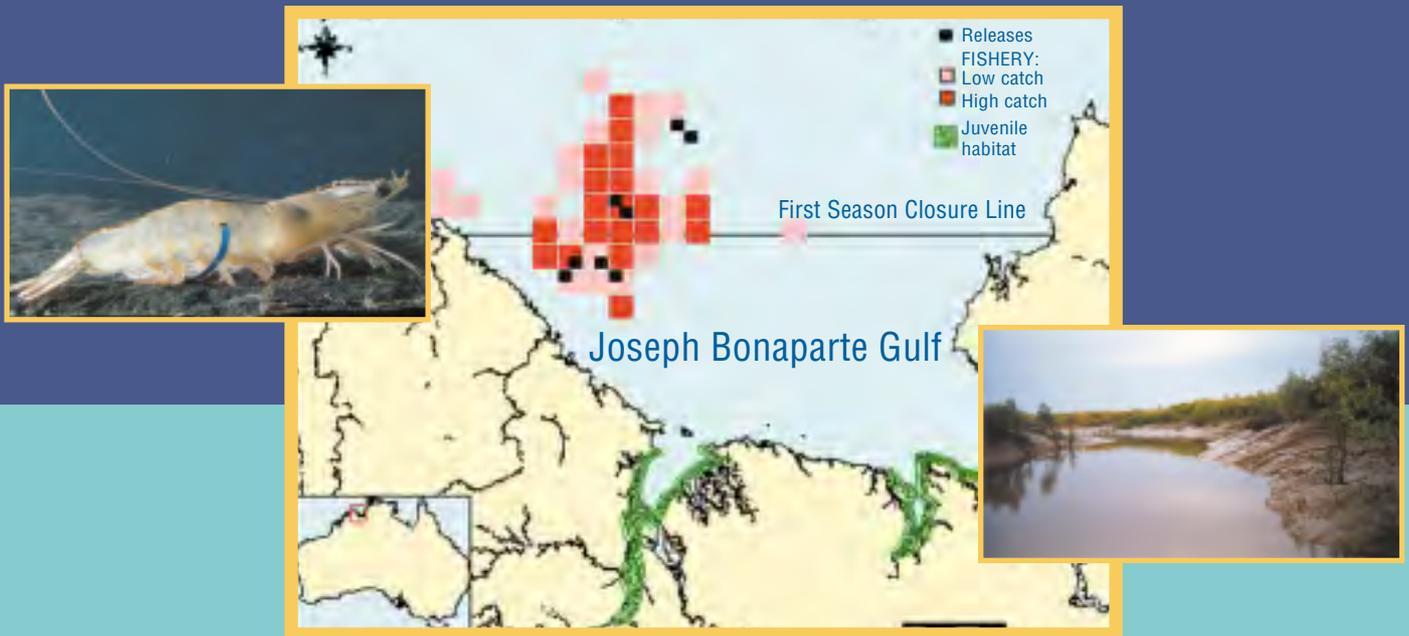


The growth, mortality, movements and nursery habitats of red-legged banana prawns (*Penaeus indicus*) in the Joseph Bonaparte Gulf



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CSIRO MARINE RESEARCH
March 2002

FRDC Project 97/105

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Project FRDC 97/105

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ISBN 1 876 996 09 9

1. *Penaeus indicus* – Australia – Joseph Bonaparte Gulf (N.T. and W.A.). 2. Prawns (shrimp) – Australia – Joseph Bonaparte Gulf (N.T. and W.A.). 3. Prawn (shrimp) fisheries – Australia, Northern. I. Loneragan, Neil. II. CSIRO Marine Research.

639.58099414

Published by CSIRO Marine Research

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2002

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Cover figure – see Figure 7.1, Page 133.

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1. CHAPTER ONE: SUMMARY

Authors: NR Loneragan, DJ Die, RA Kenyon, B Taylor, DJ Vance, FJ Manson,

97/105 The growth, mortality, movements and nursery habitats of red-legged banana prawns (*Penaeus indicus*) in the Joseph Bonaparte Gulf

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OBJECTIVES:

1. Determine the optimum exploitation rates for the management of the red-legged banana prawn fishery in Joseph Bonaparte Gulf
2. Establish a baseline dataset to identify and manage environmental and human impacts on nursery areas of the red-legged banana prawn in Joseph Bonaparte Gulf

I NON-TECHNICAL SUMMARY

OUTCOMES ACHIEVED:

This project has contributed to the ecologically sustainable management of the Northern Prawn Fishery (NPF) by providing information on the status of red-legged banana prawn stocks and the nursery habitats that support this fishery. It has achieved these outcomes by firstly completing detailed tagging studies to obtain robust estimates of growth and mortality for red-legged banana prawns. These estimates enabled per-recruit models for red-legged prawns to be revised and for the sustainability of the current fishing patterns to be assessed. The levels of estimated recruitment to the fishery are much lower than previously estimated and therefore the stocks may be more vulnerable to over-fishing than past assessments suggested. Secondly, broad-scale surveys across the inshore areas of the Joseph Bonaparte Gulf established that juvenile red-legged banana prawns are found in small, mangrove-lined creeks in the estuaries located 100 to 200 km south-east of the fishery (Fitzmaurice/Victoria Rivers to Cambridge Gulf). This means that changes in land-use that affect coastal habitats or water flow (e.g. the Ord River Stage II development) may affect the juvenile stages and the emigration of juveniles into the fishery.

The fishery for red-legged banana prawns, *Penaeus indicus*, in the Joseph Bonaparte Gulf (JBG) developed in the early 1980s. Since then, fishing effort has varied from about 700 to 2,600 boat-days per year, with total catches ranging from 200 to 1,000 t and averaging about 800 t, or about 20% of the yearly banana prawn catch for the whole Northern Prawn Fishery. Historically, fishing effort in the JBG increased when catches in other parts of the NPF were low. However, part of the NPF fleet now fishes this region on a regular basis. Despite the importance of the red-legged fishery to the overall NPF, relatively little is known of the biology of *P. indicus* in Australia, particularly its nursery habitats and population parameters such as growth and

mortality. Recent modelling studies to examine the effects of different seasonal patterns of fishing on the yield, value and egg production of red-legged banana prawns found that the model was very sensitive to the estimates of growth and mortality. This study had two main components: to establish and map the key nursery habitats for this species in the JBG and compare them with those for white banana prawns (*Penaeus merguensis*) in northern Australia (see Chapters 2 to 4); to obtain better estimates of growth and mortality for *P. indicus* in the JBG from tagging studies and revise the previous per-recruit models using these estimates (see Chapters 5 to 8).

Finding and mapping the nursery habitats (Chapters 2 to 4)

The two species of banana prawns are difficult to discriminate by eye. The first stage of this work used gel electrophoresis and a number of morphometric characters to establish whether it was possible to identify juvenile *P. indicus* from *P. merguensis* from a few, easily measured characters (Chapter 2). Measuring the distance to the first two rostral teeth and counting the rostral teeth behind the eye provided a reliable means of separating the juveniles of the two species.

Both broad-scale (across the width of the Joseph Bonaparte Gulf) and fine-scale (within three selected river systems) surveys were used to establish the nursery habitats of red-legged banana prawns and compare them with those of the white banana prawns (Chapter 3). We found a major spatial separation of the two species: juvenile red-legged banana prawns dominated the catches from the rivers in the Cambridge Gulf east to the Victoria and Fitzmaurice rivers, from 120 km south to 240 km east-south-east of the fishery. In contrast, juvenile white banana prawns dominated the catches in the rivers west of the Cambridge Gulf to Cape Londonderry (much closer to the fishery). Juveniles of both species were found in similar proportions in the Lyne River on the western side of Cambridge Gulf, which is therefore a transition zone in the distribution of species. Catches of postlarval banana prawns and juvenile *P. indicus* were highest in small, mangrove-lined creeks in estuaries, similar to the nursery habitats for *P. merguensis* in the Gulf of Carpentaria. These results imply that the larval *P. indicus* move (through an interaction between tidal currents and larval behaviour – larval advection) large distances from the spawning grounds in the fishing zone to the nursery grounds to the south and east. Conversely, the juvenile stages must emigrate large distances from the mangroves, across shallow sand into the deeper, muddier substrate (50 to 80 m deep) where the fishery operates. Understanding the process of larval advection and where the ‘effective spawning’ takes place are important questions for further work.

The distribution and extent of the mangrove habitats of juvenile red-legged banana prawns in coastal JBG were estimated using digitised 1:250,000 topographic maps from the Australian Surveying and Land Information Group (AUSLIG) (Chapter 4). We investigated the accuracy of these maps by comparing the estimates of area and length of mangroves with those from aerial photos and Landsat TM in two small creeks of the Joseph Bonaparte Gulf, and the mangroves of Weipa. The mangroves in the two creeks of the JBG formed very narrow bands lining the water’s edge. Aerial photos had the highest resolution (2 m) and gave the most accurate estimates of area and linear length. The areas of mangroves estimated from Landsat TM (30 m) were similar to those from aerial photos but the linear extent of mangroves estimated from

the two techniques differed. The area and linear extent of mangroves from topographic maps (lowest resolution) were the least accurate, except where the mangroves were greater than 50 m wide (Weipa). It would not be possible to map the area and linear extent of mangroves for the whole of the NPF from aerial photos. However, this could be feasible using Landsat TM, in combination with aerial photos and ground-truthing in zones of special interest.

Assessing fishing patterns and optimum level of fishing (Chapters 5 to 8)

An examination of historical changes in the fishery (Chapter 5) showed that catches, effort and CPUE have all varied more in the 1990s than in the 1980s when the fishery was developing. However, few new grids have been fished in the 1990s and the grids with more than 10 days of fishing effort have been consistent between years and now provide about 90% of the red-legged banana prawn catch from the Joseph Bonaparte Gulf. There has been a major shift in fishing patterns in the 1990s compared with the 1980s – in the early 1980s, most effort was expended in the later part of the year (September to December), whereas now there is a marked peak in May, with a lesser broader peak between August and November.

A total of about 8,500 and 9,500 prawns were tagged and released in each of the years 1997 and 1998 (Chapter 6). We tagged mainly sub-adult prawns before the start of the first season (April 1) and just after fishing started in each year so that we could estimate both natural and fishing mortality. The two years of tagging represented extremes of catch with amongst the highest catches on record taken in 1997 (1,017 t) and amongst the lowest on record in 1998 (288 t). The recruitment in 1997 was estimated to be between 3 and 6 times higher than in 1998. The proportion of tag returns was about twice as high in 1997 (10.8%) than in 1998 (5.4%). The Von Bertalanffy growth parameters were estimated for *P. indicus* in the JBG using two models and the estimates compared between years. Despite extreme differences in the estimated numbers of recruits, these growth parameters did not differ between years, indicating that growth was independent of density. It is proposed that the estimated growth rates could be applied to future assessment models and therefore there is no immediate need to re-estimate growth. It may be important to test whether cohorts born in different seasons also have the same growth rates.

Estimates of natural mortality rates remain uncertain (0.032 to 0.067 per week, or 0.13 to 0.28 per month), but were within the range of the values used previously in the assessment of this species (0.15 to 0.25 per month) (Chapter 6). Estimates of catchability differed greatly between tagged and untagged prawns, but this may be the result of shortcomings of the modelling and not of real differences between tagged and untagged prawns. Biases could result from the fact that the initial size of the tagged population is known and that of the untagged population is unknown. This should be investigated further. Fishing mortality rates and exploitation rates for *P. indicus* were lower than those for *P. merguensis* in the Gulf of Carpentaria. It is not known, however, whether the exploitation rates for *P. indicus* are sustainable or if they are negatively affecting the recruitment of young red-legged banana prawns. It is therefore essential to investigate the long-term impact of fishing on the productivity of the *P. indicus* stock in the JBG through more dynamic modelling approaches.

Although our tagging study was not designed to determine movement patterns, some inferences about movements can be made (Chapter 7). In the first fishing season (April to June), tagged *P. indicus* were mainly recaptured to the north-east of their release points; and mainly north to north-west in the second season (August to November). Recapture probabilities for any given 12 nautical mile grid for each fishing period were not proportional to the fishing effort in that period; they varied and were affected by the amount of effort and the fishing period. There was no evidence that *P. indicus* moved first to deep water and then returned to shallower waters during the year. The current spatial seasonal closure in the JBG prevents fishers from fishing the shallow-water stock (recent recruits to the fishery) between April to June. As there is no return migration by the prawn stocks to shallower water, our results suggest that the spatial closure does not reduce the access of trawlers to the larger prawns.

The population estimates from this study lead to an estimated population size that is much lower (10 to 15 times) than previous estimates and suggests that the fishery is sustained by a much smaller stock than previously thought (Chapter 8). Our current results suggest that management cannot focus only on maximising the yield or value of a single cohort and ignore the long-term effects of fishing on recruitment i.e. we now have to consider that fishing might reduce the spawning stock to such low levels that recruitment is also reduced. This hypothesis needs to be tested, possibly using information on catch and effort from the logbooks, combined with size information from the landings returns to estimate the proportion of recruits and spawners in the population at different times of year. Unfortunately, it would take a number of years to build the data to test this hypothesis. The precautionary principle calls for caution in managing resources when information is insufficient to define optimum levels of fishing mortality. We therefore recommend that NORMAC adopts a cautious approach in the management of red-legged banana stocks. Specifically, we recommend that NORMAC adopt measures so that effective fishing effort does not increase any further than present levels in the JBG fishery and ensures that measures aimed at protecting other prawn stocks in the NPF do not lead to increases in effort on the red-legged banana prawn fishery.

KEYWORDS: red-legged banana prawns, per-recruit models, growth, mortality, tagging, nursery habitats, mangroves, Joseph Bonaparte Gulf

II ACKNOWLEDGEMENTS

We thank the skipper (Mr. Colin Cant) and crew of the Queensland Fisheries Research research vessel “RV Gwendoline May” for their assistance in tagging prawns in 1997; and the skipper (Mr. Ric Richter) and crew of the Austfish fishing vessel “FV Libertine” for their assistance tagging prawns in 1998. Mr. Ian Boot of Austfish provided assistance on-shore. The assistance of the Northern Prawn Fishery fishers and processors for their cooperation in returning tagged prawns (particularly those NPF operators working out of Darwin) is greatly appreciated – without their enthusiasm and help, this component of the project would not have succeeded.

For vessel support for work on juvenile prawns in the inshore regions of the JBG, we thank the owner/skipper (Mr. Neil Montgomery) and crew of the “MV Makaira II” (1997) and the owner/skipper (Mr. Wayne Bishop) and skipper (Mr. Rod Cole) and crew of the “MV Ace of Spades” (1998). Sue Cheers, Vicky Smith, Michael Crouch and Anthea Koutsoukos provided assistance with sorting samples of sediments and juvenile prawns, and with data entry.

III BACKGROUND

The fishery for red-legged banana prawns in the Joseph Bonaparte Gulf developed in the early 1980s. Since then fishing effort has varied between 700 and 2,600 boat days per year, with catches ranging from 200 to 1,000 t and averaging about 800 t, or about 20% of the yearly banana prawn catch for the whole Northern Prawn Fishery. Because of the remoteness and rough sea conditions in the JBG, the intensity of fishing effort in the red-legged banana prawn fishery has been determined largely by the size of catches and economic returns from other regions of the NPF. Most effort in the JBG is now concentrated in depths of about 50-60 m and peaks around the neap tides, when tides are not so strong.

Initially, the Joseph Bonaparte Gulf fishery developed as an alternative to fishing in the Gulf of Carpentaria (GOC) and acted as a kind of “escape valve” for fishing effort in the GOC: in years of poor catches in the GOC, more fishing effort was applied in the JBG. In the early years of the JBG fishery, most effort was concentrated at the end of the year (i.e. October and November). In recent years, however, in addition to being more heavily fished in years of poor catches in the GOC, the JBG stocks are fished much earlier in the season (May or June) by a common subset of boats, regardless of the catches elsewhere in the NPF.

NORMAC is presently considering extending spatial closures in the Gulf of Carpentaria to further protect pre-spawning tiger prawns. This will probably result in fishing effort being diverted from the GOC to the JBG.

Catch rates of red-legged banana prawns (i.e. catch per unit of effort) in the Joseph Bonaparte Gulf, based on uncorrected or nominal effort, have been stable since the start of the fishery. However, our estimates of the adjusted fishing effort, which takes into account changes in effort due to factors such as increased knowledge, the introduction of Global Positioning Systems, etc, indicate that adjusted effort is now only about half of the effort in 1986. This would indicate that the catch rates based on adjusted effort have halved since the early years of the fishery. In addition to the possible concern about catch rates, the fishing industry and NORMAC are concerned about the impact that increases in effort due

to the imposition of new closures in the Gulf of Carpentaria would have on both the long and short term productivity of the red-legged banana prawns in the Joseph Bonaparte Gulf.

Although the red-legged banana prawn has been fished in the Joseph Bonaparte Gulf since the early 1980's, we know little of its biology or population dynamics. Apart from a 12-month study on red-legged banana prawns in the JBG by Northern Territory (NT) Fisheries in 1990, there have not been any studies of this species in Australia. The research by NT Fisheries suggested that growth and mortality rates, important parameters in the calculation of the effects of changes in fishing effort on stocks, could not be precisely estimated by length frequency analysis of commercial catch data. We believed that a well-designed tagging study would significantly improve the reliability of our estimates of growth and mortality of red-legged banana prawns.

A one-year project "The impact of changes in fishing patterns on red-legged banana prawns (*Penaeus indicus*) in Joseph Bonaparte Gulf" FRDC (95/16), during 1996, studied the effect of tags on the red-legged banana prawn and developed a tagged prawn cage-release system for use in the deep and rough waters of JBG. The study showed that tagging did not affect the growth and survival of *P. indicus* under laboratory conditions. This project also documented the changes in fishing patterns in JBG that were mentioned previously in this report and used a per-recruit model (SIMSYS) to estimate yield, value of the catch and egg production for the different seasonal patterns. The model showed that both yield and value can vary by as much as 15% depending on the pattern of fishing effort. However, the results of the model were sensitive to the estimates of growth and mortality that were used, which highlighted the need to obtain better estimates of these parameters (rather than the estimates from the literature and those for *P. merguensis* that were used).

Nursery habitats

In the Gulf of Carpentaria, inshore nursery habitats for juveniles of commercial prawn species have been shown to be critical for the presence of offshore commercial fisheries, for both white banana (*P. merguensis*) and tiger prawn (mainly *P. esculentus* and *P. semisulcatus*) fisheries. These juvenile habitat requirements in the GOC (mangroves and seagrass) have been well documented by CSIRO over several years.

The extent of seagrasses in the Gulf of Carpentaria has been mapped by aerial transects and field sampling. Remote sensing techniques, combined with groundtruthing have also been used to map the mangroves of the Embley River estuary in the northeastern GOC. This baseline information will allow more accurate assessment of the impacts of any future perturbations, both man-made and environmental, which might affect catches in the fisheries. It will also help to ensure that the most important juvenile habitats are adequately protected from future impacts.

In contrast to the white banana prawn (*P. merguensis*) and the tiger prawns, the juvenile habitat requirements of red-legged banana prawns (*P. indicus*) have not been documented in Australia. Overseas research suggests that, like white banana prawns, red-legged banana prawns use mangrove-lined river and creek systems. However, it is not clear what impact the extreme tidal ranges, strong currents, and scouring of rivers and creeks in the Joseph Bonaparte Gulf might have on the distribution of the juvenile prawns. They might be limited to using only a small subset of the available

river systems. The fact that there is not a large fishery for white banana prawns (*P. merguensis*) in the JBG, despite the presence of mangrove-lined rivers, also suggests that there may be some important differences in the characteristics of the nursery habitat in the JBG compared with the Gulf of Carpentaria.

IV NEED

As part of FRDC 95/16, a preliminary model of the fishery for red-legged banana prawns in the Joseph Bonaparte Gulf was developed. However, this model used growth and mortality estimates from other prawn species and from overseas studies on red-legged prawn fisheries, fisheries that operate in different circumstances to the fishery in the JBG. The model evaluated the impacts of changes in the seasonal pattern of fishing effort, as well as changes in the total annual fishing effort in the JBG. The model also helped to evaluate the effects of these changes in effort on both the yield, and the spawning biomass, of red-legged banana prawns. However, the results of the model were sensitive to the values of growth and mortality that were used. A tagging study was necessary to obtain more accurate estimates of growth and mortality for the red-legged banana prawns in the JBG fishery.

The coastal ecosystems of the Joseph Bonaparte Gulf are coming under increased pressure from mining, agricultural and tourism developments. Currently, there is work being undertaken to map the geology underlying the JBG using seismic techniques, as a precursor to possible exploratory gas drilling in inshore JBG. Furthermore, the area of cropland under irrigation in the Ord River Irrigation Area (in the catchment of JBG Rivers) is set to increase three-fold by 2010, as part of Ord Stage II. Similar threats will occur into the future. The location and extent of the juvenile nursery areas needed to be clearly defined to protect them from impacts and to help understand any fluctuations in adult abundance caused by extreme environmental fluctuations.

V BENEFITS

The majority of benefits of this project flow to the Northern Prawn Fishery, an Australian Fisheries Management Authority (AFMA) managed fishery in Northern Australia. The comparison of accuracy of different techniques for estimating the extent of prawn nursery habitats using remotely sensed data is of benefit to fisheries managers and managers responsible for terrestrial biodiversity. The finding that the nursery habitats of red-legged banana prawns are distant from the offshore fishery (and not those habitats closest to it) highlights the potential for terrestrial impacts, far from the fishery to affect the catches in the fishery.

VI FURTHER DEVELOPMENT

Since the red-legged banana prawn resource is not as extensive as previously thought, and given that possible poor catches elsewhere in the Northern Prawn Fishery may cause the fishing pressure on the red-legged banana prawns in the Joseph Bonaparte Gulf to escalate rapidly, the stock may be more vulnerable than past assessments have suggested. We recommend that the effects of fishing on *P. indicus* need to be further evaluated and specifically, whether there is a relationship between recruitment and

spawning stock. As part of this work, the feasibility of developing indices to estimate recruitment and spawning stock needs to be investigated. The exact distribution of adult *P. indicus* and *P. merguensis* in JBG is unknown, as are the annual patterns of recruitment of sub-adults to the JBG fishery. This could be achieved through analysis of catch and effort data from logbooks, combined with the collection of information on the size distribution of prawns throughout the year (from observers on vessels and sampling landings) and some fishery independent sampling.

The work on identifying the nursery habitats for red-legged banana prawns found that they are located in mangrove lined creeks 100 to 240 km to the southeast of the fishery. These distances highlight the need to identify where the effective spawning grounds for *P. indicus* are located, and the processes that enable the larvae and juveniles to move between their spatially separate habitats. It also highlights the need to evaluate the influence of potential changes in land-use in the catchments of the JBG on the fishery, particularly those that affect river flow and mangroves.

VII CONCLUSION

This project has contributed to an understanding of the optimum exploitation rates for the management of the banana prawn fishery in Joseph Bonaparte Gulf by revising per-recruit models and assessing the current fishing patterns for red-legged banana prawns (Chapter 5, 8). The tagging studies have provided robust estimates of growth parameters and estimates of mortality – the first estimates for red-legged banana prawns in the JBG (Chapter 6). These estimates provide a much sounder basis for the stock assessment in Chapter 8 and future assessments.

The project has established simple characters to separate the juveniles of red-legged banana prawns (*P. indicus*) from those of white banana prawns (*P. merguensis*) (Chapter 2). The work has been critical for establishing the broad scale spatial distribution of the juveniles of both banana prawn species: red-legged juveniles are mainly found from the Cambridge Gulf east to the Victoria and Fitzmaurice Rivers; white juveniles are found mainly from Cambridge Gulf, west to Cape Londonderry; and both species are found in the rivers of the western side of Cambridge Gulf. Within their broad distribution in the JBG, juvenile red-legged banana prawns are found in small, mangrove-lined creeks in the estuaries located 100 to 200 km southeast to south of the offshore fishery. This highlights the importance of distant habitats to the fishery and the need to evaluate the influence of changes in land-use that affect river flow and mangroves on the fishery.

The work on estimating the extent (area and linear length of mangroves) showed that in comparison to aerial photos, Landsat TM gave accurate estimates of area but not length of mangroves in the creeks of the JBG. This is mainly due to the differences in resolution of the different techniques (Aerial = 2 m and Landsat = 30m) and the very narrow bands of mangroves (<10 m wide) found in many parts of the JBG. The estimates from the AUSLIG topographic maps were the least accurate of all techniques in the JBG but gave reasonable estimates of area for Weipa, where mangroves form wider bands (about 50 m wide) than in the JBG. It would not be feasible to establish a baseline dataset for the extent of mangroves for the whole of the Northern Prawn Fishery using aerial photographs. However, it may be possible to achieve this using Landsat TM, combined with the use of aerial photos in selected

areas where mangroves are found in narrow bands, or where they are likely to be particularly significant for the fishery (e.g. Weipa, Karumba, JBG).

