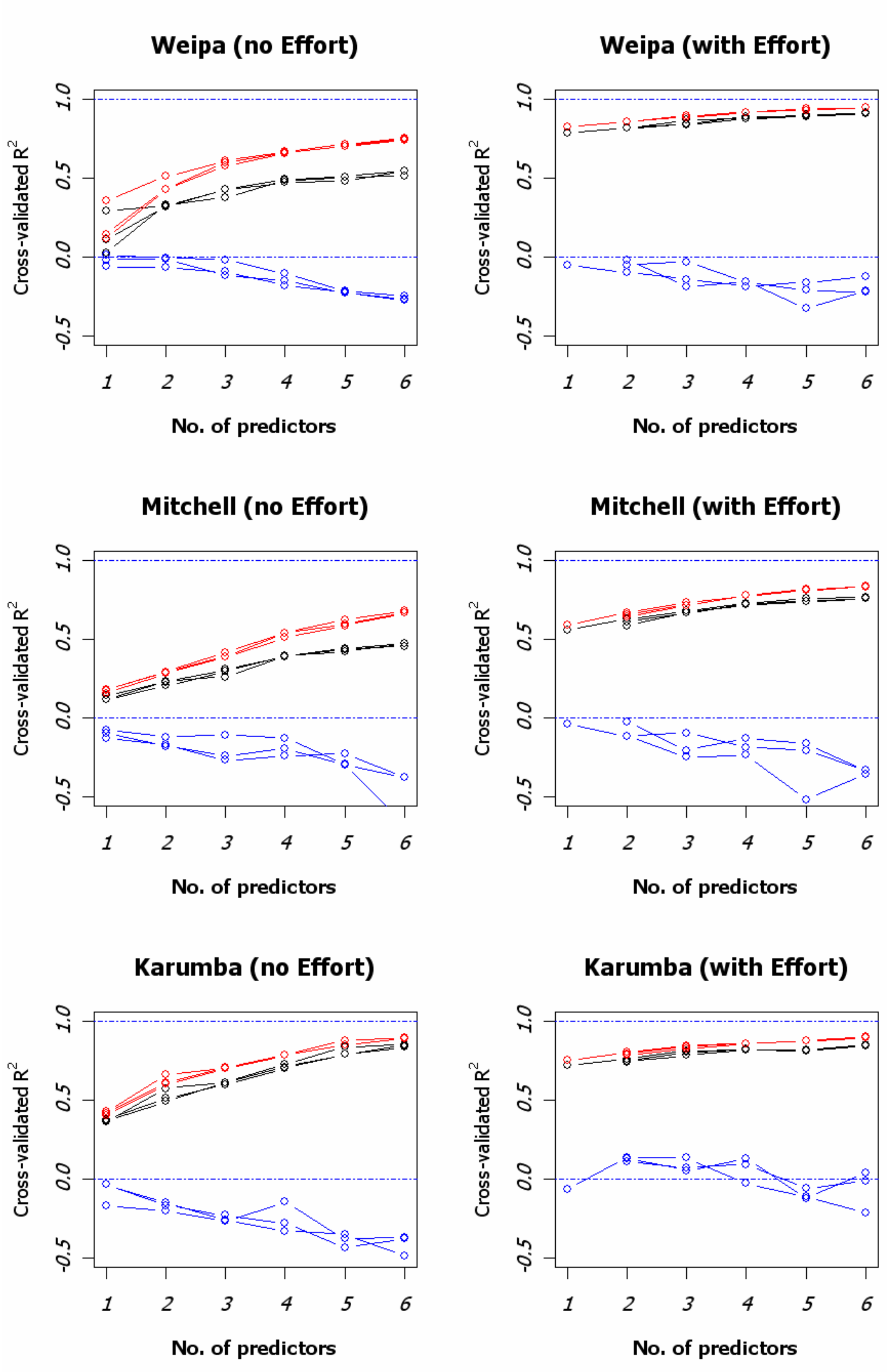

Figure 88: Standard (red lines), and cross-validated (black lines) estimates of the multiple correlation coefficient as a function of the number of predictors in the model. The blue lines show a comparison with a dummy response of independent normal variates, i.e. statistically a 'pure noise' signal. The left panels exclude log(Effort) as a predictor and the right panels include it.

For comparison (and as a check), these diagrams also show the result for 'dummy' runs of the cross-validation process where instead of the real response and simulated pure noise response is substituted.

For such a dummy response the selection effect and the standard monotone increasing property of the multiple correlation coefficient would both ensure that the standard definition yields a positive increasing (and hence biased upward) estimate. The cross-validated analogue, on the other hand, is usually negative and is mostly monotone decreasing. The separate lines in these diagrams correspond to the first, second and third best models of the original model selection process.

Discussion

The cross-validated multiple correlations are less than the standard definition, as must effectively be the case, but generally remain high and increasing, if at a rapidly diminishing rate, as the number of predictors increases. This is good evidence that the models, at least up to about 6 predictors, do have some predictive and interpretative capacity, though the picture is not as optimistic as the original estimates might suggest.

In the case of Weipa, the situation is very different depending on whether or not $\log(\mathrm{Effort})$ is included as a predictor: if it is, the catch is predictable, with some mild improvement from adding environmental predictors to it. If it is not, the catch is effectively only weakly predictable from environmental predictors alone.

For Mitchell, even with $\log(\mathrm{Effort})$ as a predictor, the catch is not as predictable as in the case of Weipa, but some environmental drivers do seem to play a stronger part.