2. CHAPTER TWO: IDENTIFICATION OF JUVENILE PRAWNS

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Note that the full details of this work have been published in the following paper: Pendrey RC, Loneragan NR, Kenyon RA, Vance DJ (1999). Simple morphometric characters, confirmed by gel electrophoresis, separate small juvenile banana prawns (*Penaeus indicus* and *P. merguensis*). *Marine and Freshwater Research* **50**: 677-680.

INTRODUCTION

The juveniles of red-legged banana prawns *Penaeus indicus* and white banana prawns *P. merguensis* are difficult to distinguish. However, the adults of these two banana prawns can be distinguished on the basis of morphological characters (Chong and Sasekumar 1982, Grey *et al.* 1983). In the estuaries of northern Australia, most juvenile *P. merguensis* are less than 10 mm in carapace length (CL) and have not developed the distinguishing morphological features of the much larger sub-adult prawns. We used gel electrophoresis (e.g. Lavery and Staples 1990) to separate the small juveniles of *P. indicus* from *P. merguensis* and then determined whether it was possible to separate the juveniles by easily measured morphometric characters.

METHODS

MEASUREMENT OF MORPHOLOGICAL CHARACTERS

Collection of adult prawns for identification

Identified sub-adult and adult banana prawns were collected for initial testing of enzyme systems. One hundred and eleven *Penaeus indicus* were collected from trawls in the Joseph Bonaparte Gulf of northern Western Australia in February 1997 (14° S, 128° E) and 117 *P. merguensis* were purchased from beam trawl fishers in the Brisbane River (26° S, 152° E) in February 1998. We identified the adults of *P. indicus* and *P. merguensis* by the presence of a distinct gastro-orbital ridge in *P. indicus* and its absence in *P. merguensis*, and a higher rostral crest for *P. merguensis* (following Grey *et al.* 1983). The mean carapace lengths (± 1 SE) for *P. indicus* were 39.8 ± 0.52 mm and for *P. merguensis*, 18.7 ± 0.37 mm.

Collection of juvenile prawns for identification

A total of 218 unidentified juvenile banana prawns were collected in beam trawls in the rivers of the Joseph Bonaparte Gulf between October and December 1997. Prawns were collected from the eastern Joseph Bonaparte Gulf (14° 50'S, 129° 30'E), Cambridge Gulf of the central JBG (14° 50'S, 128° 5'E), and the western JBG (14° 25'S, 127° 40'E). Juveniles were placed on ice, frozen and transported to the Cleveland Marine Laboratory for gel electrophoresis (using the system established for the adult prawns) and morphological measurements.

Morphometric characters

The following features of the dorsal rostral teeth (Fig. 2.1) were recorded:

- The ratio of the distance from the anterior most dorsal rostral tooth (hereafter referred to as the first tooth) to the tip of the rostrum (L_1): to the distance between the first and second dorsal rostral tooth ($L_{1,2}$). This ratio is denoted as $L_1: L_{1,2}$.
- The position of the first tooth relative to the ventral teeth e.g. between ventral teeth 3 and 4.
- The position of the first tooth in relation to the antennular peduncle (i.e. anterior or posterior to the peduncle), and
- The number of dorsal rostral teeth behind the eye (i.e. the anterior edge of the cornea).

Where possible, we measured the above four characters on all the juvenile prawns before samples from each prawn were run for gel electrophoresis to establish their identity to species. Because of damage to the carapace and rostrum, morphometric measurements were made on 138 of the 218 juvenile prawns, and all four measurements could be made on 95 of these prawns. The results from the gel electrophoresis were used to classify the juvenile prawns as *P. indicus* or *P. merguensis* and mean or modal values were calculated for each of the morphometric characters.

RESULTS AND DISCUSSION

SPECIES SEPARATION BY ELECTROPHORESIS AND MORPHOMETRIC CHARACTERS

Gel electrophoresis, with the enzyme malate dehydrogenase, clearly separated into species, both large and small prawns. Four morphological characters were measured from juvenile prawns (identified using electrophoresis): three of these provided reliable separation into species. The mean ratio of the distance from the anterior most dorsal rostral tooth (first tooth) to the tip of the rostrum (L_1): to the distance between this tooth and the second tooth ($L_{1,2}$) was higher for *P. indicus* (3.16) than *P. merguensis* (1.56). Only 5 *P. indicus* had $L_1: L_{1,2}$ values that overlapped with those of *P. merguensis*, while 6 *P. merguensis* values overlapped with those of *P. indicus*. All juvenile *P. indicus* had the first tooth posterior to the antennular peduncle, while it was anterior for all *P. merguensis* (Table 2.1).

Table 2.1: Summary of morphological measurements of juvenile banana prawns from the Joseph Bonaparte Gulf, identified by gel electrophoresis. L_1 = distance from the anterior most dorsal rostral tooth (termed the first tooth) to the tip of the rostrum; $L_{1,2}$ = distance between the first and second dorsal rostral teeth. $L_1 : L_{1,2}$ = ratio of distances.

Character	Species		<i>n</i> (<i>P. indicus</i> , <i>P.merguensis</i>)
	<i>P. indicus</i>	<i>P. merguensis</i>	
$L_1 : L_{1,2}$	3.16 ± 0.82	1.56 ± 0.084	59, 36
First tooth to ventral teeth	between 2 & 5 mode 3 to 4	Between 2 & 5 mode 3 to 4	59, 36
First tooth to ant. peduncle	posterior	Anterior	59, 36
Dorsal teeth behind eye	5: 4.5% 6: 95.5%	5: 93.9% 6: 6.1%	89, 49
Mean carapace length (mm)	8.2 ± 0.22	5.3 ± 0.27	89, 49
Carapace length range (mm)	3.1 to 16.5	3.4 to 13.1	89, 49

In our study, the modal position of the first tooth was between the 3rd and 4th ventral teeth (Table 2.1) and there was no clear difference in position between species.

The number of dorsal rostral teeth behind the eye was a good character for separating the species in the current study, with over 90% of *P. merguensis* having five teeth in this position (Table 2.1). In contrast, over 90% of *P. indicus* had six teeth behind the eye (Table 2.1). Although similar results were found for *P. merguensis* and *P. indicus* in other studies in Malaysia and India, there was more overlap between species in the number of teeth behind the cornea than found in our study.

The other important white prawn in the south-east Asian region, *P. penicillatus*, is not found in Australian waters (Dall *et al.* 1990), and only separated from *P. merguensis* in Malaysia on the ratio of $L_1 : L_{1,2}$ (Chong and Sasekumar 1982). However, *P. penicillatus* can be separated from *P. merguensis* and *P. indicus* by gel electrophoresis, using the peptidase (glycyl-leucine) enzyme system (S. Lavery, Harvard University, pers. comm.).

The lengths of the dactylus and propodus of the third maxilliped, the presence of setae on the maxilliped of males and the numbers and distribution of chromatophores have

also been used to separate *P. merguensis*, *P. indicus* and *P. penicillatus* (Muthu and Rao 1973, Chong and Sasekumar 1982). However, these characters are more time-consuming to measure than the four rostral characters that we used.

The position of the first tooth in relation to the antennular peduncle and the ratio $L_1:L_{1,2}$ provided good separation of juvenile *P. indicus* and *P. merguensis* in Australia, India and Malaysia. In Malaysia, the ratio of $L_1:L_{1,2}$ remains a consistent feature as the prawns increase in size. Because of damage to the fragile rostral tips of the small juvenile prawns, these two features could not be measured in about 30% of the individuals from Australia. However, the number of rostral teeth behind the anterior margin of the cornea could be counted on more juvenile prawns. When the number of rostral teeth behind the cornea was used in combination with the position of the first tooth, all prawns could be assigned correctly to species. Results from India and Malaysia suggest that the number of teeth behind the cornea is less reliable for larger juvenile prawns and hence care must be taken in using this feature to separate larger juveniles.

CONCLUSIONS

A reliable method of separating the juveniles of these two species using morphometrics was developed and validated by gel electrophoresis. Gel electrophoresis, with the enzyme malate dehydrogenase, clearly separated into species, both large and small prawns. Four morphological characters were measured from juvenile prawns (identified using electrophoresis): three of these provided reliable separation into species. The mean ratio of the distance from the anterior most dorsal rostral tooth (first tooth) to the tip of the rostrum (L_1): to the distance between this tooth and the second tooth ($L_{1,2}$) was higher for *P. indicus* (3.16) than *P. merguensis* (1.56). All juvenile *P. indicus* had the first tooth posterior to the antennular peduncle, while it was anterior for all *P. merguensis*. More than 90% of *P. indicus* had six rostral teeth behind the eye, while over 90% of *P. merguensis* had five teeth behind the eye. Damage to the rostrum prevented measurements of the position of the first tooth in 20 to 30% of juvenile prawns. Combining the measurements of the ratio of $L_1:L_{1,2}$ and the count of the number of rostral teeth behind the eye meant that all prawns could be unambiguously identified.

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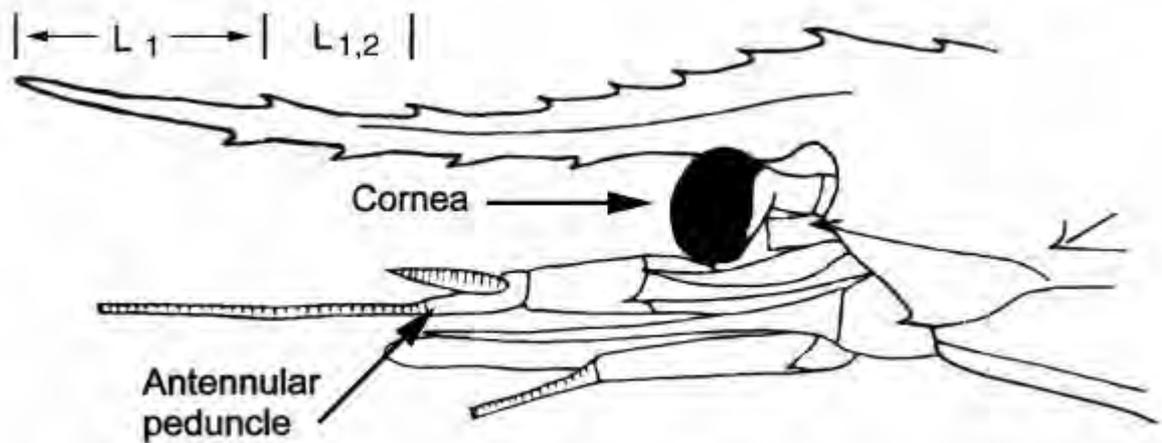


Figure 2.1 Diagram of the morphometric features that were measured in juvenile banana prawns collected from the Joseph Bonaparte Gulf of northern Australia. L_1 = distance from the anterior most dorsal rostral tooth (termed the first tooth) to the tip of the rostrum; $L_{1,2}$ = distance between the first and second dorsal rostral teeth.

3. CHAPTER THREE: DISTRIBUTION AND ABUNDANCE OF JUVENILE PRAWNS

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INTRODUCTION

In northern Australia, *Penaeus indicus* are found in a restricted geographic range – the Kimberley to Arnhem Land coasts, and the east coast of Cape York (Grey *et al.* 1983). *Penaeus indicus* is fished commercially in the western Joseph Bonaparte Gulf (Fig. 3.14) and north of Melville Island and the Coburg Peninsula (11° S, 132° E); the only Australian locations where they are commercially abundant (Somers 1994). In the JBG, *Penaeus merguensis* also is fished commercially, from the gulf's north-western extremity westward to Napier Broome Bay (14.0° S, 126.5° E). In the JBG banana prawn fishery, the main species caught is *P. indicus*, and the geographic distributions of the *P. indicus* and *P. merguensis* fisheries overlap very little in this region (Somers 1994).

Penaeus merguensis (the white banana prawn) is found over a wide area of northern Australia, from south of Moreton Bay (27.5° S, 153.3° E) on the east coast, to Shark Bay (25.5° S, 113.5° E) on the west coast (Grey *et al.* 1983). *Penaeus merguensis* is fished commercially throughout its range (Somers 1994) in locations offshore to their estuarine mangrove nursery-habitats (Staples *et al.* 1985). In Australia, it has been studied intensively for over 20 years (e.g. Crocos and Kerr 1983; Vance *et al.* 1985; Staples and Vance 1986; Vance *et al.* 1998). The life history, juvenile habitats and population biology of the species are well understood (Hill 1994). Postlarval *P. merguensis* recruit to mangrove rivers and estuaries from October to April at about 2 mm carapace length (CL), while those that recruit during October to December contribute most to juvenile populations and to the offshore fishery (Staples and Vance 1985, Vance *et al.* 1998). Benthic juvenile *P. merguensis* reside in mangrove habitats for up to 3 months, prior to emigration during December to March at a mean size of about 7-14 mm CL (Staples and Vance 1986, Vance *et al.* 1998).

In contrast to *P. merguensis*, little is known of the distribution of juvenile *P. indicus* and their population biology in Australia (Somers 1994). Although the adults of both banana prawn species are found in close proximity in the JBG, prior to this study, the broad-scale distribution patterns of their juveniles in inshore nursery habitats were unknown.

Penaeus indicus is fished throughout the Indo-West Pacific coastal waters from southern Africa and Madagascar to South-East Asia (Barus and Mahiswara 1994; Fouda 1995; Laroche and Siaviri 1995; Fennessy and Groeneveld 1997). Throughout its range, juvenile *P. indicus* are found on muddy sediments in creeks and rivers among mangrove forests (Subramanian 1985; Mohan and Siddeek 1994a). Sub-adult and adult *P. indicus* are found in coastal bays and offshore waters to a depth of about 50-80 m (Mohan and Siddeek 1994b). The Australian distribution of *P. indicus* represents the southern-most limit of its distribution in the western Pacific (Dall *et al.* 1990).

The objectives of the work on juvenile *P. indicus* were to:-

- (i) describe the broad-scale distribution patterns of postlarval and juvenile *P. indicus* in the Joseph Bonaparte Gulf,
- (ii) describe the fine scale patterns of distribution of juvenile *P. indicus* to test whether they differ between gutters, small creeks, rivers and mid-river habitats (channels and banks),
- (iii) compare the broad- and fine-scale patterns of distribution of *P. indicus* with those of *P. merguensis* in the same region.

METHODS

STUDY SITES

1997

During October, November and December 1997, we trawled estuarine habitats between Cape Londonderry (13.750° S, 126.960° E), Western Australia, and Pearce Point (14.423° S, 129.355° E), Northern Territory, in the Joseph Bonaparte Gulf (JBG) region of north west Australia to determine the broad-scale distribution of juvenile *P. indicus* (Fig. 3.1). We selected sites in the estuaries, up-river, and in open-coast locations. In the field, a Global Positioning System (GPS) receiver was used to guide us to the sites and verify our location. The tidal amplitude in the region is large (up to 7m) and we sampled during the neap tides (3-5m).

As the juvenile habitats of *P. indicus* in Australia were unknown, we selected sites where juvenile *P. indicus* were likely to inhabit as well as sites where we usually would not expect to find juvenile banana prawns. We sampled many of the habitat types in the JBG coastal zone; mangrove-lined banks in rivers and creeks, sandbanks and mudbanks, mangrove-lined beaches and sand beaches. At each site the habitats were classified descriptively. Trawls were undertaken from October to December as the timing of recruitment to the offshore fishery suggested that juvenile *P. indicus* would be abundant then, and these months correspond to annual periods of high catches of juvenile *P. merguensis* in the Embley and Norman Rivers of the Gulf of Carpentaria (Vance *et al.* 1998).

1998

In October to December 1998, we sampled three of the rivers that were sampled in 1997 to investigate the finer scale use of different microhabitats by *P. indicus*. This sampling also allowed comparisons of distribution and abundance to be made between years (1997 vs. 1998) for these three rivers. The rivers were chosen from regions in the Joseph Bonaparte Gulf with different proportions of juvenile banana prawns in the catch in 1997: Forsyth Creek in the Eastern Joseph Bonaparte Gulf, where *P. indicus* was the main species; the Lyne River in the Cambridge Gulf where both *P. indicus* and *P. merguensis* are found in about equal abundance; and the

Berkeley River in the western Joseph Bonaparte Gulf where *P. merguensis* was the main species. Each river was sampled in October/November and again in November/December of 1998.

TRAWLS

We trawled for postlarval and juvenile *P. indicus* using a 1.0 x 0.5 m beam trawl with 2 mm body mesh and a 1 mm mesh codend. Our trawls were 100 m long (3 min duration), however, in some cases, we carried out short trawls (~10 m long) in side creeks that were almost empty of water at low tide.

At each site, we recorded latitude, longitude, time, duration and length of trawl, salinity, temperature, tide phase and moon phase. The degree of turbidity of the water was measured using two methods; measuring the light penetration of the water using a secchi disc, and a qualitative categorisation of the water turbidity in four categories – clear, slightly muddy, moderately muddy, and very muddy. The catch was immediately iced, then frozen and later taken to the laboratory for sorting. Individuals of *P. indicus* and *P. merguensis* were identified using the techniques developed in Chapter 2 (see also Pendrey *et al.* 1999).

Most of the trawls (202 out of 229) that were undertaken in 1997 were made to determine the broad-scale distribution of *P. indicus* among nursery habitats in JBG (Table 3.1). Trawls were undertaken, mainly during the day, on the last third of the ebb tide when *P. merguensis* is most catchable in beam trawls (Vance and Staples, 1992). To confirm that *P. indicus* is more catchable at low tide, and to investigate differences in catch between habitats, at four selected locations in Cambridge Gulf, we trawled in a range of contrasting habitat types on the last of the ebb tide (low tide) and on the last of the flood tide (high tide) (27 trawls, Table 3.1). We trawled sandbank and channel habitats at the same time as the mud/mangrove river and creek habitats; these habitats were within about 400 m of each other. Some of the trawls made to determine distribution were also used to investigate catchability and habitat use.

In 1998, differences in catch between habitats were examined in each of the three rivers by beam trawling (164 trawls) around the time of low and high tides during the day, and at low tide and high tide during the night (Table 3.1). To look at differences in broad-scale distribution between years, on two occasions we trawled the same sites in each river at the same tide-phase and light regime as we trawled during 1997 (85 trawls, Table 3.1). Some of the trawls made to investigate finer scale habitat use were also used to confirm the distribution of *P. indicus*, as was found in 1997.

Table 3.1 The numbers of trawls undertaken in different classes of waterbody during three cruises in 1997 and two cruises in 1998. The trawls undertaken to determine the broad-scale distribution pattern of *Penaeus indicus* (“distribution” trawls) and those undertaken to determine their microhabitat preference (“habitat” trawls) are listed separately. (MS = mainstream, CH = mid-river channel, MB = mid-river bank, CK = creek, SC = sub-creek, GT = gutter, BB = beach or bay.)

Type of trawl and month of sampling	Waterbody							Total nos trawls
	MS	CH	MB	CK	SC	GT	BB	
“Distribution”								
trawls								
October 1997	29	0	0	11	18	6	0	64
November 1997	32	1	0	8	14	1	1	57
December 1997	20	0	2	17	9	5	28	81
October 1998	24	0	0	4	6	9	0	43
November 1998	24	0	0	4	6	8	0	42
Total	129	1	2	44	53	29	29	287
“Habitat” trawls								
November 1997	6	5	4	3	3	6	0	27
October 1998	24	12	12	8	12	12	0	80
November 1998	24	12	12	8	12	16	0	84
Total	54	29	28	19	27	34	0	191

ESTIMATION OF PRAWN HABITAT

Distribution of prawn habitats

We used ESRI ARCVIEW 3.1 GIS software to estimate the extent of coastal habitat types from the AUSLIG Topo250k data (AUSLIG, 1995) for the JBG region (see also Chapter 3). AUSLIG data are current to 1990 and accurate to 300m, with 90% of the data being accurate to 100m. Our aims were to estimate:-

- (i) the total area of each habitat type (as categorised by the AUSLIG data) in the JBG region, and in individual river systems,
- (ii) the linear extent of each habitat type along the banks of each river system.

The JBG was divided into four major regions and 12 sub-regions containing groups of rivers and creeks (Table 3.2). The major regions were: Eastern Joseph Bonaparte Gulf; Southern Joseph Bonaparte Gulf; Cambridge Gulf; and Western Joseph Bonaparte Gulf.

Three geographic land-types may contribute directly to prawn habitat in the Joseph Bonaparte Gulf (Table 3.2). They are categorised by AUSLIG as:-

1. **Intertidal tropical mangrove forest:** a dense growth of trees, some species of which have distinctive prop roots, which grow to a uniform height on muddy foreshore flats, and along tidal watercourses.
2. **Saline coastal flat:** A nearly level tract of land between mean high water and the extent of the highest astronomical tide.
3. **Land subject to inundation:** Low-lying land usually adjacent to watercourse or waterbody features, which is regularly covered with flood water for short periods either annually or during at least one year in ten.

We calculated the area and linear extent of these three potential prawn habitat-types along the banks of river systems in each region or sub-region of the JBG. Each habitat polygon in the coverage was defined as being within a region or sub-region and some were allocated to individual river systems. The criterion for belonging to a particular river system was proximity to the river or connected waterways. Where one polygon lay between 2 rivers, that polygon was split, and each section allotted to the nearest river.

Accuracy of the estimation of prawn habitats

Estimates of the accuracy of the AUSLIG data were made by comparing it with remotely sensed data from other techniques (see Chapter 4 - Estimating the extent of juvenile prawn habitats in JBG).

Table 3.2 The area and linear extent of dominant coastal habitats in each of four regions and 12 sub-regions (river-systems) in the Joseph Bonaparte Gulf

Habitat	Mangrove		Saline Coastal Flat		Land Subject to Inundation	
	Area (km ²)	Linear (km)	Area (km ²)	Linear (km)	Area (km ²)	Linear (km)
Region and River System						
Eastern Joseph Bonaparte Gulf						
Moon River	118	234	380	89	149	0
Fitzmaurice River	76	211	367	115	65	1
Victoria River	66	125	501	120	133	13
Keep River	87	165	587	271	505	12
Total Eastern JBG	347	735	1835	595	852	26
Total Southern JBG	19	44	829	198	53	0
Cambridge Gulf						
Delta region	83	212	401	421	14	0
Ord River	41	101	540	189	260	38
West Cambridge	32	143	779	327	26	0
Lyne River	5	28	42	66	0	0
Total Cambridge Gulf	161	484	1762	1003	300	38
Western Joseph Bonaparte Gulf						
Berkeley River	1	5	3	9	0	0
Coastal western JBG	16	53	26	30	2	0
King George River	2	16	0	0	0	0
Total Western JBG	19	74	29	39	2	0
Total JBG	546	1337	4455	1835	1207	64

ANALYSIS OF PRAWN DISTRIBUTION

We used two general linear models to look at factors affecting the distribution of *P. indicus* in JBG. The only data modelled were those data from the 229 trawls made in 1997. The first model considered the proportion of *P. indicus* juveniles in combined *P. indicus* and *P. merguensis* trawl samples taken in JBG as a function of external determining variables. These variables included location, temperature, salinity, turbidity, climatic conditions and various other site and weather variables. We also used some parameters as proxies for environmental parameters.

The second model considered the total number of *P. indicus* in a trawl and the probability of finding prawns in a trawl at all as a function of these environmental and site variables. Of the 229 trawls made, only 162 had a catch of juvenile prawns. Thus, we used a two-phase approach, estimating the probability of finding prawns first, and estimating the numbers of prawns, given that there were some, second.

A full explanation and validation of the statistics used for both of these models is presented in Appendix One of this chapter.

Model One – proportion of prawns caught

The sampling unit is the trawl and the response will take the form of a ratio:

$$P = \frac{\text{Number of } P. \textit{ indicus} \textit{ juveniles}}{\text{Total number of Banana prawn juveniles in the trawl}} = \frac{N}{T}$$

Our first aim is to model the behaviour of the proportions, P , as a function of the determining variables. For this purpose we will condition on the total number of juveniles, T . Rather than make an explicit distributional assumption, our analysis will be based on a quasi-likelihood generalised linear model (see McCullagh and Nelder 1989) with the following properties:

- $\log \frac{m}{1-m} = b_0 + s_1(x_1) + L + s_p(x_p)$, where x_1, x_2, \dots, x_p are the determining variables and s_1, s_2, \dots, s_p are flexible smooth functions for which we choose a spline family. This is usually called a logistic link function.
- $\text{Var}[P] = \frac{m(1-m)}{T/f}$, where T is the total number of juveniles and f is the scale parameter.

This guarantees that if the true proportion is near 0 or 1 then the variance of the sample proportion is low. Also, the larger the total number of juveniles in the sample the more accurate is the sample proportion as an estimate of the true proportion.

Model Two – density of prawns caught

Data

The high number of trawls that caught no prawns, together with some trawls that caught over 200 prawns (1280 maximum) suggested a two-phase approach. Firstly, estimate the probability of finding *any* prawns in the trawl, and later estimate the numbers of prawns found, given that there were some.

Logistic regression models for presence of any prawns

A natural tool to use to estimate the probability of finding any prawns under the conditions existing in the survey is logistic regression. If p is the probability of finding any prawns in a shot, logistic regressions model the relationship between p and the determining variables as:

$$\log \frac{p}{1-p} = b_0 + b_1 x_1 + L + b_k x_k$$

where the b_j s are regression coefficients and the x_j s are the determining variables. We will generally use spline bases to allow a flexible contribution from each of the determining variables, which amounts to using a whole group of linear terms for one genuine predictor variable and rating the term not by coefficients but by a plot of the contribution of the whole composite term to the logistic transform of the probability. It is therefore more natural to think of the model as having the form:

$$\log \frac{p}{1-p} = b_0 + S_1(x_1) + L + S_k(x_k)$$

where the $S_j(x)$ terms are called the *partial contributions* to the logistic transform.

The determining variables we considered for this model are as follows:

- Temperature,
- Salinity (with a few sporadic values less than 29 promoted to 29 to guard against undue influence of outlying points in the determining variables),
 - Pelite (as a percentage of the sediment sample),
 - Cloud cover,
 - Secchi depth,
 - Sediment (a categorical variable with three levels: mud (152 stations), intermediate (33 stations) and sand (44 stations)),
 - Water Type (a categorical variable with three levels: Coastal (29 stations), Creek (100 stations) and River (100 stations)),
 - Salt Flat (a categorical variable with two levels: No (115 stations) and Yes (114 stations)).
- Distance travelled by the trawl itself.
- Location along a Northwest-Southeast axis as a surrogate for other unmeasured determining variables (as in companion paper on composition).

The initial model used natural splines for continuous variables with 4 degrees of freedom (except for Cloud which had too few distinct values and so the spline term had three degrees of freedom) and separate constants for each level of the categorical variables.

Presence of *P. indicus* and *P. merguensis* in the trawl-catches that contain prawns

The data set has 129 stations where *P. indicus* were caught and 100 where the species was not. We can repeat the above analysis checking for the presence or otherwise of *P. indicus* only. Similarly, we can repeat the analysis checking for the presence of *P. merguensis* only. The data set for *P. merguensis* has 107 stations where the species was caught and 122 where it was not.

Density of prawns caught

In this section we attempt to explore by standard modelling techniques the total number of prawns caught per metre of trawl distance, either of *P. merguensis* or *P. indicus*, separately. We use two different modelling techniques, namely a generalised linear model with a quasi-likelihood error structure, log link and variance proportional to the mean and secondly a tree-based model that seeks to find the major drivers of prawn density using recursive partitioning of the data.

Density of *P. indicus* and *P. merguensis* using a parametric model

We will consider a quasi-likelihood generalised linear model with log link and variance function proportional to the mean. The response will be

$$\frac{\text{No. of } P. \text{ indicus}}{\text{Distance travelled in the trawl}}$$

Under some optimistic assumptions this variable could be approximately proportional to a Poisson random variable, suggesting a variance proportional to the mean. Our study of *P. merguensis* density will parallel the analysis for *P. indicus*.

Density of *P. indicus* and *P. merguensis* using a tree-based model

A simpler approach to predicting density is to use the idea of recursively partitioning the data and producing a binary tree predictive device of the same style as botanical keys. The data is partitioned into increasingly homogeneous groups with respect to density by a binary splitting on the most effective determining variable, at the most effective place, at each recursive stage. For more details see, for example, Venables and Ripley (1999, Chapter 10), and references therein. After an initial tree is formed cross validation techniques are used to see the degree of complexity in the tree is warranted. The tree is then optimally pruned to the degree of complexity suggested by the cross validation so that it is neither too simple (which would result in seriously biased predictions) or too complex (which would result in the errors in the training set being reproduced in the predictions).

RESULTS

THE PHYSICAL ENVIRONMENT OF JOSEPH BONAPARTE GULF

The water temperature in the coastal areas of the Joseph Bonaparte Gulf ranged from 26.8-34.2°C depending on time of day. The range in water temperatures was similar in the different regions of the JBG and Cambridge Gulf. The salinity in the JBG ranged from 30 to 36 among the rivers in all of the regions, except for the Ord River in the Cambridge Gulf region where at some sites salinities were to <1. The low salinity in the Ord River is due to freshwater flows from the release of irrigation water from the Kununurra Diversion Dam throughout the year.

The turbidity of the rivers in the JBG varies much more with region than either temperature or salinity varies. In most of the eastern JBG and Cambridge Gulf, turbidity is very high (secchi depths < 0.2 m) due to extremely high sediment loads in the riverine water column. The turbidity was lower at a few sites with an oceanic influence. In contrast, turbidity in the western JBG is lower, with the secchi depths ranging from 0.2-4.5 m. The riverine waters in this region do not have such high sediment loads as those in the eastern JBG. Turbidity in the Lyne River, (near the seaward opening of Cambridge Gulf), was intermediate between that of the eastern and western regions of the JBG, with secchi depths ranging from 0.2 to 1.6 m. This river was less turbid than areas in the eastern and the upper Cambridge Gulf, where secchi depths of about 0.1 m were recorded.

HABITATS IN COASTAL JOSEPH BONAPARTE GULF

The largest area and linear extent of mangrove forests in the JBG are found in the extensive river systems of the eastern JBG (347 km² and 735 km, respectively; Table 3.2). The rivers in this region are large with extensive mud/mangrove habitats in the lower and middle reaches. The Cambridge Gulf also has extensive mangrove forests (161 km² in area and 484 km in linear extent), with a particularly large area found in the north-east (Table 3.2). The area and linear extent of mangroves in the western JBG was much lower than either of the above regions. The river and creek systems in the western JBG are shorter than those in the east or Cambridge Gulf, often with sandy substrates and surrounded by rocky escarpments. The mangroves in these areas occur in narrow bands along the river edges, rather than in extensive forests. In this region and the southern JBG combined, the total area of mangroves is 38 km² and their linear extent is 118 km (Table 3.2).

In the eastern JBG, Cambridge Gulf and southern JBG, each river system has an extensive area and linear extent of saline coastal flats behind the fringing mangroves and stretching many kilometres inland to higher ground (Table 3.2). In the western JBG, rocky escarpments and sand dunes restrict the area and linear extent of saline coastal flat in this region to the lower reaches of the rivers and creeks (28 km² and 39 km, respectively). The distribution of “land subject to inundation” between the river systems is similar to that of saline coastal flats (Table 3.2).

GEOGRAPHIC RANGE OF SAMPLE SITES

In 1997, we caught an estimated 43,918 postlarval banana prawns, 6,650 juvenile *P. indicus* and 7,189 juvenile *P. merguensis* in 202 trawls made at 185 sites in the Joseph Bonaparte and Cambridge Gulfs; ranging from an un-named creek east of Pearce Point (14.462° S, 129.475° E) to a bay south east of Cape Londonderry (13.955° S, 127.118° E) (Fig. 3.1). These sites were spread over about 500 km of coastline.

DISTRIBUTION OF *P. INDICUS* AND *P. MERGUIENSIS* IN THE RIVERS OF COASTAL JOSEPH BONAPARTE GULF

In 1997, postlarval banana prawns were abundant in the Cambridge Gulf (up to 1,500 postlarvae·100m⁻²) and the rivers in the western JBG (Fig. 3.2a). They were not abundant in the eastern JBG (apart from the Keep River) or the southern JBG. However, only 3 trawls could be completed in the southern JBG, as it was difficult to access this region. Juvenile banana prawns were abundant in the eastern JBG, Cambridge Gulf and western JBG (Fig. 3.2b). No juvenile prawns were caught in the three trawls made in the southern JBG.

In the eastern JBG and Cambridge Gulf, over 96% and 73% (respectively) of juvenile banana prawns were *P. indicus* (Fig. 3.3) and their densities were greater than in the western JBG (Fig. 3.2b). The catch rates of *P. indicus* were higher in the Fitzmaurice (58.1±17.3 prawns·100m⁻²), Victoria (116.9±61.8 prawns·100m⁻²) and Keep (323.4±233.4 prawns·100m⁻²) Rivers of the eastern JBG, than in the Berkeley (34.8±27.4 prawns·100m⁻²) and King George Rivers (0.2±0.2 prawns·100m⁻²) and the many coastal creeks (13.2±10.7 prawns·100m⁻²) of the western JBG (Fig. 3.2b).

Conversely, in the western JBG over 93% of the juvenile banana prawns were *P. merguensis* (Fig. 3.3). Their catch rates were greater (e.g. 357.6±91.4 prawns·100m⁻² in the Berkeley River; 332.7±180.9 prawns·100m⁻² in western JBG creeks) than those in the eastern JBG and most of Cambridge Gulf (<16.6 prawns·100m⁻²) (Fig. 3.2b).

In the Cambridge Gulf, *P. indicus* was the main species in the “Cambridge Delta” near Cape Domett (43.3±18.4 100m⁻²) and in the rivers of the southern and western Cambridge Gulf (146.3±64.2 100m⁻²). The Lyne River of the north-western Cambridge Gulf was the only location where the catch rates of both species were high and similar in magnitude (*P. indicus*, 314.1±272.0 prawns·100m⁻² and *P. merguensis*, 332.6±233.8 prawns·100m⁻²). In the east-arm of Cambridge Gulf and the Ord River neither species was abundant (Fig. 3.2b).

In the southern JBG, only 23 postlarval banana prawns were caught from the three trawls. Most of these were caught on sand beaches. Because of the low numbers of trawls and the small catches, these sites were excluded from further analyses.

In 1997 and 1998, three rivers were sampled in both years and the proportions of *P. indicus* and *P. merguensis* in the catch was similar (Fig. 3.4). Among the rivers, the Forsyth Creek in eastern JBG had > 98% *P. indicus* in both years; the Berkeley River in western JBG had <10% *P. indicus* in both years; and the Lyne River in Cambridge

Gulf had a mixture of both species (49% *P. indicus* in 1997 and 30% *P. indicus* in 1998). The proportion of *P. indicus* in the Lyne River showed some variation, however, in each year the river was characterised by a mix of both banana prawns, rather than predominantly one or the other. Although we did not sample as many sites in JBG in 1998 as we had in 1997, the proportion of *P. indicus* and *P. merguensis* in the catch from the three regions of the JBG confirms that the distribution of the two species was similar in both years.

Size of *P. indicus* and *P. merguensis* in the rivers of coastal Joseph Bonaparte Gulf

In 1997, with the exception of the Victoria River, over 85% of juvenile *P. indicus* within all of the rivers of the JBG were < 9 mm CL. In the Victoria River, over 70% of juvenile *P. indicus* were < 9 mm CL, while about 25% were in the 10-14 mm CL size range. Many of these larger prawns were caught in the lower reaches of the main river channel.

The size distribution of juvenile *P. merguensis* was more variable than that of *P. indicus*. Within many of the river systems of the JBG (Fitzmaurice, Berkeley and King George Rivers, rivers and creeks of Cambridge Gulf and west JBG), a high proportion of juvenile *P. merguensis* (over 90%) were < 9 mm CL. However, only about 65% of juvenile *P. merguensis* in the Victoria River in eastern JBG, and about 74% of juvenile *P. merguensis* in the Lyne River in Cambridge Gulf, were < 9 mm CL.

FACTORS AFFECTING THE DISTRIBUTION OF *P. INDICUS* IN JOSEPH BONAPARTE GULF

Model One – a generalised linear model for the proportion of *P. indicus* in the total prawn catch

Figure 3.5a shows the actual proportions of *P. indicus* observed the 162 stations (trawls) where at least some banana prawns were caught. The proportions presented in this figure are based on widely different numbers of animals and so have variable accuracy. Nevertheless it is clear that the stations with high proportions of *P. indicus* are concentrated near the mouths of the larger rivers and in the southwest of the JBG.

Of the available determining variables, we considered a reduced set as potential predictors: *Temperature*, *Salinity*, *Secchi* depth, *Pelite* (mud) in the substrate, *Mangroves* (presence or absence), and two location variables. The two location variables were not latitude and longitude but a coordinate system tilted at 45° so one axis, *NWSE*, runs from south-east to north-west and the other, *SWNE*, runs from south-west to north-east. Since the orientation of the major coastal system for our purposes is along the *NWSE* axis, this choice of system minimises the necessity for inclusion of interacting terms. We anticipate that the orthogonal axis, *SWNE*, will play little part in the model.

It is clear from Table 3.3 that the term in *NWSE* was necessary, although from a biological point-of-view it is not a very satisfactory explanatory variable as it corresponds to no topographic or physical feature of the landscape. At best we can assume that it is a surrogate for other, unmeasured explanatory variables that would

be more generally applicable. We included it in our model, however, to check if other explanatory variables have additional explanatory power.

Salinity has been modified for modelling purposes. Two stations were far enough inland for the salinity to be very low. These greatly influence the modelling process and distort the graphical representation of the component. In the fitted model if the salinity is less than 29 units we replace it by 29. At low salinities the proportion of *P. indicus* is essentially zero in any case and this modification does not materially affect the model in any other way.

The proportion of *P. indicus* in the catch increases as the location moves from NW to SE. This is the dominant effect (Table 3.3). Possibly *P. indicus* has a preferred temperature range (about 30-32 °C), but the effect is smaller. There may be a preferred salinity range, with less saline water (<32) preferred. The contribution of secchi depth in explaining the distribution of *P. indicus* is only barely significant, though it shows they prefer more turbid water.

Table 3.3 Significance of terms included in model one

Component	Degrees of freedom	F statistic	P value
$s_4(NWSE)$	4, 145	36.733	0.000
$s_4(\text{Temperature})$	4, 145	3.590	0.008
$s_4(\text{Salinity})$	4, 145	4.063	0.004
$s_4(\text{Secchi})$	4, 145	2.291	0.062

We can gain some idea of how well the model is accounting for the observed proportions by comparing a similar plot to Figure 3.5a using the proportions that were estimated by the model, as shown in Figure 3.5b.

There is a clear separation of regions with very low proportions of *P. indicus* from those where their proportion is very high, but the fit of the model is possibly not good enough apart from some interpretative purposes. Accurate prediction seems not to be possible. Note, also, that these estimates are based on observed proportions based on numbers of individuals that differ very widely. This difference in accuracy makes interpretation difficult.

We investigated possible explanations for feature variables for which the *NWSE* variable may be a surrogate. A plot of secchi depth against the coordinate in the *NWSE* axis clearly shows that the SE corner of the JBG has a much lower secchi depth than the more NE parts (Appendix One). Importantly, it is *consistently* low. The main feature of the plot, though, is the large difference in variance along the line. If the data is smoothed in two directions using both latitude and longitude the smooth curve shown in this diagram is very little different. This suggests that the *NWSE* axis is a good surrogate for the “consistent mean turbidity” in the area. In the SE corner, not only is the secchi depth low (and hence turbidity high), but it is consistently low in all neighbouring regions. Outside the SE corner there are large variations in turbidity. This high variance in the predictor in parts of the range may well explain

why it does not act as well as the NWSE predictor, especially if high spatial variation is also accompanied by high temporal variation. *Penaeus indicus* may require consistently high turbidity, not just temporary high turbidity.

Model Two - a logistic regression model for the presence of any prawns in trawls

Pruning the model by maximising the Akaike Information Criterion (AIC) led to a reduced variables regression retaining only *Salinity*, *Cloud*, *Sediment* and *Pelite*. The significance of each of these terms is shown in Table 3.4.

Table 3.4 Contributions of each remaining term to the pruned logistic regression model

Term	df	Deviance	p-value
<i>ns(max(Salinity, 29),4)</i>	4	25.90538	0.00003
<i>ns(Cloud,3)</i>	3	12.28874	0.00646
<i>Sediment</i>	2	32.46126	0.00000
<i>ns(Secchi,4)</i>	4	21.88625	0.00021

The four partial contributions to the regression model suggest that the animals are most likely to be found in turbid water (low secchi depth) with muddy sediments and high salinity on a cloudy day. However, the standard error lines on the graphs warn that the picture is not strikingly clear for much of the range.

Presence of *P. indicus*

When we investigate the presence of *P. indicus* in trawls that caught either species of banana pawn and use the same suite of candidate predictors, more remain as significant contributors to the model. Table 3.5 shows the terms in the final model. Note that the first term, a spline term in the NW-SE axis location, is a surrogate for unmeasured variables that they themselves are progressively distributed along this axis. The interesting point to notice is that the remaining terms are all significant *separately* and *in addition* to this location term, suggesting that they have some biological significance.

Table 3.5 Remaining contributions to the model predicting the presence of *P. indicus*

Term	df	Deviance	p-value
<i>ns(NW-SE, 6)</i>	6	18.1337	0.0059
<i>ns(Temp, 4)</i>	4	13.8309	0.0079
<i>ns(Cloud, 3)</i>	3	10.4028	0.0154
<i>ns(Saln29, 4)</i>	4	18.2579	0.0011
<i>ns(Secchi, 4)</i>	4	14.6427	0.0055
<i>Sediment</i>	2	28.9737	0.0000

Figure 3.6 shows the partial contributions of each variable to the fitted model. *Penaeus indicus* are more abundant in the southeast of the study area, in turbid waters on muddy sediments in small water-bodies, such as creeks.

Presence of *P. merguensis*

A similar analysis to assess how the probability of finding *P. merguensis* (in trawls that contain banana prawns) varies with predictor variables reveals a simpler model with a stronger dependence on the NW-SE location variable. The terms remaining in the pruned model are shown in Table 3.6.

Table 3.6 Significant terms in the model for predicting presence of *P. merguensis*

Term	df	Deviance	Pr(Chi)
<i>ns(NW-SE, 6)</i>	6	26.3378	0.0002
<i>ns(Secchi, 4)</i>	4	13.8510	0.0078
<i>Sediment</i>	2	10.9978	0.0041
<i>Water Type</i>	2	6.4482	0.0398

The terms themselves are shown graphically in Figure 3.7. The abundance of *P. merguensis* is greater in the northwest of the study area and they too are found in turbid waters, on muddy sediments in creeks.

The diagrams in Figure 3.8 (a) and (b) show the stations arranged in groups so that the predicted probability of finding *P. indicus* or *P. merguensis*, respectively, is steadily increasing. This gives some indication that, for *P. indicus*, the probability is not dominated by the NW-SE location variable, while of *P. merguensis*, there is a stronger dependence on the NW-SE variable.

Density of prawns caught

Density of *P. indicus* and *P. merguensis* using a parametric model

Using the same suite of variables as possible predictors that we used for *P. indicus* in the previous case (i.e. predicting the probability of finding the species), the terms shown in Table 3.7 appear to carry useful information.

Table 3.7 Significance of terms in a quasi-likelihood GLM for the number of *P. indicus*

Term	df	Deviance	F Value	Significance
<i>ns(NW-SE, 4)</i>	4	154.6478	6.7587	0.0000
<i>ns(Secchi, 4)</i>	4	238.3981	10.4189	0.0000
<i>ns(Cloud, 3)</i>	3	74.6338	4.3491	0.0053
<i>Water Type</i>	2	351.1422	30.6926	0.0000

As with many quasi-likelihood models the significance of each term has to be treated with some caution. There seems little doubt that these terms do have some predictive capacity in this context, but it is not always clear how this is achieved. About the only really clear message is that the density of *P. indicus* in the creeks is higher than in either the river or coastal regions. Graphical representations of the partial contributions of these terms to the linear predictor are given in Figure 3.9. However, the capacity of the model to predict with any accuracy is quite limited. There is some ability for the model to select the trawls that will have the larger density but accurate prediction seems not to be possible.

A quasi-likelihood parametric model for *P. merguensis* suggests a more complex picture than that for *P. indicus*, but with a greater reliance on the NW-SE location variable surrogate (there are more *P. merguensis* in the northwest). The terms remaining in the parsimonious model and their significance are shown in Table 3.8. Similar qualifications apply to the significance column in this case as applied for the previous one. Nevertheless it seems clear that these terms do have some predictive capacity for the distribution of density. Graphical representations of the terms are shown in Figure 3.10.

Table 3.8 Terms in the predictive model for density of *P. merguensis* and their significance

Term	df	Deviance	F-Value	Significance
<i>ns(Secchi,4)</i>	4	29.4738	4.0210	0.0037
<i>ns(Temp,4)</i>	4	25.5776	3.4895	0.0088
<i>Sediment</i>	2	13.3564	3.6444	0.0278
<i>Water Type</i>	2	42.5568	11.6118	0.0000
<i>ns(Saln29,4)</i>	4	35.4971	4.8428	0.0009
<i>ns(NW-SE,4)</i>	4	242.0877	33.0273	0.0000

Density of *P. indicus* and *P. merguensis* using a tree-based model

The standard procedure applied for *P. indicus* to the same response variable yields a tree of 5 or 6 terminal nodes. We have selected the one with 5 terminal nodes and the diagram is shown in Figure 3.11.

Note that, for *P. indicus*, the same four variables are chosen as in the parametric model. The first split is on water type, with the river and coastal zone trawls going to the left and the creeks to the right to be further subdivided. The creek trawls are then subdivided on secchi depth and each group further subdivided on a separate variable.

Again the predictive capacity of this model is not great, but it does suggest that these variables at least have some interpretive value.

The same tree construction and pruning process for *P. merguensis* suggests that it is somewhat problematical whether or not the tree model idea works. The tree of 4 terminal nodes shown in Figure 3.12 must therefore remain somewhat speculative. Nevertheless it does select from the main variables suggested by the parametric model and in roughly the same order. The heights of the vertical bars in these diagrams are

proportional to the effectiveness of the splits in reducing the residual sums of squares. In this case, it is interesting to note that the most effective split in this sense is on cloud cover, but only for the creek trawls in the north-western part of the sample range.

ABUNDANCE OF *P. INDICUS* AND *P. MERGUIENSIS* IN DIFFERENT MICROHABITATS IN COASTAL JOSEPH BONAPARTE GULF

The abundance of *P. indicus* varied between sites at the same location (i.e. between different water bodies, e.g. a creek branching off a river) and between different locations. In creeks and rivers in close proximity, the abundance of prawns varied from less than 10 prawns 100 m⁻² to over 1,000 prawns 100 m⁻². Similarly, the abundance of postlarval banana prawns and that of *P. merguensis* varied in the same way.

In both 1997 and 1998, the mean catch rates of banana prawn postlarvae and juveniles were greater in near-bank habitats than in mid-river habitats. Less than 3.5 postlarval prawns or 1.5 juvenile prawns 100 m⁻² were found on the bottom of river-channels or in the shallows on mid-river mudbanks at any site or time, even though these habitats were sometimes only 100 m from the near-bank mangrove habitats where juveniles were abundant.

Among the mud/mangrove near-bank habitats of the Cambridge Gulf in 1997, the mean catch rates of *P. indicus* were far higher (20 to 50 times) in gutters (1,056.3 ± 710.6 prawns 100m⁻²) and sub-creeks (411.5 ± 371.0 prawns 100m⁻²) than in creeks (17.8 ± 12.1 prawns 100m⁻²) or main rivers (0.7 ± 0.4 prawns 100m⁻²). Similarly, the mean catch rates of banana prawn postlarvae in gutters (11675.0 ± 7252.8 postlarvae 100m⁻²) and sub-creeks (2943.1 ± 1448.4 postlarvae 100m⁻²) were 10 to 100 times higher than those in creeks (205.0 ± 105.6 postlarvae 100m⁻²) and the main rivers (132.5 ± 66.5 postlarvae 100m⁻²). However, the mean catch rates of *P. merguensis* were higher in the medium-sized water-bodies (sub-creeks (292.5 ± 187.2 prawns 100m⁻²) and creeks (104.5 ± 101.2 prawns 100m⁻²)) than in the small gutters (23.9 ± 17.5 prawns 100m⁻²) or the main rivers (1.1 ± 1.1 prawns 100m⁻²).

In 1998, a more widespread and rigorous sampling regime in the mud/mangrove habitats of the JBG and the Cambridge Gulf showed similar results. The mean catch rates of banana prawn postlarvae were far higher (five to 100 times) in creeks, sub-creeks and gutters (from 195.8 ± 168.5 to 1770.2 ± 719.2 postlarvae 100m⁻²) than in the main rivers, either in near-bank (<40 postlarvae 100m⁻²) or in mid-river habitats (< 3.5 postlarvae 100m⁻²) (Fig. 3.13a).

In the Forsyth Creek, the mean catch rates of *P. indicus* were far higher (eight to 15 times) in smaller waterbodies (sub-creeks (417.9 ± 165.2 prawns 100m⁻²) and gutters (1,754.4 ± 636.9 prawns 100m⁻²)) than the main river (54.8 ± 47.4 prawns 100m⁻²) (Fig. 3.13b). Similarly, the mean catch rates of *P. indicus* were higher in smaller waterbodies (sub-creeks (6.2 ± 2.8 prawns 100m⁻²) and gutters (21.5 ± 11.7 prawns 100m⁻²)) than the main river (1.8 ± 0.7 prawns 100m⁻²) in the Lyne River (Fig.

3.13b). No waterbodies that were categorised as creeks were sampled in the Forsyth Creek or the Lyne River. Few *P. indicus* were caught in the Berkeley River.