With Karumba, however, environmental drivers seem to be as important as $\log(\mathrm{Effort})$ for prediction purposes, if not more so in the aggregate. Notice that even with only one environmental predictor the multiple correlation estimate is much higher than for either of the other two stock areas, and with 6 predictors it stands at essentially 0.9 whether or not $\log(\mathrm{Effort})$ is one of them. This is in stark contrast to Weipa or Mitchell. We have seen that the major predictors of catch in this case, with or without $\log(\mathrm{Effort})$, are rainfall means.

Summary and conclusions

With an observational study as we have here it is extremely difficult, if not logically impossible, to attribute causal relationships to observed associations. These studies can, however, be useful in generating hypotheses and testing links between potential drivers and observed outcomes that under some conceptual model of the system might be expected to occur.

Following on from the prior work of Vance and others, we have settled on precipitation measures and their analogues and surrogates as the most likely environmental correlates of banana prawn catch in the Eastern NPF. Unlike Vance and his colleagues, however, we have largely used broad, catchment-wide environmental measures rather than point measures from some of the key available weather recording stations. We do not claim any necessary advantage for this policy, other than that it represents a slightly different direction of attack, and that the recently published SILO data provides a convenient uniform foundation on which to base aggregate measures. We acknowledge that the effects of interpolation in the data are unknown, but contend that averaging over the catchment is likely to render any such effects somewhat secondary for our purposes.

Using both aggregate, SILO-based catchment-wide measures and actual daily measures from two key recording stations, in Weipa and Normanton respectively, we were able to show that in both cases either measure behaved similarly, particularly for prediction purposes such as we were proposing.

Also, using rainfall records from individual stations, we were not able to show any convincing evidence of a long-term change in the rainfall pattern over the duration of the fishery. This is important for Weipa, especially, as if we could show strong associations between catch and environmental predictors, presumably mainly rainfall, we would need to be able to show some change in the overall rainfall pattern at Weipa for environmental explanations of the downturn in catch in the area to have any credence.

The daily rainfall records over the period 1969-2004 for the catchments allow us to study similarities between the catchments themselves on this basis, and we showed that they fall into three main groups, namely North-East, South-East and Western groups, within which the rainfall history is very similar. A study of the logbook data also shows that banana prawn fishing patterns in the regions are largely confined to

a) Albatross bay and immediately offshore from it,
b) Offshore from the Mitchell catchment, and to a lesser extent the mouth of the Staaten and Coleman rivers
c) Offshore from the Norman catchment, and other nearby rivers.

We settled on using the Embley, Mitchell and Norman catchments as the basis for generating potential environmental drivers of catch for these three regions. The similarity between catchments should imply that if others were important, the chosen catchments should serve as good surrogates for them. This seemed reasonable, given that the study was largely concerned with identifying possible drivers, only.

As most of the influences on catch are likely to be multiplicative rather than additive, the models we considered focused on log (Catch) as the response and, where appropriate, used log (Effort) as one of the predictors. As this is largely a pulse fishery with a large part of the effort concentrated in a short burst at the beginning of April, it also seemed appropriate to use total annual catch for the stock area as the response rather than try to deal with it on any finer temporal scale. This carried with it the disadvantage of reducing the effective sample size to 35 observations, which makes serious regression modelling somewhat artificial, but in this case inevitable.

As a predictor of catch, log (Effort) is clearly inappropriate as it is unknown prior to the opening of the season. However as an explanatory variable, log(Effort) is entirely reasonable, but attributing any kind of causal link to it would need at least an assumption that the mechanism by which effort levels are set is independent of catch levels. In the case of banana prawns, such an assumption is at best contentious. Given the communal (if not cooperative) way the banana fishing activity is conducted and given the possibility of alternative fishing grounds if the initial evidence of abundance through catch rates is unpromising, it seems that effort levels must be set by some combination of pre-planning and adaptive change during fishing itself.

The key question for Weipa seems to be whether or not the observed dramatic collapse of the banana prawn catch is attributed to external influences, or whether it is simply due to a reduction of effort in searching for product, occasioned by the contraction of the season, the reduction in the fleet and the promise of simpler and more plentiful catches elsewhere in the limited time available for fishing. This key question cannot be addressed directly with observational studies like this one, but some indirect light can be thrown upon it.

Our main reason for fitting models both with and without log (Effort) as a predictor was to allow the existence of environmental drivers, independent of and in addition to effort to be established. This seems to have been established most clearly in the case of Karumba, where rainfall measures clearly play an important part in predicting banana catch. In the case of Mitchell environmental predictors are clearly present but are less effective than for Karumba, and for Weipa the evidence of links with environmental drivers is still strong, even though those links themselves appear to be weak and fairly ineffective for prediction when used alone.

One curious outcome of this study is to show that the relationship between catch and effort, *mutatis mutandis,* it itself somewhat different in the three areas. For Weipa it seems to be ‘super proportional’ with, roughly

$$\text{Catch}\ \mu\ \text{Effort}^{1.5}$$

In Mitchell it is very close to strict proportionality

$$\text{Catch}\ \mu\ \text{Effort}$$

and for Karumba is ‘sub-proportional’ with

$$\text{Catch}\ \mu\ \text{Effort}^{0.5}$$

These approximate relationships may only reflect the different degrees of importance given to environmental drivers in the three areas, but they could also suggest that the catch in Weipa is much more sensitive to changing effort levels than either of the other two.

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