In the Berkeley River, where their numbers were greatest, the catch rates of *P. merguensis* were higher in medium-sized creeks (360.7 ± 139.8 prawns 100m^{-2}) than the small sub-creeks (199.5 ± 129.3 prawns 100m^{-2}) or the main river (116.9 ± 47.6 prawns 100m^{-2}) (Fig. 3.13b). In the Lyne River, the catch rates of *P. merguensis* were similar in the sub-creeks (29.8 ± 18.4 prawns 100m^{-2}) and the gutters (23.8 ± 10.0 prawns 100m^{-2}), which were four times higher than the main river (5.7 ± 2.2 prawns 100m^{-2}) (Fig. 3.13b). In the Forsyth Creek, the only numbers of *P. merguensis* of consequence that were caught were in the gutters (62.7 ± 31.9 prawns 100m^{-2}) and a few in sub-creeks (6.9 ± 6.5 prawns 100m^{-2}). No waterbodies that were categorised as gutters were sampled in the Berkeley River.

Size of *P. indicus* and *P. merguensis* in different microhabitats of coastal Joseph Bonaparte Gulf

The majority of trawls to examine differences in microhabitats were done in 1998 (164 out of 201 trawls), so the catches from each year were grouped. In 1997 and 1998, juvenile *P. indicus* near the banks of the gutters and sub-creeks of JBG (> 95% of juveniles < 9 mm CL) had similar carapace length distributions as those near the banks of the large creeks (> 70% of juveniles < 9 mm CL) and rivers (> 95% of juveniles < 9 mm CL). A much higher proportion of larger *P. indicus* (100% of juveniles \geq 9 mm CL) were found in the mid-river channels and mudbanks (although few prawns were caught in these habitats) than in the near-bank habitats.

The length frequency distributions of *P. merguensis* were similar to those of *P. indicus* in the near-bank habitats - the gutters (76% < 9 mm CL), side-creeks (96% < 9 mm CL), creeks (95% < 9 mm CL) and riverbanks (88% < 9 mm CL). However, in contrast to *P. indicus*, the majority of *P. merguensis* in the mid-river channels (100% < 9 mm CL) and mudbanks (>77% < 9 mm CL) were also small prawns.

DISCUSSION

DISTRIBUTION

Juvenile banana prawns are abundant throughout the coastal mangrove habitats of the JBG and Cambridge Gulf; similar to their abundance in mangrove habitats in the Gulf of Carpentaria (Staples 1980, Vance *et al.* 1990, Vance *et al.* 1998). However, in the Joseph Bonaparte Gulf, the two species of banana prawns show a major difference in their distribution patterns. In both 1997 and 1998, over 95% of juvenile banana prawns in the eastern JBG were *P. indicus*, while over 93% of juvenile banana prawns in the western JBG were *P. merguensis*. The northwest corner of the Cambridge Gulf seems to be a transition zone, where both species were abundant.

The difference in distribution pattern of the two species of prawn coincides with some major gradients in geomorphology and physical characteristics of river systems across the JBG. In the eastern JBG, river systems are long and wide with large catchments, extensive floodplains and high turbidity. These rivers contrast with rivers in the western JBG that are much smaller, have smaller catchments, are confined by sandstone escarpments and have much clearer water. The hilly landforms around the Lyne River in north-west Cambridge Gulf (where both *P. indicus* and *P. merguensis* are abundant) are the less-rugged than the escarpment country of the east Kimberley region (the coast of west JBG), but more elevated than the floodplains of east JBG. This area seems to be “transition zone” for the local geomorphology that matches the “transition zone” of banana prawn species distribution. Elsewhere in Cambridge Gulf, where *P. indicus* are common, large turbid rivers with extensive floodplains also dominate.

The changes in the geomorphology and the river systems are characterised by differences in the extent of banana prawn habitat in the eastern and western JBG. The large rivers and floodplains of the east JBG support the extensive mangrove habitats, as well as the saline coastal flats, which we quantified for the region from the AUSLIG data. Although not ground-truthed to any significant extent over most of the study area, we visually confirmed the presence of these habitats during our extensive travels to trawl-sample throughout it. There seems to be no direct relationship between the extent of habitat in a river-system and abundance of either species of banana prawn in that river. However, 92% of all *P. indicus* that were caught in 1997 were caught in the eastern JBG or Cambridge Gulf where the extent of mangrove habitat is greatest.

In contrast, the smaller rivers that run through gorges and low, rocky hills in the western JBG have very little flat floodplain associated with them and limited areas of mangrove and saline coastal flat, as quantified from the AUSLIG data. Near the river mouths, a small estuary may support mangrove habitats and saline flats; however, over most of the length of the river, mangroves are reduced to a narrow fringe and saline flats are non-existent.

Although *P. merguensis* are clearly associated with extensive mangrove habitats in other locations around Australia (Vance *et al.*, 2001), over 85% (95% if the Lyne River is included) of all the *P. merguensis* that were caught in 1997 were caught in the creeks and rivers of the western JBG. In these rivers, their mangrove habitats may be limited to a well-developed, but narrow, fringe of mangroves or even a few sparse mangroves on a relatively sandy beach in the upper-reaches of the river; yet large numbers of postlarval and juvenile *P. merguensis* prawns were caught at these sites. The question arises – why *P. merguensis* were not abundant in the extensive mangrove habitats of the eastern JBG and Cambridge Gulf (coexisting with *P. indicus*) – and no obvious explanation is evident. However, the high turbidity of the water in the eastern JBG, compared to the west, may be a factor. It is possible that *P. indicus* is more tolerant of extreme turbidity than *P. merguensis*.

Our modelling supported the contention that turbidity has a significant effect on the distribution of *P. indicus* in JBG. Part of the variation in the proportion of *P. indicus* in the catch (Model One) was explained by secchi depth (a measure of turbidity). The most significant term in the regression was the trend for the proportion of *P. indicus* to increase from the northwest to the southeast. Further analysis suggested that this

term could be an effective surrogate for consistent turbidity, which is high and consistent in the southeast (with a high proportion of *P. indicus*) and low and variable in the northwest (with a low proportion).

Modelling the total number of *P. indicus* in a sample (Model Two) showed that significantly greater numbers of *P. indicus* were found in very turbid waters with low secchi depths (<0.5 m). Turbidity (secchi depth) had a significant but lesser influence on the numbers of *P. merguensis*. Both species were found on mud sediments, rather than sediments with a high sand content. The modelling also showed that they are significantly more abundant in smaller water bodies (creeks and gutters) than the rivers and coastal locations.

HABITAT PREFERENCE

Juvenile *P. indicus* were found associated with mangrove-lined mudbanks in estuaries and rivers of JBG, similar micro-habitats to those identified for *P. merguensis* in the Gulf of Carpentaria (Vance *et al.* 1996, Vance *et al.* 1998); and those identified for *P. indicus* elsewhere in the Indo-Pacific (Subramanian 1985, Mohan and Siddeek 1995a). In these habitats they were associated strongly with mud substrates, as they are in other locations (Mohan and Siddeek 1996). Repeated trawls in adjacent mangrove-lined riverine habitats showed that *P. indicus* are most abundant in small waterbodies, usually side-creeks and gutters, compared to rivers. They were particularly abundant (often >1000 prawns·m⁻²) in remnant waters in the small gutters that drained the mangrove forests; presumably where they have accumulated at low tide as the water level in the surrounding mangroves recedes (Vance *et al.* 1996, Vance *et al.* 2002). They were only found in very low numbers in mid-river habitats, such as channels and mudbanks.

In the JBG, at low tide juvenile *P. merguensis* also accumulate in the shallow near-bank habitats of mangrove-lined waterways, as they do elsewhere (Vance *et al.* 1998). However, in both 1997 and 1998, their abundance was greater in large creeks than small creeks or rivers, a different pattern to *P. indicus*. As has been found elsewhere in tropical Australia, they were not abundant on mid-river banks and in channels (e.g. Staples *et al.* 1985).

The contention that high densities of *P. merguensis* are found in large creeks, while *P. indicus* are more abundant in small creeks and gutters, is affected by the range of habitats found in the different regions of the JBG. Not all habitats were found and sampled in each of the 3 main regions where the microhabitat distribution of banana prawns was studied. For example, in the eastern JBG and Cambridge Gulf, where *P. indicus* is abundant, no habitats were classified as “Creeks”. Conversely, in the eastern JBG where *P. merguensis* is abundant, no habitats were classified as “Gutters”. However, “Sub-creeks” were common to all regions of the JBG, and comparisons show that *P. indicus* were more abundant in gutters than sub-creeks in Forsyth Creek, and that *P. merguensis* were much more abundant in creeks than sub-creeks in the Berkeley River.

RELATIONSHIP TO THE OFFSHORE FISHERY

The offshore fishery for *P. indicus* takes place in the north-western offshore waters of the JBG (in water depths of 50-80 m, around 14° S, 128° E). Thus, the juvenile phase of *P. indicus* is found in estuarine habitats up to 120 km south and 240 km east-south-east of the southern and eastern limits of the JBG *P. indicus* fishery (Fig. 3.14). The juvenile phase of *P. merguensis* is found in estuarine habitats in the western JBG, about 50 km to the south west of the *P. indicus* fishery, offshore. Although these mangrove habitats are the closest inshore habitats to the fishery, they are not used by *P. indicus*. These results suggest that the larvae of *P. indicus* resulting from spawning in the fishing, are advected large distances to the south and east to their nursery habitats. They also imply that the emigrating juveniles and sub-adults migrate from the mangrove nursery habitats, north and west, across shallower sand substrates (30 – 40 m deep) to the deeper-water fishery (on mud substrates about 50-80m deep).

A caveat on the probable large distance of advection by *P. indicus* postlarvae would be the possibility of an “effective spawning population” (Rothlisberg *et al.* 1995; Rothlisberg 1996) inshore of the main fishery. Perhaps some young adult prawns spawn as they move seaward to the fishing grounds. The distribution of adult *P. indicus* in the mid-shore regions of the JBG should be further examined to identify any possible unknown spawners.

If postlarval *P. indicus* advect such large distances (minimum of 170 km), the “advection envelope” (Rothlisberg *et al.* 1996; Condie *et al.* 1999) for *P. indicus* in JBG must be large (Fig. 3.15). The exact determinants of advection depend of the behaviour of the postlarvae and local hydrology (Rothlisberg *et al.* 1995; Vance *et al.* 2001). However, a quick estimate suggests that the advective envelope might be about 17000 km²; and this is perhaps 10 times the size of advective envelopes of *P. merguensis* in locations in the Gulf of Carpentaria where effective spawning may occur only 44 km offshore (Rothlisberg *et al.* 1996). The large tides (7 m) and strong tidal currents (4 km h⁻¹) in JBG probably contribute to the large size of the advection envelope for the prawn postlarvae (Condie *et al.* 1999).

The juvenile *Penaeus merguensis* found in the rivers of the western JBG may recruit to these areas from outside the JBG, possibly further west where the Kimberley prawn fishery operates. However, the hydrologic processes that transport the larvae are unclear. The exact nature of the advective processes for both species needs further investigation.

As juvenile *P. merguensis* are only abundant in regions where the aerial and linear extent of mangrove habitats are limited, (e.g. the western JBG and the north-west corner of the Cambridge Gulf), their contribution to the offshore fisheries of the JBG may be considerably less than that of *P. indicus*. *Penaeus indicus* are abundant in the eastern JBG and southern Cambridge Gulf where mangrove habitats are extensive. The combination of high abundance and the extensive areas of habitat in these regions means that they are likely to be very significant for the productivity of the offshore banana prawn fishery in JBG.

Furthermore, our results highlight the risk when attempts are made to link offshore fishery production with the extent of adjacent inshore habitats (Staples *et al.* 1985). In the JBG, the most productive juvenile habitats for this fishery are not those closest

to it, but those about 200 km distant. A sound knowledge of the hydrodynamics associated with adult emigration and postlarval advection, to and from offshore fisheries, is crucial for adequate fishery management.

REMOTE DETERMINATION OF HABITAT

Attempts to link the productivity of inshore nursery habitats to offshore fishery productivity rely on the accurate measurement of the extent of inshore habitats. We used topographical data to estimate the broad scale extent of coastal habitats in the region. However, it is important to note that these data are much less accurate than those from aerial photographs or Landsat TM (see Manson *et al.* 2001 and Chapter 4 for full details). Comparisons of the estimates of area and linear extent of mangroves in two rivers with those from aerial photographs and Landsat TM shows that the topographical data underestimates the area and linear extent of mangrove habitats (Manson *et al.* 2001). Thus, the values we used for area and linear extent of prawn habitat are potentially poor estimates and they may lead to unsatisfactory conclusions about the influence of habitat on fishery productivity.

Our study shows that the use of information on the extent of coastal habitats in models that link habitat with offshore fishery production must take into account the scale and precision of the source-data on habitat. The scale of the data, and their source can provide estimates of the extent of habitats that vary by more than 400% (Manson *et al.* 2001).

MANAGED RIVER-FLOW REGIMES DUE TO IRRIGATION ARE DETRIMENTAL TO JUVENILE PRAWN HABITATS

Our results show that the distribution of *P. indicus* and *P. merguensis* in the Ord River has probably been affected greatly by freshwater discharge from the Ord River Irrigation Scheme. The all-year-round discharge from the irrigation scheme lowers the salinity in the east arm of the Cambridge Gulf, i.e. the estuary of the Ord River (Rodgers *et al.* 2000 and our measurements). At low tide, the salinity is 0-5 just upstream from its confluence with the west arm of Cambridge Gulf. Few (virtually no) juvenile banana prawns were found in the Ord River estuary. In fact, we ceased sampling further upstream in the Ord River because no prawns were caught at several up-estuary sites and the water was fresh. This contrasts with the catches at sites in the western arm of the Cambridge Gulf and the rivers and streams that flow into it. These areas have comparable habitats, but higher salinities (around 33-35), and the catch rates of juvenile banana prawns were high.

Historically, the streamflows in the Ord River have occurred mainly in January, February and March, after wet-season rains (O'Boy *et al.* 2001). Like most of the dry-tropics of Australia, virtually all the rainfall in the Ord River catchment occurs during the monsoon season from November to March, with peaks in January and February (Rodgers *et al.* 2000; O'Boy *et al.* 2001). Thus, streamflow follows the peak rains (January-March), and from about May to November, virtually no runoff and streamflow occurs. Prior to the damming of the Ord River, runoff from late April to early November was negligible and the river would have had salinities roughly equal to ocean-seawater (about 35). The Ord River was dammed by the Kununurra

Diversion Dam in 1963 and the Ord River Dam in 1972 (Rodgers *et al.* 2000). Since then, regulated flows and water discharge from the irrigation scheme have altered the streamflow to an all-year-round discharge and hence altered the salinity in the lower Ord River all year round. Currently, about 6 gigalitres d⁻¹ are released from the Kununurra Diversion Dam to the lower Ord. This flow may be reduced by further irrigation development in the Ord River Irrigation Area (ORD Stage II Irrigation Scheme), as the water is used for more extensive irrigation (Waters and Rivers Commission, 1999; Rodgers *et al.* 2000).

Although water management infrastructure will be engineered to avoid water discharge, some discharge may occur into the Keep River as part of the ORD Stage II Irrigation Scheme. Consequently, changes to river flows that alter the salinity regime (i.e. inputs of fresh water) in the Keep River may reduce the estuarine habitat available to juvenile prawns and other estuarine fauna in the Keep estuary at some times of the year. The Keep River flows into a significant embayment in Eastern JBG, which has extensive areas of mangrove forest habitat that is used by juvenile banana prawns. Such changes would have similar effects (i.e. lowering the abundance of juvenile prawns in the system) to those in the Ord River in the western Joseph Bonaparte Gulf system

CONCLUSIONS

Until recently, the distribution and abundance of the juvenile *Penaeus indicus* and *P. merguensis* in the coastal nursery habitats of JBG was unknown. In 1997 and 1998, we trawled in estuarine habitats over 500 km of coastline in Joseph Bonaparte Gulf to determine their distribution.

We found major differences in the broad-scale spatial distribution of the juveniles of the two banana prawns. In eastern JBG and Cambridge Gulf, over 96% and 73% (respectively) of juvenile banana prawns are *P. indicus*. Conversely, in the western JBG over 93% of the juveniles are *P. merguensis*. In the Lyne River in north-western Cambridge Gulf, both species are abundant in what appears to be a transition zone.

Thus, the juvenile phase of *P. indicus* is found in estuarine habitats 120 km south and 240 km east-south-east of the southern and eastern limits of the JBG *P. indicus* fishery. The juvenile phase of *P. merguensis* is found in estuarine habitats about 50 km to the south west of the *P. indicus* fishery in JBG. Although these mangroves are the closest inshore habitats to the fishery, they are not used by *P. indicus*.

These results suggest that postlarval *P. indicus*, spawned offshore, must use tides and currents to travel large distances to the south and east to nursery habitats. They also imply that juveniles and sub-adults migrate north and west, across shallower sand substrates (30 – 40 m deep) to the deeper-water fishery (50-80m deep). *Penaeus merguensis* may recruit to their habitats in west JBG from areas outside JBG, further west; but the hydrologic processes that transport the larvae are unclear.

Juveniles of both *P. indicus* and *P. merguensis* were found associated with mangrove-lined mudbanks in estuaries and rivers, similar habitats for juvenile banana prawns to those identified elsewhere in Australia and the Indo-Pacific. Repeated trawls among different riverine habitats in close proximity showed that the catch rates of juvenile banana prawns were much greater (50 to 100 x) in creeks and gutters, than in rivers. Both species were found in very low numbers mid-river - on mudbanks and in channels.

FURTHER DEVELOPMENT

The exact nature of the advective processes for both species needs further investigation. In JBG, the advective envelope for *P. indicus* seems to be much larger than for *P. merguensis* in the Gulf of Carpentaria. In JBG, the offshore fishery is much further offshore from coastal nursery habitats than elsewhere in the NPF. Our work for Chapter Five showed that the benthic habitat between the estuaries and the offshore fishery does not seem favourable to adult *P. indicus*. Investigation of the “effective spawning stock” for the red-legged banana prawn fishery is warranted, as the possibility of a mature spawning stock remaining inshore seems slim.

Our results highlight the risk when attempts are made to link fishery production to the extent of adjacent inshore habitats. In the JBG, the most productive habitats for this fishery are not those closest to it, but those about 200 km distant. A sound knowledge of the hydrodynamics associated with adult emigration and postlarval advection to and from fisheries is crucial for adequate fishery management.

We also show in Chapter Four that error and discrepancy may occur when estimating the extent of coastal habitats, depending on the source of the habitat data. The results of Chapter Four, together with those from this Chapter that show that juvenile habitat may be very distant from the fishery and this introduces the likelihood of error in models that link habitat extent and juvenile prawn abundance to the production of offshore fisheries. These factors should be taken into account in future studies, although measuring the effects of hydrodynamic processes and the error in remotely sensed data would be costly.

Relationship between the distribution of adults and juveniles

- The project showed that the distribution of juvenile *P. indicus* and *P. merguensis* is markedly different throughout coastal JBG. *Penaeus indicus* is mostly found in the east JBG and Cambridge Gulf (in southern JBG), while *P. merguensis* is mostly found in the west JBG.
- The exact distribution of adult *P. indicus* and *P. merguensis* in JBG is unknown, as are the annual patterns of recruitment of sub-adults to the JBG fishery. However, in the areas in northwest JBG that are fished, the proportion of *P. indicus* is much greater than the proportion of *P. merguensis*. Furthermore, the fishery for *P. merguensis* is further west, mostly outside JBG. Thus, the separate distributions of juvenile *P. indicus* and *P.*

merguiensis may be explained by hydrological processes that advect the postlarvae of each species inshore over different pathways, or it may be a consequence of different habitat preference or survival of individuals once in the coastal rivers.

- Determining factors that might affect the survival of each species in the rivers would be difficult. However, a project to begin to understand the pathways and processes of juvenile recruitment in JBG would be to sample the postlarval recruits entering the rivers in east, south and west JBG simultaneously with the population of juveniles in near-bank habitats within the rivers of each region. If the ratio of *P. indicus* to *P. merguiensis* entering the rivers was the same as that of the resident juvenile population, then the hydrodynamic process within the JBG may be delivering the larvae of the two species in different ways within the Gulf, i.e. most *P. indicus* postlarvae are delivered to the east and south Gulf, while *P. merguiensis* postlarvae are delivered to the west Gulf. However, if the ratio of *P. indicus* to *P. merguiensis* entering the rivers (perhaps 50:50 throughout the Gulf) is not the same as that of the benthic postlarvae, then the postlarvae and juveniles in the rivers must be suffering different level of mortality due to environmental conditions in the rivers.

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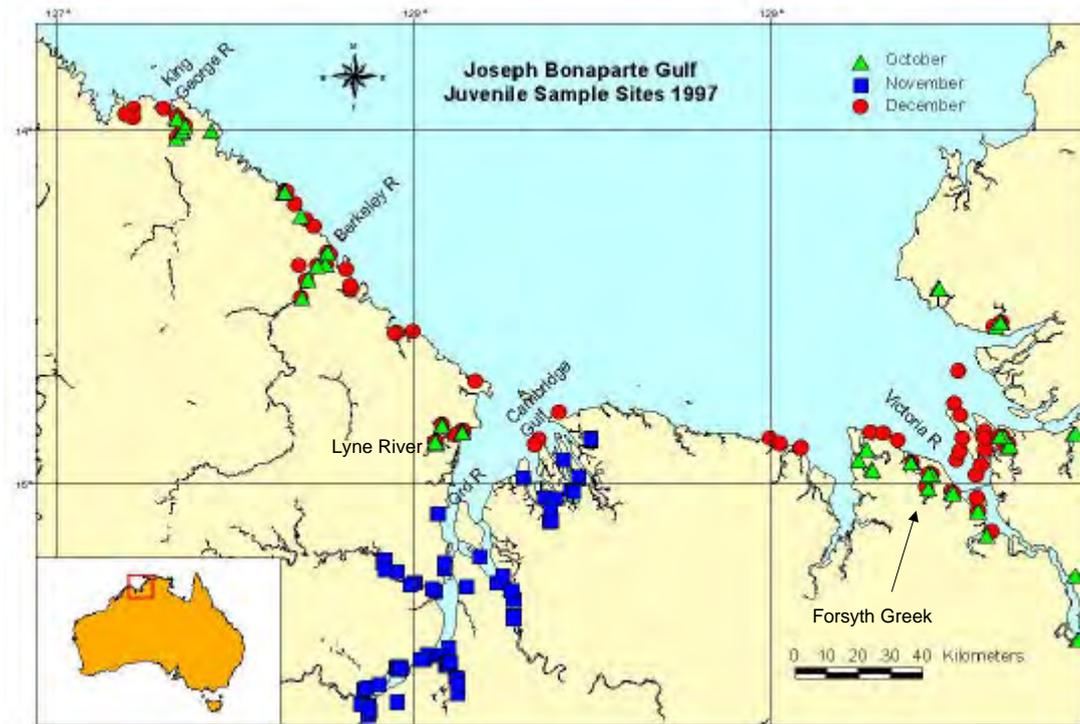


Figure 3.1 Study sites trawled for postlarval and juvenile banana prawns during three cruises undertaken in Joseph Bonaparte Gulf during 1997.

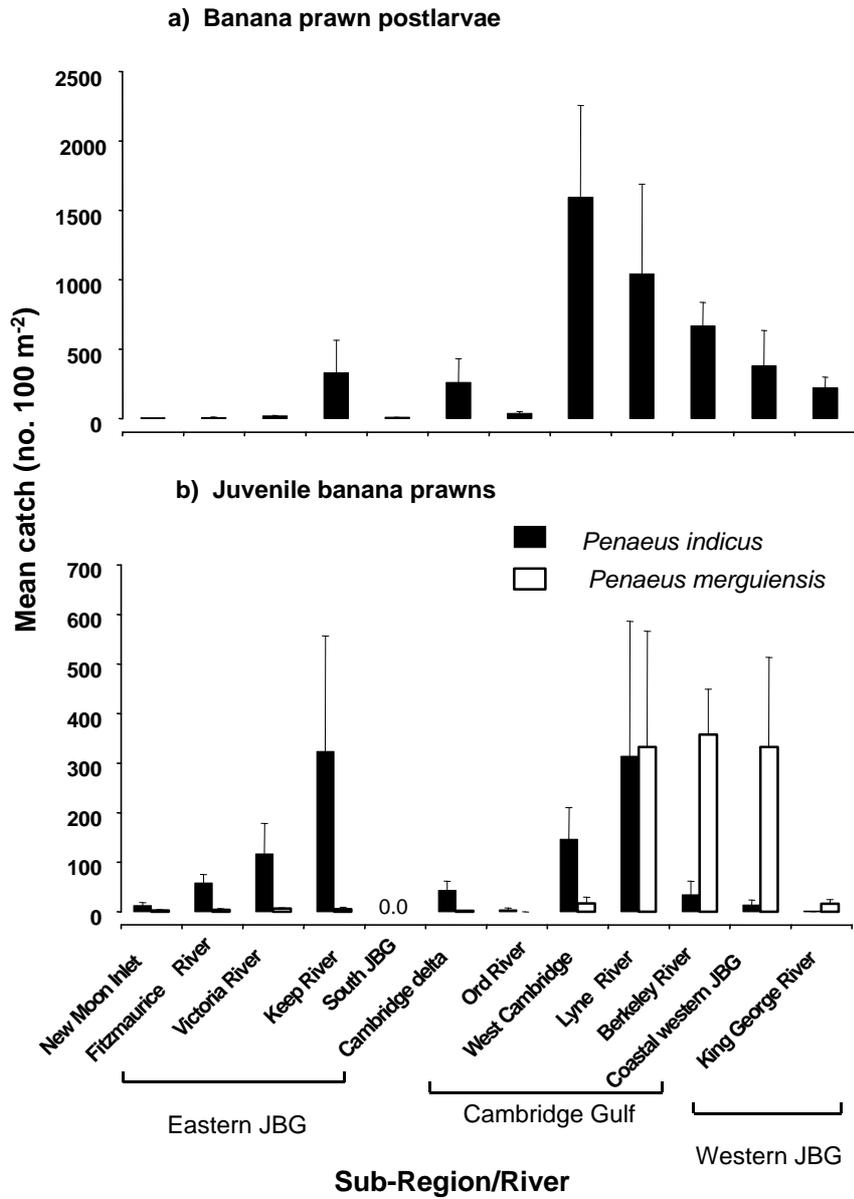


Figure 3.2 Mean catch (± 1 SE) of postlarval banana prawns and juvenile banana prawns (*Penaeus indicus* and *Penaeus merguensis*) in beam trawls from 12 sub-regions in Joseph Bonaparte Gulf during October – December 1997.

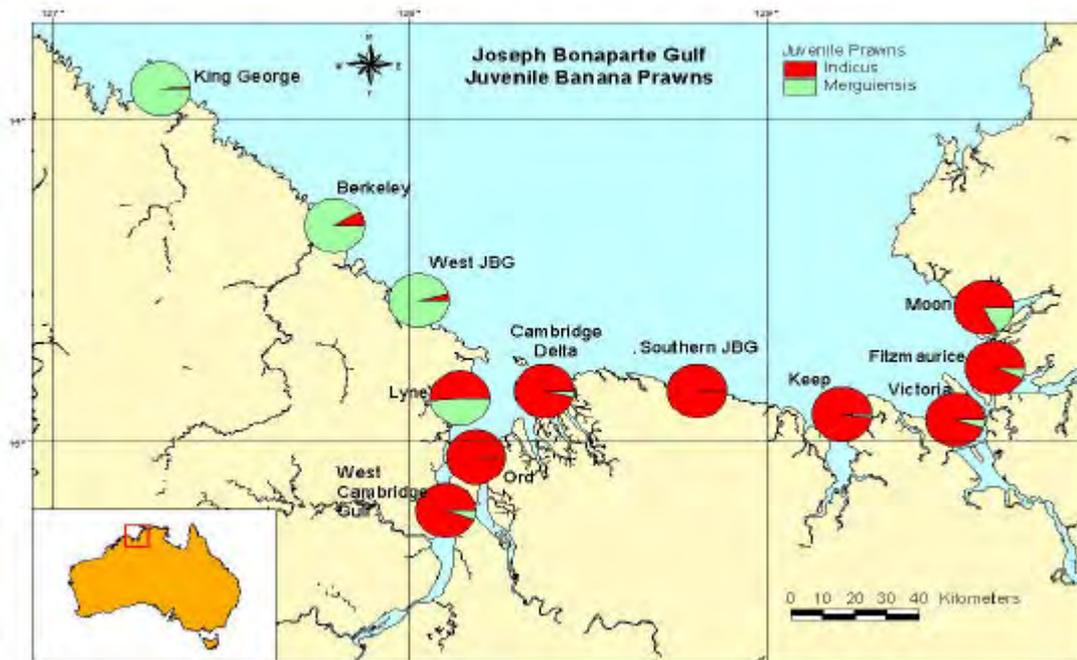


Figure 3.3 Proportion of *Penaeus indicus* and *Penaeus merguensis* in the juvenile prawn catch from 12 sub-regions in Joseph Bonaparte Gulf in 1997.

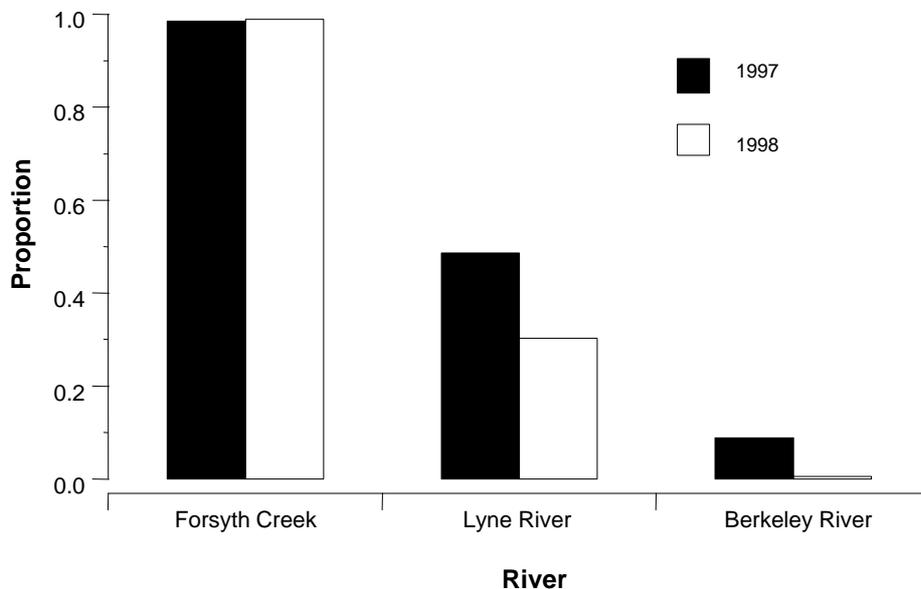


Figure 3.4 Proportion of *Penaeus indicus* in the juvenile prawn catch from three rivers in eastern and western Joseph Bonaparte Gulf, and the Cambridge Gulf, that were sampled in both 1997 and 1998.

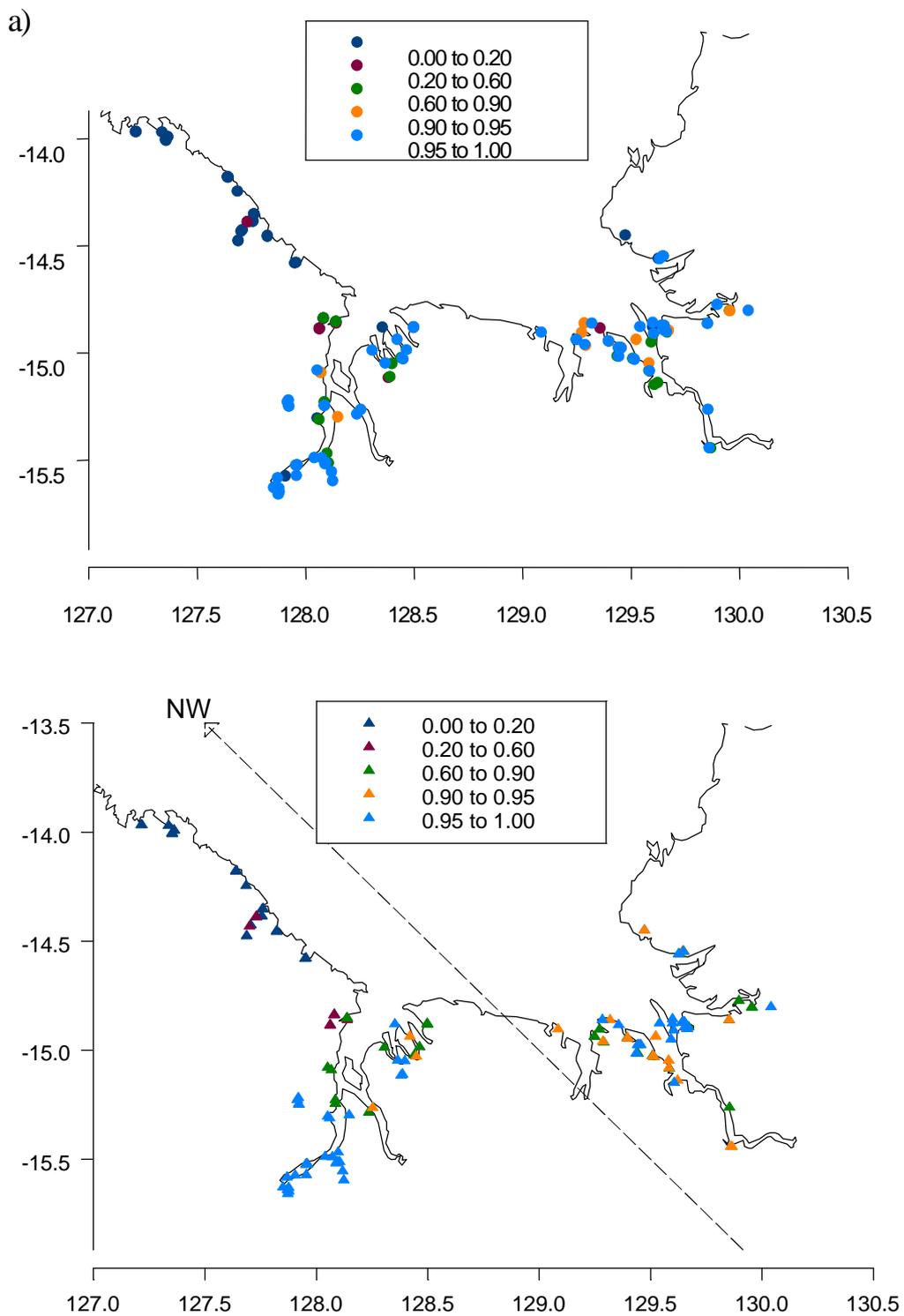


Figure 3.5 a) Stations classified by the raw proportions of *P. indicus*, and b) Proportions of *P. indicus* estimated from fitted model

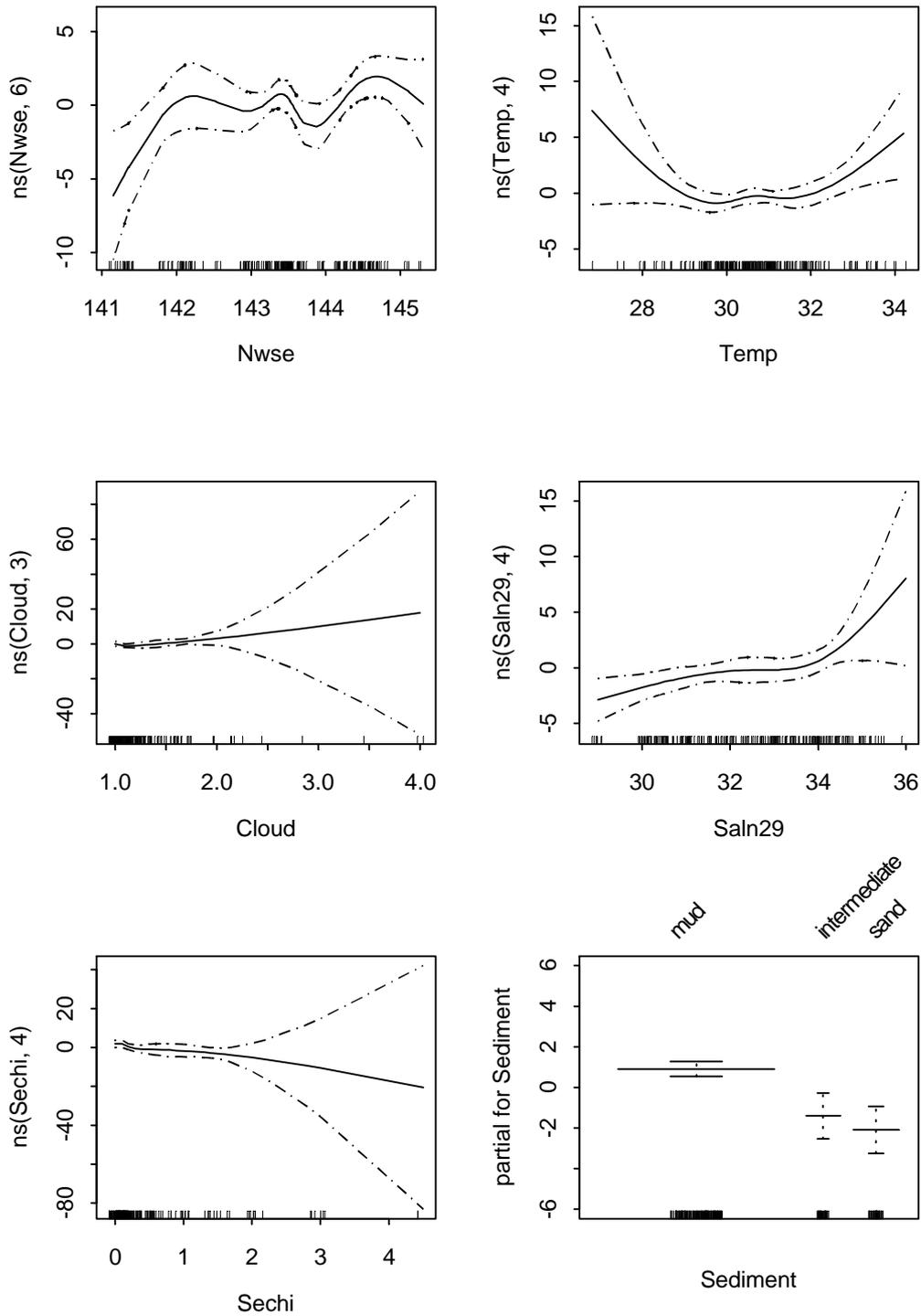


Figure 3.6 Partial contributions to the linear predictor for the *P. indicus* presence model

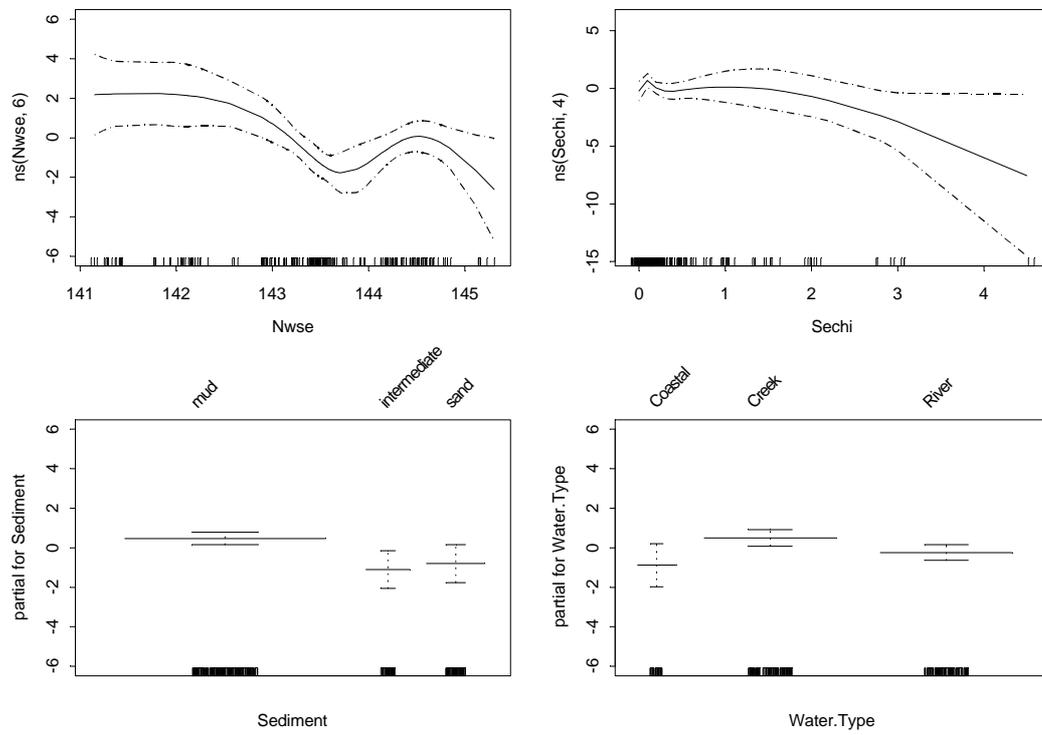
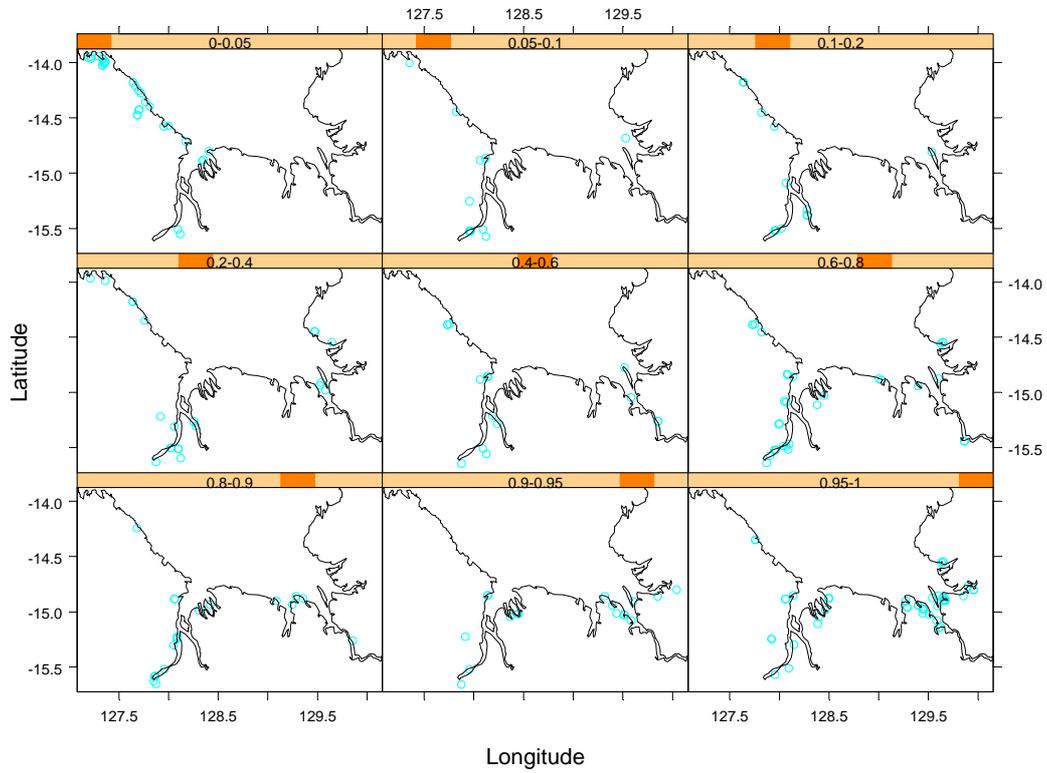


Figure 3.7 Partial contributions to the model predicting presence of *P. merguensis*.

a) *Penaeus indicus*



b) *Penaeus merguensis*

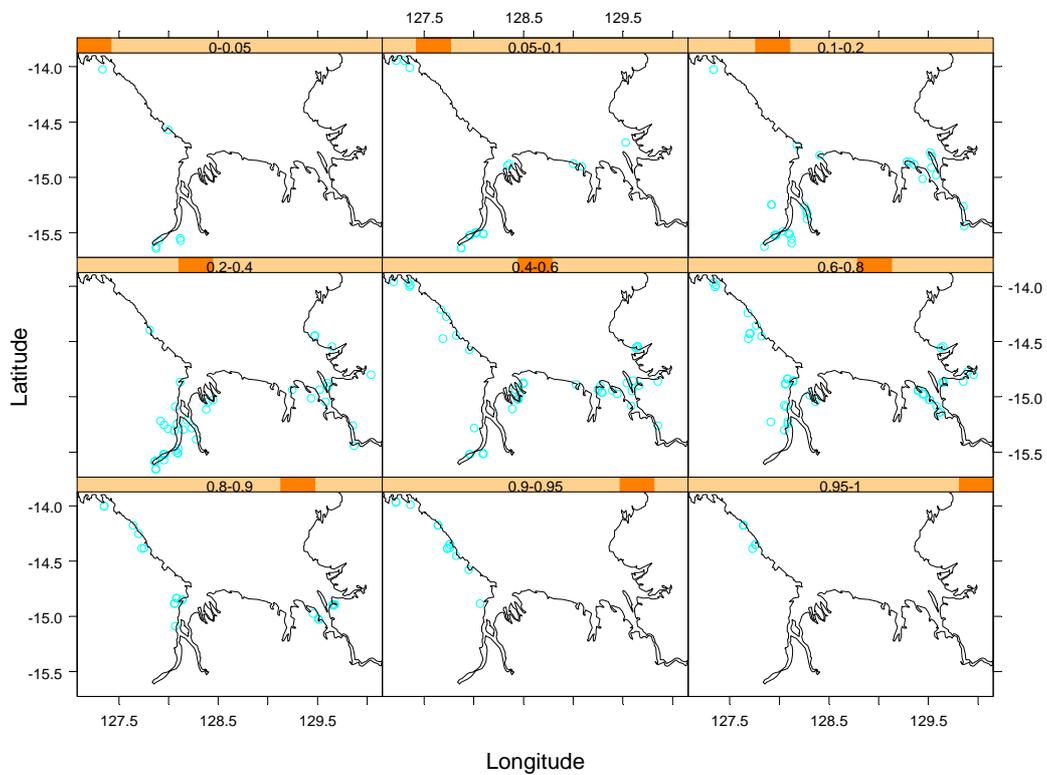


Figure 3.8 Spatial disposition of stations according to the probability of finding (a) *P. indicus* or (b) *P. merguensis*

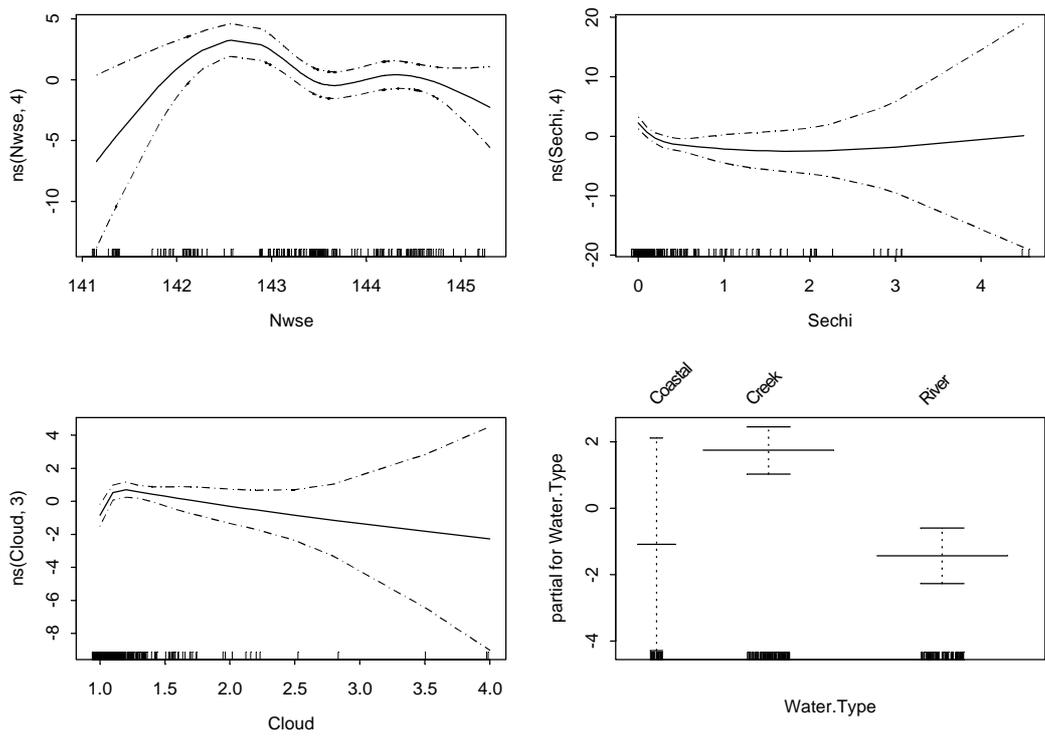


Figure 3.9 Partial contribution of terms to the predictive model for the density of *P. indicus*

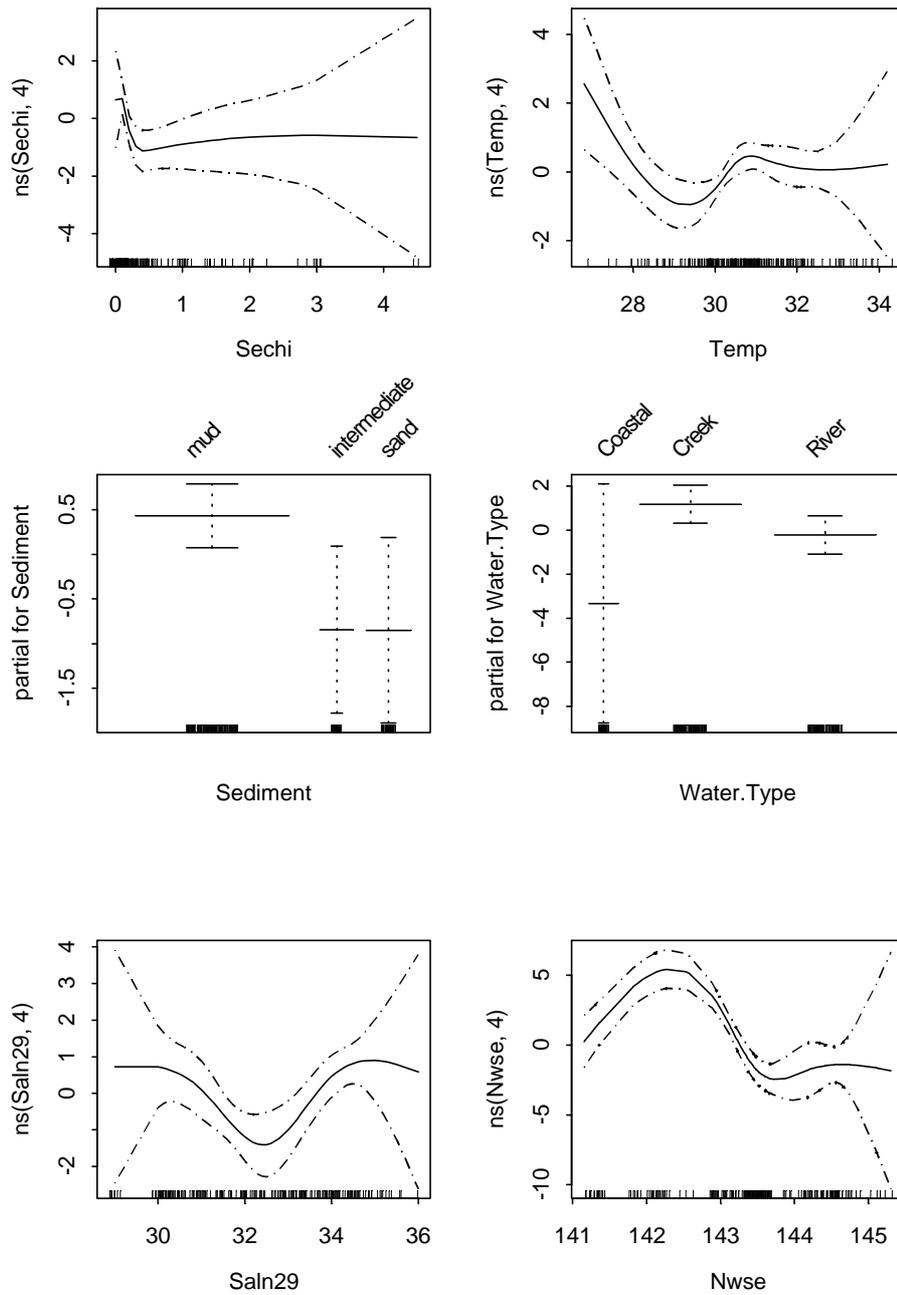


Figure 3.10 Partial contributions of terms to the predictive model for density of *P. merguensis*

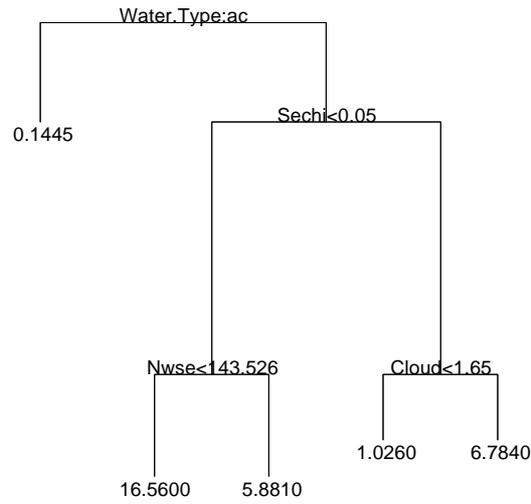


Figure 3.11 Pruned tree diagram for predicting density of *P. indicus*

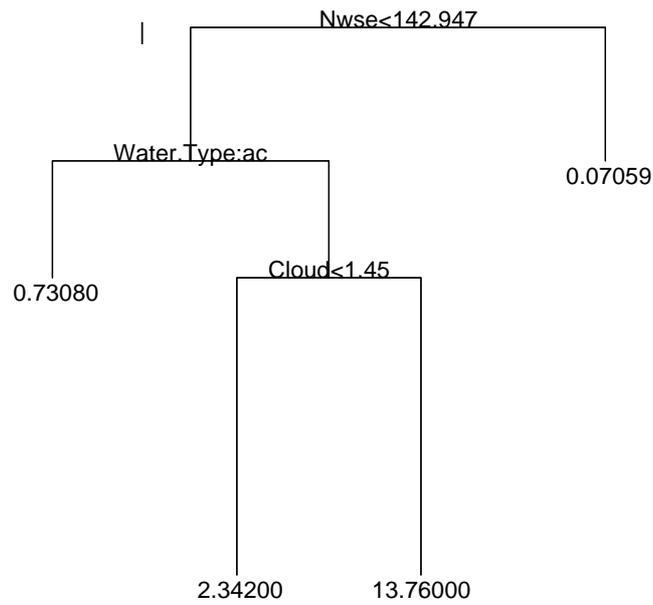


Figure 3.12 Tree-based model for density of *P. merguensis*

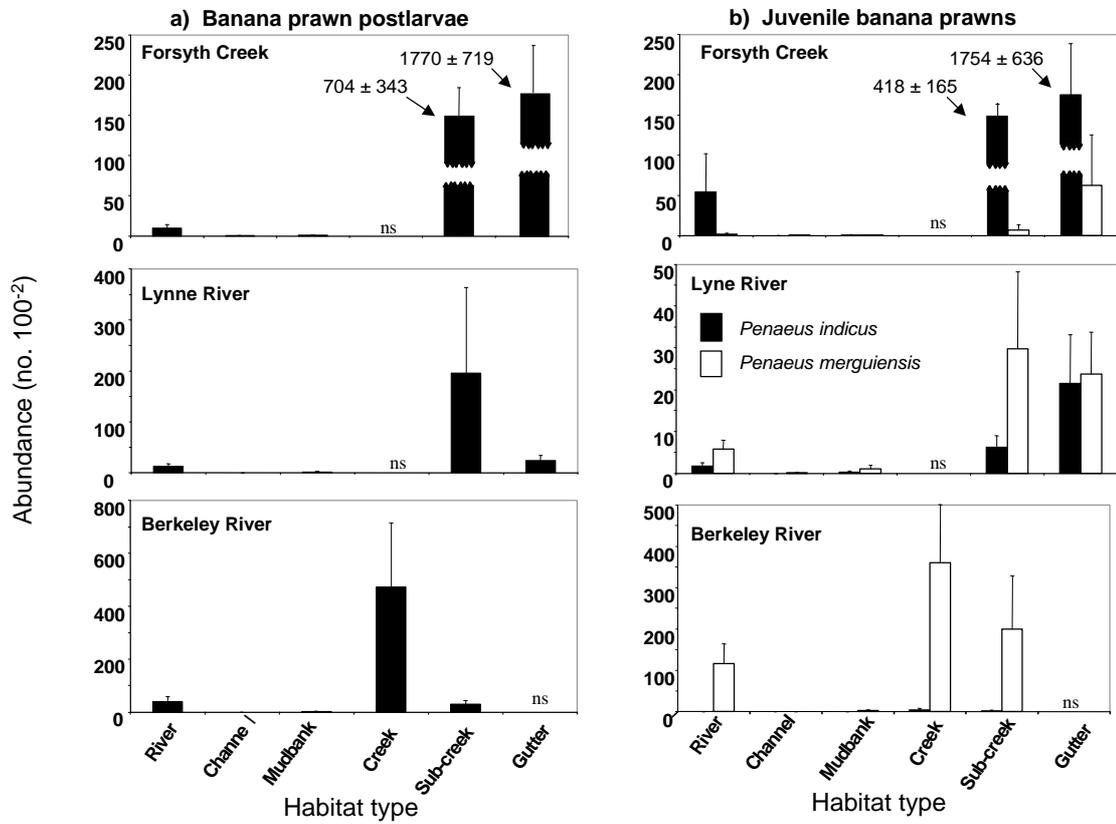


Figure 3.13 Abundance of postlarval and juvenile banana prawns (*Penaeus indicus* and *Penaeus merguensis*) among five microhabitats in Joseph Bonaparte Gulf in October to December 1998. ns = not sampled.

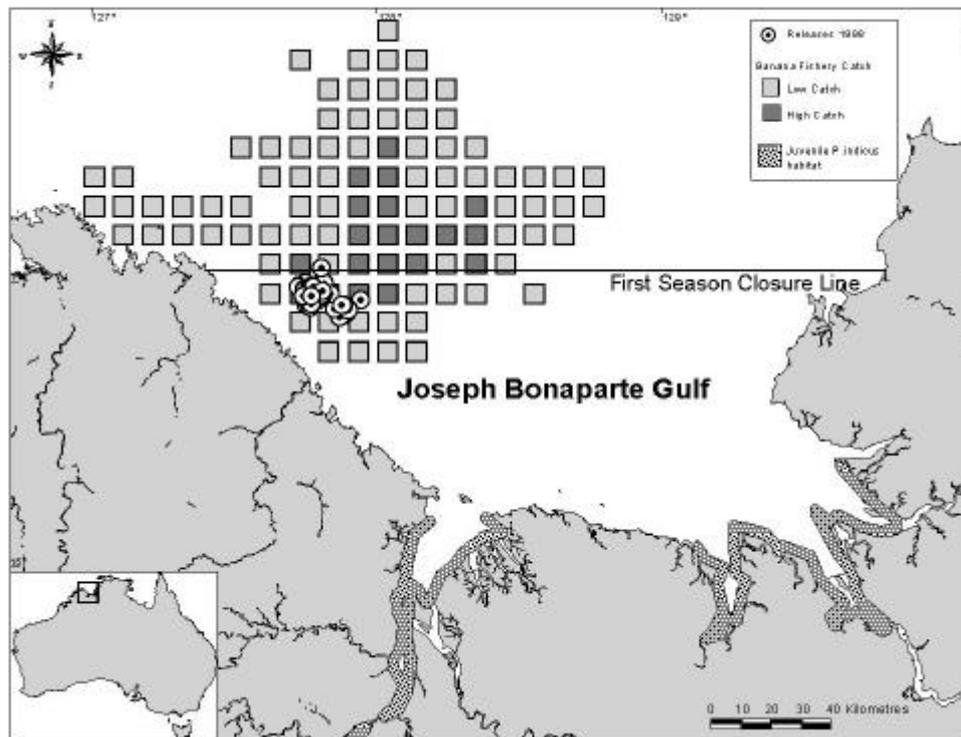


Figure 3.14 Distribution of fishing effort relative to the location of the inshore juvenile nursery habitats of postlarval and juvenile *Penaeus indicus* in Joseph Bonaparte Gulf in 1998. The release sites where recently emigrated adult prawns were found and tagged (as part of the project) are also marked.

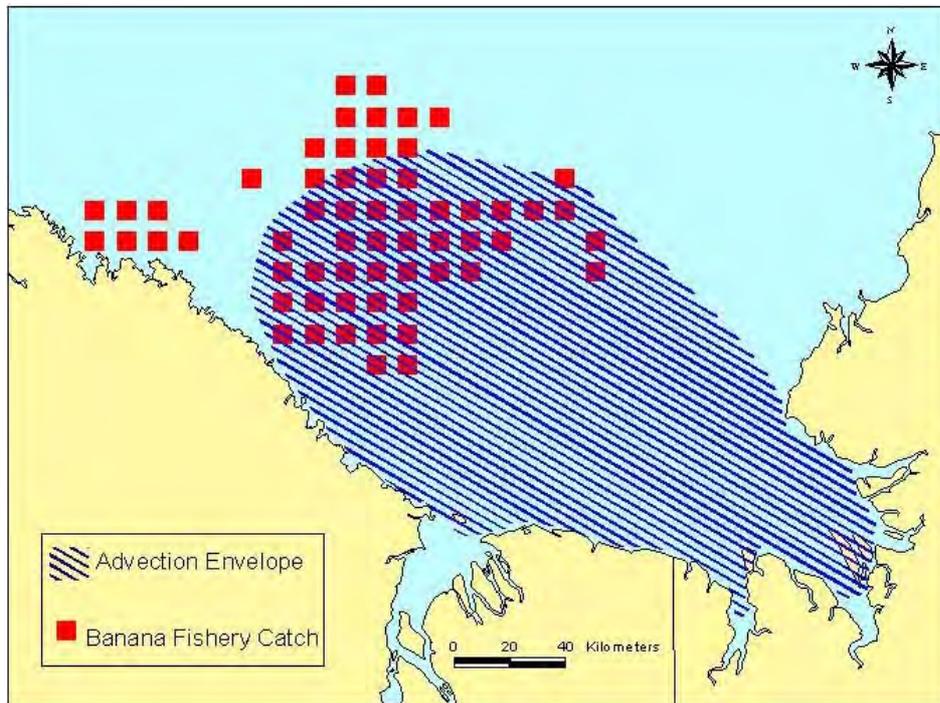


Figure 3.15 The size of the probable advective envelope for postlarval *Penaeus indicus* in Joseph Bonaparte Gulf.

4. CHAPTER FOUR: ESTIMATING THE EXTENT OF JUVENILE BANANA PRAWN HABITATS IN JOSEPH BONAPARTE GULF

(Authors: FJ Manson, NR Loneragan, IM McLeod, and RA Kenyon)

In this Chapter, we present a summary of the key findings from this component of the work. The full details of the work have been published in the following paper:

Manson FJ, Loneragan NR, McLeod IM, Kenyon RA (2001). Assessing techniques for estimating the extent of juvenile prawn habitats: topographic maps, aerial photographs and Landsat TM imagery. *Marine and Freshwater Research* **52**: 787-792.

INTRODUCTION

Juvenile banana prawns (*Penaeus merguianensis* and *P. indicus*) in northern Australia use mangroves and saline coastal flats as nursery areas (see Staples *et al.* 1985). The availability and distribution of these habitats are, therefore, important in the life-cycle of the prawns. Because of this link with fishery production, it is important for fishery managers to have accurate estimates of the extent of these habitats. The objectives of this study were to compare the estimates of the area and linear extent of coastal habitat (particularly mangroves) from three techniques for two rivers in the Joseph Bonaparte Gulf. Comparisons have also been made with results from the Embley River estuary in the north-eastern Gulf of Carpentaria, where the mangroves extend further from the edge of the water than in the Joseph Bonaparte Gulf.

METHODS

We used three methods (topographical data, aerial photography and Landsat Thematic Mapper (TM) satellite imagery) to estimate the area and linear extent of these habitats in the Berkeley River and the Lyne River in Joseph Bonaparte Gulf. The Australian Land Information Group (AUSLIG) topographical dataset is a commercially-available dataset, which has been digitised from topographical maps at a scale of 1:250,000, and includes such features as mangroves, saltflats, land subject to inundation, and rivers. Black and white aerial photographs were obtained from the West Australian Department of Conservation and Land Management (CALM); these were digitally classified to identify mangroves and saltflats. Landsat TM satellite imagery was acquired, and used to classify the mangroves and saltflats. For each method, the area and linear extent of each type of habitat were calculated. Ground-truthing was carried out in both rivers to verify the results of the classifications.

RESULTS AND DISCUSSION

For the Lyne and Berkeley Rivers, the aerial photographs provided the most accurate estimates of both area and linear extent of habitats, as verified by ground-truthing, while the topographical data was the least accurate (Table 4.1, Figure 4.1). Landsat TM imagery gave good estimates of the area of habitats, but underestimated the linear extents (Table 4.1). The differences in the estimates of mangrove extent are attributed to differences in the resolution of each of the methods. The mangroves of the Joseph Bonaparte Gulf region typically form narrow fringes (<50 m wide) along the river and creek banks, which can only be detected with high-resolution techniques. Aerial photographs, with their 2 m pixel resolution, are able to identify these narrow mangrove fringes, while Landsat TM (30m pixels) can only discriminate the larger mangrove stands. The AUSLIG topographical dataset is unable to consistently identify mangrove forests that are less than 50 m wide. Work done in the Embley River, Gulf of Carpentaria, where mangroves form more extensive forests (50-1000 m wide), shows that the accuracy of both AUSLIG data and Landsat TM imagery is better where mangroves are broader and less linear in shape. It can be concluded that, while aerial photographs give the most accurate results at the scale of individual river systems, Landsat TM imagery and topographical data can be useful tools in broader-scale studies.

Table 4.1 Area (km²) and linear extent (km) of mangrove and saltflat habitats of the Berkeley and Lyne Rivers from the Australian Land Information Group (AUSLIG) topographical data (1991-1994), aerial photograph classifications (August 1994) and Landsat TM classifications (July 1994). Also shown are area and linear extent of mangroves in the Embley River.

River and Habitat	Aerial photographs	AUSLIG	Landsat TM
Area of Habitats (km²)			
Mangrove			
Berkeley	1.31	0.72	1.53
Lyne	18.05	4.98	17.51
Embley	30.20	29.70	25.50
Saltflat			
Berkeley	2.38	2.58	2.22
Lyne	7.40	42.05	6.79
Linear Extent of Habitats (km)			
Mangrove			
Berkeley	36.45	5.04	17.76
Lyne	124.18	27.78	50.31
Embley	117.00	81.20	NA
Saltflat			
Berkeley	0.00	9.30	0.27
Lyne	0.00	66.36	0.00

This work has shown that topographic maps at scales of 1:250,000 or coarser can underestimate the area and linear extent of mangroves, particularly in localities such as north-western Australia, where rivers are typically lined by a very narrow fringe of mangroves. This could have serious implications for ecological studies that use these data, including attempts to model the relationship between habitat area and the productivity of commercial fisheries. However, since the AUSLIG dataset is relatively cheap to buy (AU\$50 per tile per theme), and is simple and quick to use, these maps are certainly still useful for obtaining a first-pass view of an area, before using higher-resolution techniques, such as aerial photography and Landsat TM imagery. These are readily available, and can achieve far better estimates of habitat extent, enabling improvements in the accuracy of ecological models to be made. The use of aerial photographs for fine-scale studies, and of Landsat TM or other satellite imagery over larger areas, provides the most cost-effective approach to accurate habitat mapping.

CONCLUSIONS

- The work in Chapter 3 has shown that the critical nursery habitats for red-legged banana prawns (*P. indicus*), like those for white banana prawns (*P. merguensis*) are mangrove-lined creeks and rivers. Establishing a baseline for the extent of mangroves (both area and linear length) is therefore important to:
 1. assess future changes in production of banana prawns; and
 2. the potential impacts of developments that remove coastal habitats on banana prawn production.
- The comparison of topographic maps, aerial photographs and Landsat TM imagery in 2 small creeks to estimate the extent of mangroves and saltflats in Joseph Bonaparte Gulf, showed that the accuracy of the estimates varies greatly between techniques. Aerial photographs had the highest resolution of the three techniques (2 m) and gave the most accurate estimates of habitat extent. Landsat TM has a resolution of 30 m and was able to discriminate mangroves except where the mangrove fringe is very narrow. This technique gave similar estimates of area to aerial photos but the estimates of linear extent of mangroves differed from those of aerials. AUSLIG topographic maps were the least accurate, except where the mangrove forests were greater than 50 m wide, but are still useful for broad-scale studies.
- The most appropriate technique to use will depend on the scale required and the extent of the area of interest. The choice of techniques for mapping coastal habitats is a trade-off between the resolution of the technique (and, therefore, its accuracy) and the costs of acquisition and processing. For example, it would not be feasible to establish a baseline for the whole of the Northern Prawn Fishery using aerial photographs. It may be possible to achieve this using Landsat TM.

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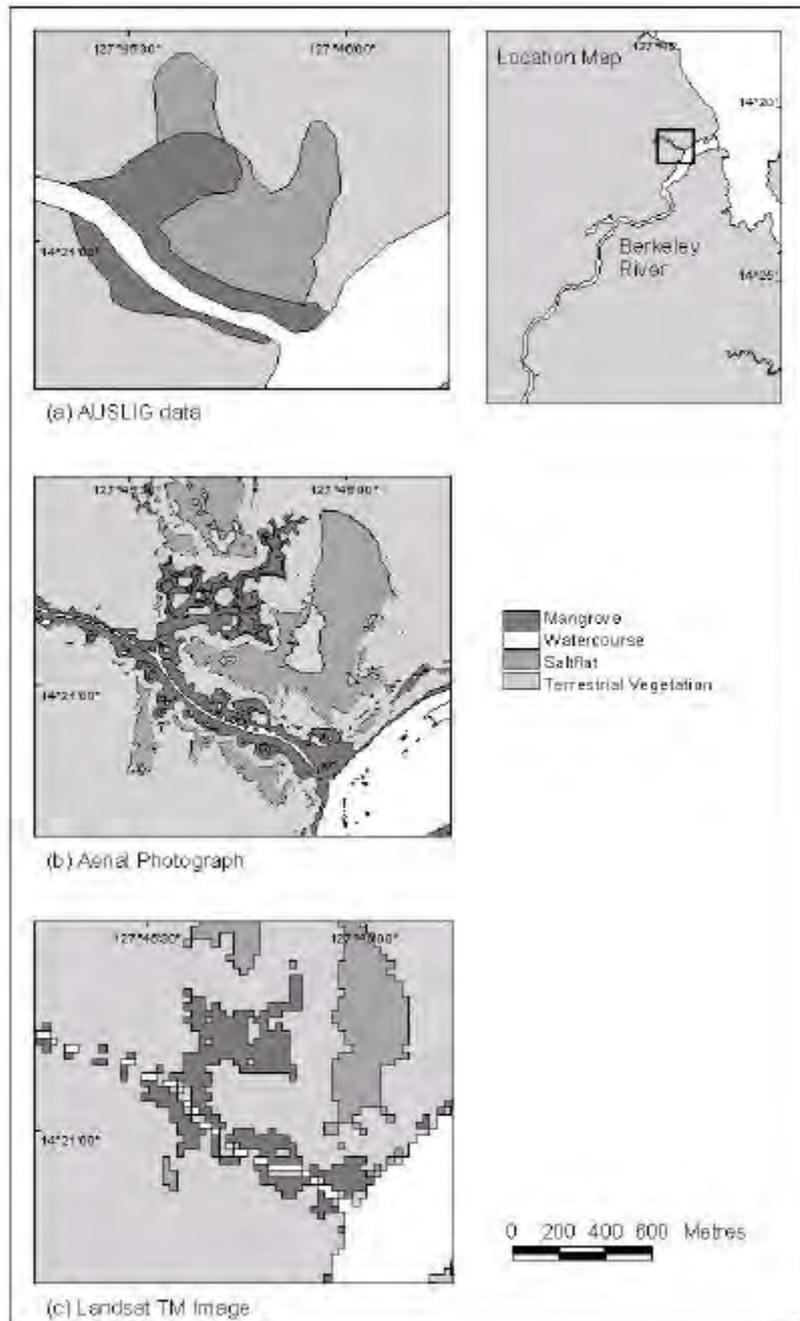


Figure 4.1 A comparison of the three mapping methods. The habitats (mangroves, saltflat, river and terrestrial vegetation) are shown for a side creek of the Berkeley River. (a) AUSLIG data, (b) classification of an aerial photograph, (c) classification of a Landsat TM image.

5. CHAPTER FIVE: DESCRIPTION OF THE FISHERY FOR RED-LEGGED BANANA PRAWNS IN THE JOSEPH BONAPARTE GULF

(Authors: NR Loneragan, DJ Vance, DJ Die)

INTRODUCTION

Banana prawns (*Penaeus merguensis* and *P. indicus*) are distributed widely throughout the Indo-West Pacific region where they contribute to important commercial and traditional fisheries. In Australia, the white banana prawn *P. merguensis* extends from Shark Bay on the west coast, across northern Australia into northern New South Wales on the east coast (Grey *et al.* 1983). In contrast, the red-legged banana prawn, *P. indicus*, is restricted to tropical waters, north of 15° S.

The Northern Prawn Fishery (NPF) is Australia's most important prawn fishery with total annual catches ranging from 6,000 to 8,000 t in the last 5 years (Sharp *et al.* 2000). Catches of banana prawns can vary greatly from year to year, but have accounted for about 40 to 50% of the total prawn catch in the Northern Prawn Fishery, with those of red-legged banana prawns in the Joseph Bonaparte Gulf (JBG) accounting for about 20% of the total annual banana prawn catch in the NPF in the last 10 years (range = 8 to 38%). Fishing for prawns in the NPF was based initially on white banana prawns in the Gulf of Carpentaria in the mid-1960s, followed by the discovery of tiger prawns in the 1970s. The red-legged banana prawns in the JBG were only discovered in the early 1980s.

Unlike the fishery for *P. merguensis*, which is a daytime fishery targeting schools of prawns in shallow waters, the fishery for *P. indicus* takes place in deeper waters and in the day or night. In addition, *P. indicus* are fished throughout the fishing seasons of the NPF, while the fishing for *P. merguensis* takes place mainly in the first 4 weeks of fishing, which now starts on April 1. The fleet then starts fishing tiger prawns (mainly *Penaeus esculentus* and *P. semisulcatus*) or red legged banana prawns in the Joseph Bonaparte Gulf.

Due to the large tidal amplitude range in the JBG (up to 7m), *P. indicus* are fished on the neap tides, when tidal currents are least. Thus, over a tide cycle, fishing effort is high on the late spring-neap, neap and early neap-spring tides, and low to non-existent at other times when the fleet moves to fishing grounds north of Melville Island and Port Essington, outside the JBG. The extra steaming time that this fishing pattern generates, together with the remoteness of the JBG and the lower price of *P. indicus* in comparison to other species of prawns, makes the JBG a less attractive area to fish than other parts of the NPF. As a result, the annual fishing effort in the JBG fishery is mostly dependent on the catch levels elsewhere in the NPF; if catches are good elsewhere, effort in JBG is low. Over the last decade, however, as catch levels elsewhere have declined (Wang and Die, 1996), the JBG fishery has become one of the main fisheries in the NPF and there is increasing concern on the status of *P. indicus* stocks.

The aims of this Chapter are to describe the fishery for red-legged banana prawns and the logbook and landings information system that provide the data for stock assessments. This Chapter also provides some of the background to the detailed tagging studies to estimate growth and mortality (Chapter 6), indications of movement patterns (Chapter 7) and the per-recruit modelling of yield, value and egg production (Chapter 8).

MATERIALS AND METHODS

CATCH AND EFFORT DATA

Catch and effort data for the Northern Prawn Fishery come from two sources: the daily logbooks of fishers and the landing returns from processors, both held by the Australian Fisheries Management Authority. Data from these sources are recorded by commercial species groups (banana prawns = *P. merguensis*, *P. indicus*; tiger prawns = *P. esculentus*, *P. semisulcatus*; endeavour prawns = *Metapenaeus endeavouri*, *M. ensis*; and king prawns = *P. latisulcatus*, *P. longistylis*). Since 1994, the total catches from logbooks are virtually the same as those from the landings returns.

ESTIMATES OF CATCH AND EFFORT

The catch of banana prawns was estimated by adjusting the reported catch from logbooks to match the total landings from processors' returns. This involved an adjustment factor of about 2 in the early 1970s to less than 1.05 in the 1990s (Saschse 1994). The nominal fishing effort was then estimated as the ratio between processor landings and the catch per unit effort (CPUE) calculated from the logbook data. This estimation assumes that the CPUE from logbooks is an unbiased estimate of the average CPUE for the whole fishery.

Fishing effort was allocated to either the banana prawn 'fishery' or the tiger prawn 'fishery' based on the composition of banana prawns in the catch: when banana prawns exceeded 50% of the catch, or when the catch was zero, effort was allocated to the banana prawn fishery, otherwise it was allocated to the tiger prawn fishery. Within each fishery, the catch was assigned to each species of banana prawn by the geographical distribution of the species determined from research surveys and sampling the catch of commercial vessels (Somers 1994). The effort was allocated to the species of banana prawns that was the highest proportion of the catch. The two species of banana prawn show virtually no overlap in their patterns of distribution. This method of allocating effort to the different species groups is currently being reviewed.

The level of effective fishing effort was not calculated. However, for stock assessments of *P. indicus* an adjustment to effort should be calculated due to likely increases in fishing power. This adjustment should lie somewhere between those for tiger prawns and those for *P. merguensis*. For tiger prawns, the average fishing power has been assumed to increase by 5% each year (Buckworth 1992, Somers 1994, Wang and Die 1996), and is currently being reviewed by the NPF Assessment

Group. The last major reduction in the number of boats operating in the NPF was in 1993 and about 125 boats have fished since this time. Data from the 1980s (1983 to 1989) have been compared with those from the 1990s (1990 to 1999) by calculating the mean, standard error and coefficient of variation for catch, effort and CPUE in each 'decade'.

CHANGES IN CLOSURES IN THE NPF

During the history of the NPF, various spatial and seasonal closures have been implemented at different times. Fishers were able to trawl throughout the year in most regions of the NPF until 1987, when an end of year (1 December to March/April) and a mid-year (June to August) closure were introduced. In the JBG, various areas have been closed to fishing in the first part of the year to protect juvenile prawns. The major area closed to fishing has remained the same since 1988.

These closures can be grouped into 4 main time periods:

- 1981-84: fishing though out the year
- 1985-86: closure from Cape Ford to Koolan Island (December to February/April); 1986 coastal strip in southwest JBG 1 January to 1 April)
- 1987: end of year NPF wide closure (1 December to 15 April); mid-year NPF wide closure (22 June to 1 August); inshore JBG closure (15 April to 1 August)
- 1988 – present: end of year NPF wide closure (1 December to March/April); mid-year NPF wide closure (22 June to 1 August); Cape Rulhieres to Cape Dombey closure (1 December to 1 August).

The percentage of total annual effort in each month was calculated for each year and the mean percentage of boat days in each month was then determined for each of the first 3 time periods above and from 1988-1992 and 1993-1999.

HISTORICAL CHANGES IN THE SPATIAL DISTRIBUTION OF EFFORT

Note that because of confidentiality agreements, catch and effort for grids that were fished for less than 10 days and where fewer than 5 boats fished cannot be published. We therefore used the AFMA daily logbook system to calculate the annual fishing effort and catch for each 6' x 6' grid in the fishery, and then estimated two indices to define the extent of the fishing grounds (Table 5.1). The first index is based on catch per grid. We ranked all grids according to the annual catch and selected those with the greatest annual catch (referred to as "most productive grids") that produced 80% of banana prawn catches. The second index was based on effort; for any given year we define the area of the fishing grounds as those grids with more than 10 fishing days a year (referred to as "most visited grids"). In contrast, the area encompassing all grids fished at least once is referred to as the "area searched". We defined the first year that a given grid became part of the fishing grounds as the "year of discovery" of that grid, and the last year the grid was ever fished as the "year of abandonment" (Table 5.1). Finally, we defined the "currently fished grids" as the combination of all the most visited grids in the period 1993-1999. We then calculated the catch produced by the currently fished grids during the entire history of the fishery.

Table 5.1 Indices used to define the change in extent of the fishing grounds in the Joseph Bonaparte Gulf, using the AFMA daily logbook system.

Index	Definition
Most productive grids	Grids that produce 80% of the catch
Most visited grids	Grids with > 10 fishing days
Area searched	All grids with recorded effort
Year of discovery	First year that the grid was fished
Year of abandonment	Last year that the grid was fished

RELATIONSHIPS BETWEEN CATCH, EFFORT AND RAINFALL

The relationship between catch of red-legged banana prawns and rainfall was investigated by a stepwise multiple regression analysis of annual catch with the total annual rainfall from July of one year to June of the following year and the monthly rainfall from November until April. A second multiple regression was used that included the annual effort and finally the annual CPUE was regressed against the rainfall variables. The distribution of the variables was checked for normality and where appropriate, the data were transformed before analysis. The rainfall data for this analysis came from the monthly average of 22 Bureau of Meteorology recording stations in the region.

RESULTS AND DISCUSSION

CATCH, EFFORT AND CPUE

Since 1981, between 43 and 94 (1986) vessels have operated in the Joseph Bonaparte Gulf. In recent years the number of vessels operating in the JBG has declined from about 60 in 1990 to 41 in 1995.

The data on species composition collected from the JBG suggest that, since 1984, *Penaeus indicus* have comprised over 90% of the banana prawns caught in the JBG banana prawn fishery. The estimated catches of *Penaeus indicus* from the banana prawn fishery increased rapidly from 3 t in 1980 to about 700 t in 1982 as the fishery developed (Fig. 5.1). Between 1983 and 1987 catches varied between 600 and 800 t, declined to 200 t in 1992 and then increased to 800 t in 1993. Catches varied by more than 300 t between 1996 and 1999, with the greatest fluctuation between 1997 (1, 000 t) and 1998 (300 t). The maximum estimated catch of *P. indicus* from the tiger prawn fishery in the JBG is only 31 t.

The number of days fished in the JBG increased to a peak of about 2, 300 boat days in 1986 and then declined to 670 boat days in 1992 (Fig. 5.1b). The variation in effort from 1993 until 1999 was less than in the 1980s as the number of boats operating in the NPF has stabilised. The catch per boat day between 1981 and 1991 was relatively stable at about 400 kg day⁻¹ (Fig. 5.1c). The catch per boat day has exceeded 400

kg·day⁻¹ in all years since 1992, except in 1998 (350 kg·day⁻¹). It has also varied more in recent years than before 1992.

The mean catch of *P. indicus* was about 100 t lower in the ‘1990s’ (576 t) than in the ‘1980s’ (686 t) (Table 5.2). However, the coefficient of variation was nearly three times higher in the 1990s than in the 1980s. The mean nominal effort in the 1990s (1082 boat days) was about 70% of the mean effort in the 1980s (1681 boat days). The coefficients of variation for effort in these two ‘decades’ were similar in magnitude. The mean catch per boat day was higher, and more variable in the 1990s (mean = 521 t, CV = 32%), than in the 1980s. (mean = 415 t, CV = 13%, Table 5.2).

Table 5.2 Summary for catch (estimated catch of *Penaeus indicus*) and effort statistics for the banana prawn fishery in the Joseph Bonaparte Gulf (JBG). CV = coefficient of variation.

Species and region	Years	
	1980s (1983-1989)	1990s 1990-1999
Catch (tonnes)		
Mean (± 1 SE)	686 \pm 32	576 \pm 75
Range	583 – 836	209 – 983
CV	13.0%	40.9%
Nominal Effort (boat days)		
Mean (± 1 SE)	1681 \pm 115	1082 \pm 79
Range	1257 – 2341	667 – 1445
CV	19.3%	23.0%
Nominal CPUE (kg per boat day)		
Mean (± 1 SE)	415 \pm 21	521 \pm 53
Range	320 – 490	310 – 860
CV	12.8%	31.9%

SPATIAL PATTERN OF FISHING

The total number of grids visited in the Joseph Bonaparte Gulf increased to a high of about 160 in 1986 and then declined to about 60 in 1994 (Fig. 5.2a). Since then it has only varied from 66 to 82 grids. The number of grids discovered in the JBG peaked in 1983 (60) and again in 1986 (40) (Fig. 5.2a). The number of abandoned grids also peaked in these two years. Few grids have been discovered or abandoned since 1990.

The proportion of the catch coming from the most visited grids in recent years (1993 to 1999) has exceeded 80% since 1992 and 90% since 1994 (Fig. 5.2b). However, the proportion of the catch taken in these grids varied from 60 to 80% between 1984 and 1991. In the early years of the fishery (1980-83), it varied from 17 to 60% (Fig. 5.2b).

The increased variation in both catches and CPUE in the 1990s compared with 1980s, despite the stabilisation in the grids that are fished in the 1990s is cause of concern. The reasons for this increased variation are unknown but might be related to changes in environment, or more effective targeting of prawns in the 1990s. They should be investigated in future assessments of the red-legged banana prawn stocks in the JBG.

In the combined years from 1981 until 1984, before seasonal closures to fishing were introduced, most fishing effort in the Joseph Bonaparte Gulf was completed between October and December, with peak effort in September (c. 25%) and October (c. 30%) (Fig. 5.3a). In 1985 and 1986, when an end of year closure was in place from December until February/April, most fishing was completed between June and September, with a peak in August of about 25%.

After the introduction of the mid-year closure in 1987 (June to August), the distribution of fishing effort became markedly bimodal, with a major peak in effort in May (c. 30 to 40%), and a second, much broader peak between August and November (effort levels of around 10%, Fig. 5.3b). This represents a major shift in patterns of fishing effort over the history of the fishery: in the early years of the fishery most effort was spent in the later part of the year (September to December), compared with the current situation of a marked peak in May, with a lesser broader peak between August and November.

RELATIONSHIPS BETWEEN CATCH, CPUE, EFFORT AND RAINFALL

January rainfall was the only variable fitted to the multiple regression for annual catch with rainfall variables and explained about 20% of the variation in the relationship (Table 5.3a). When effort was added to the independent variables, it accounted for 50% of the variation in catch (Table 5.3b). Annual rain and November rain were also fitted to this multiple regression and the three variables in the multiple regression together accounted for about 72% of the variation in catch. Annual rainfall and November rain were both fitted to the multiple regression equation for CPUE and together accounted for about 55% of the variation in CPUE (Table 5.3c).

Table 5.3 Percentage of variation explained by significant variables fitted to the multiple regression between catch and rainfall and effort. Data for annual rainfall and CPUE were $\log_{10}(n)$ transformed before analysis. Superscript shows significance of the variable in multiple regression.

Multiple regression and variables entered in the equation	R^2 and P for each variable
(a) Annual catch with rainfall only	
January rain	19.6 ^{0.05}
(a) Annual catch with rainfall and effort	
Annual effort	50.7 ^{<0.001}
Annual rain	13.7 ^{0.02}
November rain	7.7 ^{0.05}
(c) Annual CPUE with rainfall	
Annual rain	43.2 ^{0.002}
November rain	12.8 ^{0.04}

CATCHES IN THE GULF OF CARPENTARIA

In the Gulf of Carpentaria, annual total catches in the banana prawn fishery have varied between 2, 000 and 4, 000 t between 1980 and 1999 (Fig. 5.5). Total annual catches in the tiger prawn fishery declined from about 7, 000 t in the early 1980s to about 3, 300 t in 1986. Since then, they have ranged from 2, 900 t (1999) to 5, 100 t (1995).

Both catch and effort in the banana prawn fishery of the Joseph Bonaparte Gulf were negatively correlated with total catches from the banana prawn fishery, tiger prawn fishery and both fisheries in the Gulf of Carpentaria (Table 5.4). However, the correlations were either similar, or higher for effort than catch. The highest correlation was between total catch from both fisheries in the GOC and effort in the JBG, which accounted for about 34% of the variation in this relationship ($r = -0.59$, Table 5.4). These results suggest that the dynamics of the fishery in the JBG are affected by catch rates in the Gulf of Carpentaria and this factor needs to be incorporated in future assessments of the status of red-legged banana prawn stocks in the JBG.

Table 5.4 Pearson correlation coefficients between catch of *Penaeus indicus* and banana prawn effort in the Joseph Bonaparte Gulf (JBG), and total catches in the banana and tiger prawn fisheries of the Gulf of Carpentaria (GOC). N = 19 in each case.

Fishery in the GOC	Banana prawn fishery in the JBG	
	<i>P. indicus</i> catch	Effort
Banana	-0.40	-0.37
Tiger	-0.11	-0.52
Both fisheries	-0.25	-0.59

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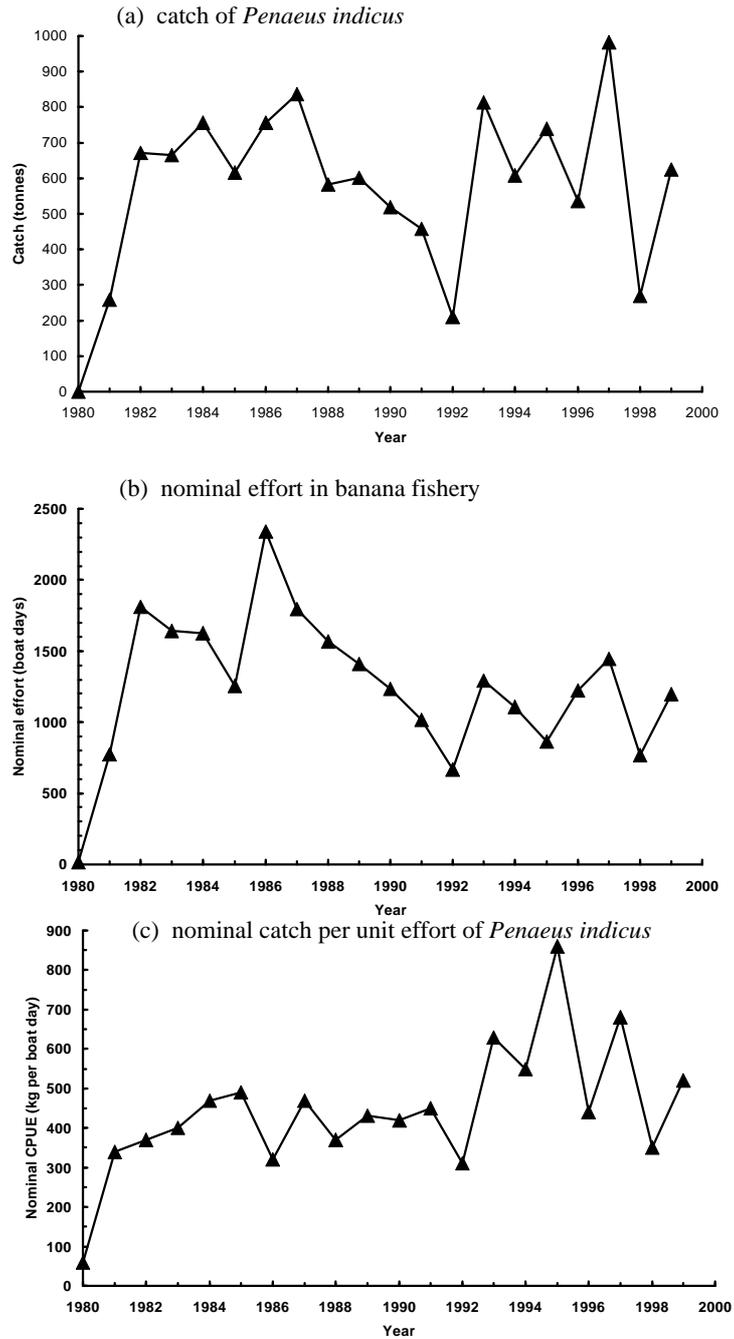


Figure 5.1 Annual (a) estimated catch of *Penaeus indicus* (b) effort and (c) catch per unit effort for the banana fishery in the Joseph Bonaparte Gulf

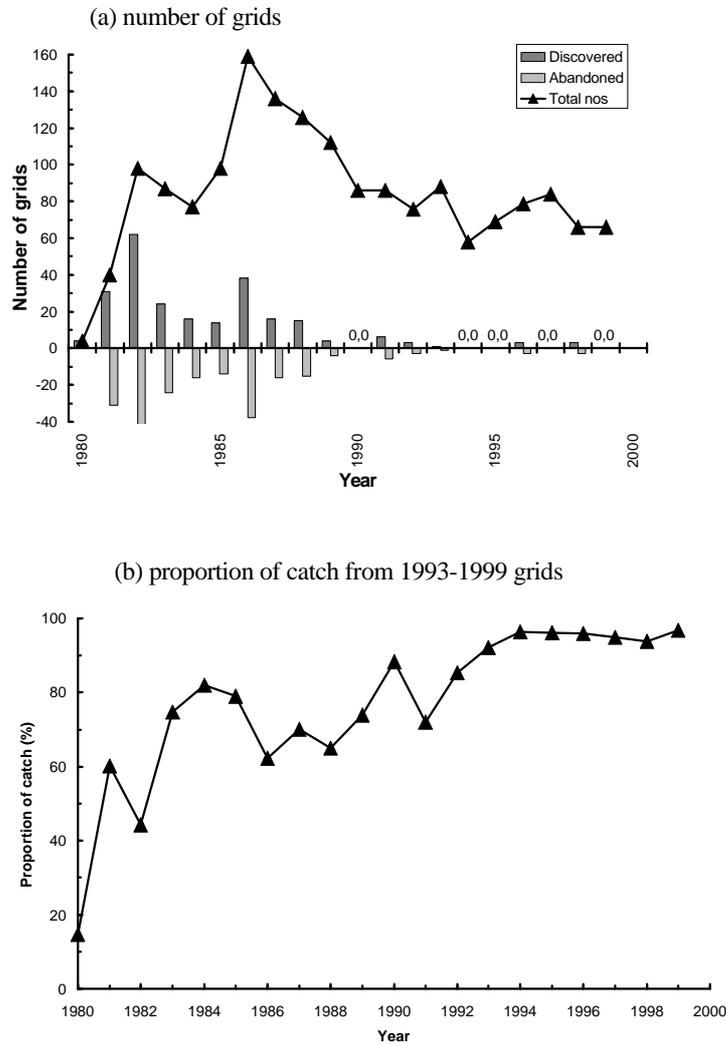


Figure 5.2 Summary of changes in fishing patterns in the Joseph Bonaparte Gulf for (a) the total, discovered and abandoned grids and (b) the proportion of catch coming from the most visited grids from 1993 until 1999.

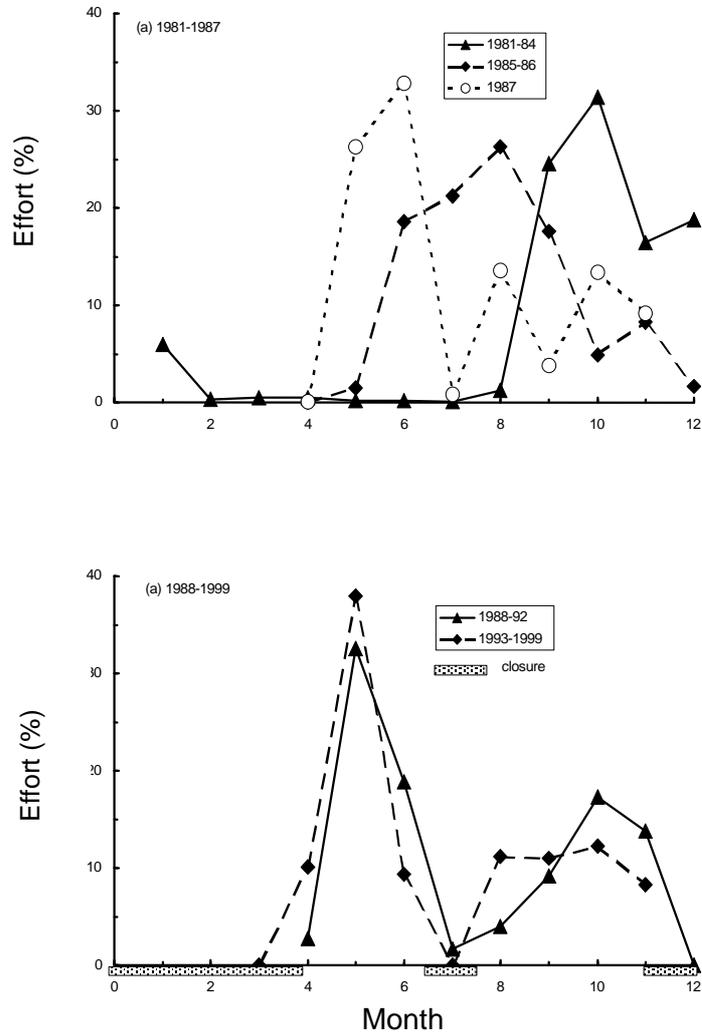


Figure 5.3 Percent of effort in the banana prawn fishery for groups of years with different closure regimes in the Joseph Bonaparte gulf. See text for description of exact times of seasonal closures

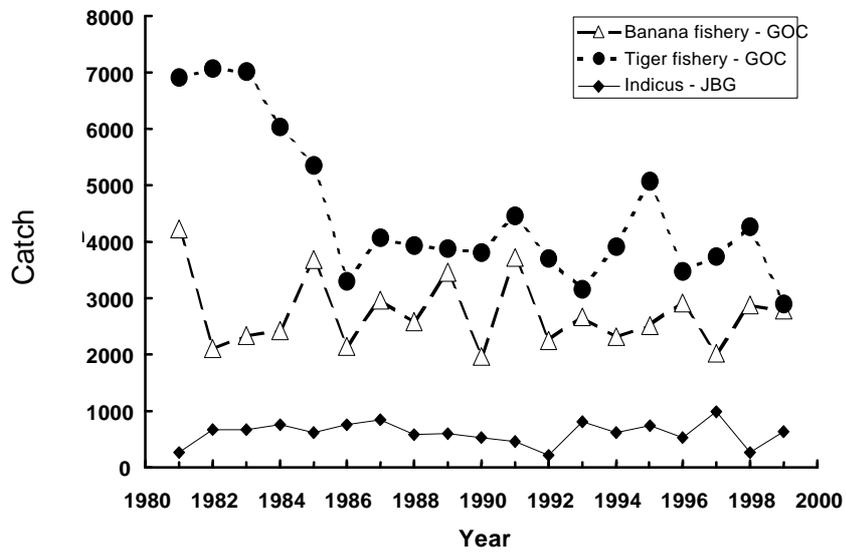


Figure 5.4 Total annual catch for the tiger and banana prawn fisheries in the Gulf of Carpentaria and annual catches of *Penaeus indicus* in the banana prawn fishery of the Joseph Bonaparte Gulf between 1981 and 1999

6. CHAPTER SIX: GROWTH AND MORTALITY OF RED-LEGGED BANANA PRAWNS

(Authors: DJ Die, NR Loneragan, RA Kenyon, B Taylor)

INTRODUCTION

The red-legged banana prawn fishery in the Joseph-Bonaparte Gulf (JBG) is an important, but little studied component of the Northern Prawn Fishery (see Chapter 5). The closure regimes in the JBG are the same as those introduced primarily to manage tiger prawns and banana prawns (*P. merguensis*) in the Gulf of Carpentaria. A recent evaluation of these closure regimes and their impact on yield, value and egg-production per-recruit found that the results of the model were sensitive to the values of growth and mortality used in the model (Loneragan *et al.* 1997). The only values for these parameters available at the time were literature values for other species (particularly *P. merguensis*) in other regions.

In 1997 and 1998, a tag-release-recapture experiment was undertaken in the JBG to estimate the growth and mortality of the *P. indicus* population in this region. Most tagging experiments make a number of assumptions about the tagging and recapture process: the two most important assumptions are that each tagged animal has the same probability of recapture and that this probability is the same as that of capturing an untagged animal from the population. Before estimating the mortality rates, these assumptions about the tagging were tested. Similar tagging studies have been undertaken for other NPF prawn species (Somers and Kirkwood 1984, Somers 1987); and other species elsewhere (Glaister *et al.* 1987, Derbyshire *et al.* 1990, Montgomery *et al.* 1995). The new estimates of growth and mortality from our tagging study were used to revise the stock assessment completed by Loneragan *et al.* (1997) (see Chapter 8).

METHODS

FIELD TAGGING AND RELEASE

The tagging program was designed to tag prawns twice in each of two years (1997 and 1998), before fishing started in the JBG (i.e. before April 1). This was done to allow tagged prawns to mix with untagged prawns before fishing started and would have allowed both natural mortality and fishing mortality to be estimated.

We decided to focus our analysis on the main cohort in each year. This was achieved by identifying this cohort from the size frequency distribution of the first set of catches in the first tag and release cruise. Only those animals within the size range defining this cohort were tagged. Prior to the second cruise, we predicted the size range of that main cohort from growth information (CSIRO, unpublished data) and only tagged animals in this size range. This procedure was designed to ensure that the

two groups of tagged animals belonged to the same cohort before the start of fishing. Restricting the tagging to the main cohort of prawns helped maximise the chances that animals from both sets of tag-release cruises had the same probability of recapture.

In 1997, the first tagging was completed in March. However, the second tagging was delayed until just after fishing had started in April because of a tropical cyclone in the JBG. We restricted our tagging to prawns that were less than 31.5 mm CL in March and less than 32.5 mm CL in April. In 1998, we tagged prawns in February and March, before any fishing in the region. The prawns were larger in 1998 than in 1997 and tagging was restricted to prawns less than 36 mm CL in February and less than 39 mm CL in March.

To reduce damage to the prawns, short trawls (about 10 min duration) were made with otter trawls, before the catch was winched on-board and sorted. All live prawns were transferred to flow-through seawater tanks. The prawns were allowed to acclimatise for about an hour, before they were measured (carapace length to the nearest 0.1 mm) and sexed, then tagged with streamer tags (see below) through the 2nd abdominal segment. The tagged prawns were transferred to holding baskets in flow-through tanks and allowed to acclimatise before being transferred to the release cage, and released overboard. Prior to release tagged prawns were checked for swimming response and those not actively swimming were discarded. They were released in batches of between 100 and 200 prawns per release cage. The number of tagged prawns that died before release as a consequence of tagging and handling (handling mortality before release) was also recorded in the hope that it indicated the overall condition of prawns in a given release. The water temperature of the holding tanks was about 28-30°C and the flow rate of the circulating seawater was in excess of 50 l min⁻¹.

Prawns were released on the bottom of the JBG in 45-65 m of water. A release cage was used to transfer prawns from the surface to the bottom. It consisted of a rectangular aluminium cage with one complete side in the form of a flap, which opened when activated by a heavy stainless steel “sender” on the rope that lowered and retrieved the cage.

TAGS

Polyethylene streamer tags (Hallprint streamer tags, numbers 5 and 7; 77 mm by 3 mm and 57mm by 3mm, respectively) were inserted using an attached needle which was daubed in Aureomycin antibiotic ointment. Each tag was individually numbered to identify each prawn.

RELEASE SITES

In 1997, the majority of tagged prawns were released in an area towards the southern extent of the fishing grounds, as defined by the area where catch is relatively high (Fig. 6.1a). The release sites were chosen in two localities within a relatively small area, to ensure good mixing of the tagged-prawns and the non-tagged population for mortality estimation. One group of releases was made just south of the first-season closure line, while a second group was made just north of the closure line (Fig. 6.1a).

Most of these latter releases were made during April/May, when prawns were caught further north than in March. A third group of releases, (735 prawns or 8.7 % of all releases) was made in the northern portion of the fishing grounds, about 50 km northeast from the majority of release sites (Fig. 6.1a).

In 1998, tagged prawns were released in the southern portion of the fishing grounds, similar to the majority of releases in 1997 (Fig. 6.1b). All prawns were released south of the first-season closure line, except one batch that was released on the line (Fig. 6.1b).

SIZE AT RELEASE OF TAGGED PRAWNS

In 1997, 8,474 tagged *P. indicus* were released, compared with 9,538 tagged prawns in 1998 (Table 6.1). In 1997, the mean carapace length (± 1 SE) of tagged male prawns was 27.2 ± 0.16 mm in March and 29.0 ± 0.10 mm in April (Table 6.1). The corresponding sizes for females were 26.8 ± 0.19 mm in March and 30.1 ± 0.13 mm in April (Table 6.1). The mean size of tagged and released prawns was about 2 to 6 mm larger in 1998 than in 1997 (Table 6.1).

Table 6.1 The number and size of prawns released in two releases in (a) 1997 and (b) 1998. Release 1 = March for 1997 and February for 1998. Release 2 = April for 1997 and March for 1998.

Parameter	Release 1		Release 2	
	Male	Female	Male	Female
(a) 1997	(March)		(April)	
Number released	2,030	1,832	2,900	1,712
(Total nos)	(3,862)		(4,612)	
Mean size (mm \pm SE)	27.2 ± 0.16	26.8 ± 0.19	29.0 ± 0.10	30.1 ± 0.13
Size range (mm)	21.7 – 35.8	20.8 – 31.8	24.0 – 32.2	25.8 – 33.7
(b) 1998	(February)		(March)	
Number released	2,500	1,870	3,249	1,919
(Total nos)	(4,370)		(5,168)	
Mean size (mm \pm SE)	29.8 ± 0.12	32.3 ± 0.23	30.4 ± 0.12	33.2 ± 0.23
Size range (mm)	24.8 – 35.7	25.7 – 37.2	27.8 – 35.5	29.2 – 38.4

RETURN OF TAGGED PRAWNS

A novel tag-reward scheme was used to encourage a high and consistent return rate for tagged prawns and promote awareness of the tag-release-recapture experiment among the fishing fleet. The rewards consisted of ‘Scratch-it’ tickets, costing \$3 each. This could lead to a prize of up to \$10,000 or no reward at all. For a subset of the returned prawns (all those with tags ending in “9”), we offered an additional cash reward of \$50, to test whether the ‘Scratch-it’ tickets provided enough incentive to ensure a high reporting rate of tagged prawns. Fishers were asked to provide details of the location, depth, date and time of the recapture. Recaptured prawns were collected from Darwin, Cairns, Karumba and Perth in June and November each year i.e. immediately following the mid-year and end of year closures. On-shore processing plants were contacted to check whether tagged prawns may have been missed on the trawlers. No tagged prawns were recovered from the processing plants and all tag returns came from commercial fishers. All prawns were identified, sexed and measured after being collected and taken back to the Cleveland Laboratory.

ESTIMATION OF GROWTH RATES

We used size-at-release, size-at-recapture and time-at-liberty data from tag-returns from 1997 and 1998 to model growth rates using the following procedure:

1. Investigate differences in growth rates between sexes and years
2. Group data when no differences were found between sexes or years
3. Fit data to a growth model that incorporates variability in L_8 and measurement error

To determine whether there were differences between sexes and years we used the Fabens’ (1965) model because its simplicity lends itself better to hypothesis testing than other models. Although the Fabens’ model may produce biased estimates of growth parameters, the test of differences between years and sexes should not be affected by the bias. It is well known (Die 1992a) that if the distributions of length at release are very different between data sets, testing of differences in growth with the Fabens’ model can be misleading. To make sure of the robustness of our tests we examined the distributions of length at release and length at recapture. Adjusted R^2 for all non-linear fits were calculated as:

$$R_{adj}^2 = 1 - \frac{(n-1)(1-R^2)}{n-p}$$

(6.1)

where n is the number of observations and p the number of parameters.

We then chose to fit the data to a model that incorporates variability in growth. The model is by Wang (1995) and only attempts to estimate individual variability in $L\mu_8$,

$$\Delta L = [L_\infty + \beta\{L_1 - E(L_1)\} - L_1] (1 - e^{-K\Delta t}) + \varepsilon$$

(6.2)

where ΔL is the increase in length between release and recapture, L_1 is the length at release, Δt is the time spent at sea, L_8 and K are the von Bertalanffy growth parameters, β is a parameter measuring the amount of variability in L_8 and ε is the unexplained error (includes model and measurement error). As suggested by Wang (1995) we fitted this model by a least squares procedure.

ESTIMATION OF MORTALITY RATES

Prior to using the tagging data to estimate mortality rates, we attempted to test some of the assumptions made by the survival models used to estimate mortality rates.

Testing the basic assumptions of tagging experiments designed to estimate survival rates

Most tagging experiments make a number of assumptions about the tagging and recapture process (Cormack, 1968). The two most basic assumptions are :

1. every tagged animal has the same probability of recapture, and
2. the probability of recapture is the same for tagged animals and those from the untagged population (Ricker 1975).

Ensuring that the tagged population is selected randomly from the wild population contributes towards having a probability of capture for the tagged population similar to the probability of capture for the untagged population. It does not, however, guarantee that these probabilities will be equal. The process of releasing tagged individuals into the wild and the mixing of these individuals with the wild stock also affects these probabilities. For assumption two to be fulfilled, the tagged and untagged populations must mix thoroughly. This assumption is difficult to test as the spatial distribution of most mobile animals is rarely known and often changes with time. In addition, tagging is an expensive and logistically difficult process. The number of sites and times when animals can be collected, tagged and released are often constrained. Because of these constraints, it is often not possible to select and release animals at random from the population. It is therefore essential to attempt to test the assumptions of equal probability of capture for tagging studies.

The recapture probability of tagged prawns can be affected by the characteristics of the tagged animals (size, sex), the tagging procedure (tag type, handling mortality), the conditions at release for each batch of tagged animals (location, date, time) and

the level of cooperation of fishers (size of reward). It is difficult to say how these different factors affect the tag-recapture rate, and ultimately, the estimates of survival rates. It is known, however, that small prawns are less likely to be captured if their size is smaller than the size selected by the commercial gear and targeted by fishers. Larger rewards may also increase the reporting rate of tagged prawns by commercial fishers, and thus the recapture rate.

For the purposes of this analysis tag release times were classified into four groups, midday (11:00 – 14:00), afternoon (14:00 – 17:00), dusk (17:00 – 20:00) and night (20:00 – 24:00).

Given the time and date of release a relative tidal speed was calculated as:

$$speed = \left| \frac{h_{t-0.01} - h_{t+0.01}}{0.02} \right| \quad (6.3)$$

where h_t is the tidal height at release time t (in hours). Approximate tidal heights at time t were estimated from Australian National tide tables for Cape Domett (14.8°S, 128.4°E) and the interpolation method proposed in these tables.

During tagging, prawns were sexed and measured and this information was recorded together the type of tag and the location and time of release. Two types of streamer tags (large, 77 mm long and small, 57 mm long) were used to test whether there was an optimum tag type for the size of prawns being tagged. The number of tagged prawns that died before release as a consequence of tagging and handling (handling mortality) before release) was also recorded in the hope that it indicated the overall condition of prawns in a given release.

To test the effect of all the above variables in the probability of recapture we used a generalised additive model (GAM) to identify the different factors affecting tag recapture rates. This model allows for linear and non-linear terms to be added, with the advantage that no parametric form needs to be assumed for the non-linear terms. With so many factors to test at the same time, any procedure is likely to have difficulty in converging on a solution unless the data are extensive and very informative. Therefore, we reduced the complexity of the analysis by initially only using the data for the first tagging cruise in March 1997. This left us with a model with one continuous variable (length) and six categorical variables (sex, tag type, time, date, reward and tagger). We implemented the following generalized additive model in SPLUS,

$$R = \alpha + \beta_1 time + \beta_1 date + \beta_1 reward + \beta_1 sex + \beta_1 tagtype + \beta_1 tagger + f(length) \quad (6.4)$$

where $f(length)$ is a non-parametric spline function. We used a binomial distribution as link function.

Estimation of mortality rates

From testing the assumptions about tagging (see Results section below), size-at-release affected the probability of recapture in 1997 but not in 1998. This is probably because in 1997, many of the tagged prawns were smaller than the size at full selection (i.e. the size when all prawns are retained in the codend) when they first became available to the commercial fishing fleet. In 1998, however, tag releases were made earlier in the year and fishing started later in the year. As a result all tagged prawns had grown beyond the size at full selection, which would explain why there were no differences in recapture rates between prawns released at different sizes in 1998. Because of these differences between the two years, we used two types of model to estimate survival. The first model was size structured, and could accommodate the differences in recapture rates between prawns released at different sizes. This model was used to analyse the 1997 tagging data. The second model was not size structured and therefore ignored differences in recapture rates with size – it was used to analyse data from both 1997 and 1998.

Size-structured model

A population model was developed to estimate the rate of natural mortality. The population model attempts to predict the number of recaptured prawns $R_{c,t,l,i}$ from each cruise c , time period t , length at release l and sex i , as a function of the original number of prawns $T_{c,l,i}$ released in each cruise, of each length at release and sex. The predicted number of recaptures is assumed to be proportional to the ratio of fishing and natural mortality in period t ,

$$R_{c,t,l,i} = \left(N_{c,t+1,l,i} - N_{c,t,l,i} \right) \frac{F_{c,t,l,i}}{F_{c,t,l,i} + M} \quad (6.5)$$

Where $F_{c,t,l,i}$ is the fishing mortality rate, M is the natural mortality rate and $N_{c,t,l,i}$ is the number of tagged prawns having survived to time t calculated as,

$$N_{c,t+1,l,i} = N_{c,t,l,i} e^{-(F_{c,t,l,i} + M)}$$

and (6.6)

$$N_{c,0,l,i} = T_{c,l,i}$$

Fishing mortality is assumed to be a function of fishing effort f_t , the catchability coefficient and the selectivity $S_{c,t,l,i}$ for each length at release and sex at time t ,

$$F_{c,t,l,i} = f_t q_i S_{c,t,l,i} \quad (6.7)$$

where selectivity is assumed to be a logistic function of the length $L_{c,t,l,i}$ attained at each time t by prawns released with length l ,

$$S_{c,t,l,i} = \frac{1}{1 + e^{a-bL_{c,t,l,i}}} \quad (6.8)$$

where a and b are parameters of the logistic function. $L_{c,t,l,i}$ is calculated from the length at release and the sex-specific von Bertalanffy parameters,

$$L_{c,t,l,i} = L_{\infty,i} + e^{-k_i} (L_{c,t-1,l,i} - L_{\infty,i})$$

and

$$L_{c,0,l,i} = l$$
(6.9)

The parameters of the von Bertalanffy equation used were those estimated from the analysis of growth data by the Faben's model (see Results Table 6.5). Estimates of M , q_i , a and b were obtained by the least-squares method using the non-linear minimiser SOLVER found in EXCEL. The sum of squares minimized was,

$$SSQ = \sum_c \sum_t \sum_i \left(r_{c,t,i} - \sum_l R_{c,t,l,i} \right)^2$$
(6.10)

where $r_{c,t,i}$ is the observed number of recaptured prawns for a given time period, sex and cruise. Note that, for simplification, we do not use the information of the observed length at recapture in the estimation of survival parameters. Our model assumes that there is no individual variability in growth rates and therefore that all prawns released at a given size are the same size at any time t . The time period used for the calculations was 15 days and fishing effort was calculated from the logbooks as the number of fishing days in the Joseph Bonaparte Gulf where more than 50% of the catch was banana prawns or when fishing was taking place but no catch was reported. Most effort on banana prawns in 1997 took place 15 to 45 days after the opening of the first season on April 1 (Fig. 6.2). A second, smaller peak of effort was recorded during the first 45 days following the opening of the second season on August 1 (Fig. 6.2).

Non size-structured model

This model aims to predict the number of tagged and untagged prawns surviving at each time period, regardless of sex and size. It uses information on the number of tagged prawns $r_{c,t}$ from each cruise c recaptured per 15 day time period t and also on the total number of untagged prawns caught $C_{y,t}$ each year at each time period. The latter was estimated from the weight of banana prawns recorded in the logbooks $W_{y,t}$ and the average weight of prawns $P_{y,t}$ landed during that period,

$$C_{y,t} = \frac{W_{y,t}}{P_{y,t}}$$
(6.11)

Data on landings by commercial count $L_{y,t,cc}$ were provided by Newfishing Australia and were used to estimate the average prawns weight for each time period in the analysis (Table 6.2). Landings by Newfishing Australia represented about 15% of total landings of redleg banana prawns from the Joseph Bonaparte Gulf. Average prawn weight was estimated by assuming that average weight per commercial count category p_{cc} was constant during both years and, when possible, equal to the weight of the mid point of the category (Table 6.3).

$$P_{y,t} = \frac{\sum_{cc} L_{y,t,cc} p_{cc}}{\sum_{cc} L_{y,t,cc}} \quad (6.12)$$

Note that on average, prawns were larger in 1998 than in 1997, but the number landed was much greater in 1997 (Tables 6.2, 6.3).

The model then predicts the abundance of the untagged and tagged portions j of the population,

$$N_{j,t+1} = N_{j,t} e^{-(F_{j,t} + M)} \quad (6.13)$$

and where the initial number of prawns in the tagged populations are equal to the total number of tagged prawns released during each cruise c and the initial number of prawns in the untagged population is equal to the recruits Q_y for that year y ,

$$N_{j=c,0} = T_c \quad N_{j=y,0} = Q_y \quad (6.14)$$

Table 6.2 Average individual weight (g) of *Penaeus indicus* landed in the Joseph Bonaparte Gulf by Newfishing Australia, and estimated total number of prawns caught (in thousands) by the whole fleet for each 15 day time period during 1997 and 1998. Period 1 starts on April 14th in 1997 and April 16th in 1998. * No data available for this period and weight was assumed to be the same as that for the next period. Note that only time periods used in the analysis of tagging data are presented here. A small quantity of prawns was landed outside these periods.

15 day Time period	Average weight (g)		Numbers landed (x 10 ⁻³)	
	1997	1998	1997	1998
1	29.2	37.7*	518	60
2	26.3	37.7	7,475	2,528
3	25.8	36.4*	12,750	1,580
4	25.6	36.4	4,533	1,025
5	28.1		1,727	
6				
7				
8				
9	30.9*		4,335	
10	30.9		1,496	
11	40.4		1,337	
12	40.7		295	
13	35.5		187	
14	31.3*		287	
15	31.3		114	

Table 6.3 Assumed average count and average weight (g) of individual prawns for each commercial category.

Category	Average Count per pound	Average Weight per prawn (g)
U10	8	57
U15	13	35
10/20	15	30
15/25	20	23
21/30	26	17
31/50	40	11

The fishing mortality rates are assumed to be proportional to the observed fishing effort and the catchability coefficient for each group of prawns,

$$F_{j,t} = f_t q_{j,t} \quad (6.15)$$

the numbers of prawns caught in each group $Y_{j,t}$ is then modelled as,

$$Y_{j,t} = (N_{j,t+1} - N_{j,t}) \frac{F_{j,t}}{F_{j,t} + M} \quad (6.16)$$

Estimates of M , $q_{j,t}$ and Q_y were then obtained by the least-squares method using the non-linear minimiser SOLVER found in EXCEL. The sum of squares minimised was,

$$SSQ = \sum_j \sum_t h_j (X_{j,t} - Y_{j,t})^2 \quad (6.17)$$

where h_j is the relative weight given to each portion of the population and where,

$$X_{j=c,t} = r_{c,t} \quad Y_{j=y,t} = C_{y,t} \quad (6.18)$$

relative weights were set to $h_{j=c} = 1$ and $h_{j=y} = 10^{-9}$ so that the contribution to the sum of squares for each portion of the population was of the same order of magnitude.

We investigated four model options to fit the data well, but minimise the number of parameters to be estimated (Table 6.4). The simplest model is option A where catchability is considered to be constant for all time periods (t), cruises (c) and years (y) but differs between tagged and untagged groups i.e. only two catchability parameters are estimated – one for tagged prawns and the other for untagged prawns. Option B assumes that catchability differs between groups, i.e. between cruises, years and between tagged and untagged prawns and estimates five catchability parameters. Option C (9 catchability parameters) is similar to Option B but in addition, assumes that in 1997 catchability changes after the mid year closure. Option D is a less complex model than Options B and C – it makes the same assumptions about catchability for untagged prawn, but for tagged prawns assumes that catchability changes between releases (release 1 = March 1997 and February 1998); release 2 = April 1997 and March 1998) but not between years (5 parameters). Note that during 1998, not enough tagging and catch data were available to estimate parameters for the time period after the mid-year closure.

Table 6.4 The catchability parameters estimated for each option of the non size-structured model for year y, time period t and cruise c.

Model option (nos parameters)	Catchability parameters
A (2)	$q_{y,t} = q_1$ $q_{c,t} = q_2$
B (6)	$q_{y,t} = q_y$ $q_{c,t} = q_c$
C (9)	$q_{y,t=1,\dots,8} = q_{y,1}$ $q_{y,t=9,\dots,15} = q_{y,2}$ $q_{c,t=1,\dots,8} = q_{c,1}$ $q_{c,t=9,\dots,15} = q_{c,2}$
D (5)	$q_{97,t=1,\dots,8} = q_{97,1}$ $q_{97,t=9,\dots,15} = q_{97,2}$ $q_{98,t=1,\dots,8} = q_{98,1}$ $q_{1,t} = q_1$ $q_{2,t} = q_2$

RESULTS

RETURN OF TAGGED PRAWNS

In 1997, a total of 916 tagged prawns were returned (10.8% return rate), compared with 512 tag returns for prawns released in 1998 (5.4% return rate). Information on size and location of capture could be obtained for over 97% of the returned prawns (892 prawns in 1997 and 506 in 1998, Table 6.4). In 1997, about 650 tagged prawns were returned from the first half of the 1997 fishing season (i.e. before June 15th), and about 250 were returned from the second-half of the season (August 1st to November 30th) (Fig. 6.3). In 1998, only 16 prawns were returned during the second half of the season. No tagged prawns released in 1997 were caught during the 1998 season.

The largest male prawn returned measured 35.7 mm CL and the largest female returned was 46.3 mm CL (Table 6.4).

Table 6.5 The number and mean size (carapace length \pm 1 SE) of prawns recaptured from different releases during (a) 1997 and (b) 1998. Number refers to the number of prawns that could be measured.

Parameter	Release 1		Release 2	
	Male	Female	Male	Female
(a) 1997	(March)		(April)	
Nos returned	290	198	237	167
Mean size (mm)	30.8 \pm 0.09	34.6 \pm 0.25	30.0 \pm 0.10	33.0 \pm 0.28
Size range (mm)	25.5 – 35.7	27.5 – 45.2	24.3 – 35.0	26.4 – 43.1
(b) 1998	(February)		(March)	
Nos returned	162	95	145	104
Mean size (mm)	32.4 \pm 0.07	38.8 \pm 0.21	32.0 \pm 0.11	38.0 \pm 0.24
Size range (mm)	30.5 – 35.1	28.0 – 42.7	29.3 – 39.4	31.4 – 46.3

The number of recaptures during 1997 was clearly a function of the fishing effort (Fig. 6.2) and the catch of *P. indicus* obtained by the NPF fleet (Fig. 6.3). The highest numbers of recaptures were made at the times of highest catches – five and seven weeks after the opening of the first season (Fig. 6.2). There was a clear decrease in the number of recaptures over time.

The catches of banana prawns and the fishing effort in the Joseph Bonaparte Gulf were much higher in 1997 (1, 019 t, 1504 boat days) than in 1998 (288 t, 812 boat-days, Chapter 5, Sharp *et al.* 2000). During 1997, about one tagged prawn was taken per tonne of catch, while during 1998, two to three tagged prawns were taken per tonne of catch.

During both 1997 and 1998, virtually all (\geq 94%) of the tagged prawns recaptured during the first season were taken in the first four weeks of fishing.

ESTIMATION OF GROWTH RATES

Complete information for the growth analyses was obtained from 844 of the returned prawns in 1997 and 474 prawns in 1998. Prawns that were at liberty for less than 10 days were excluded from the growth analyses.

The size frequency distribution of tagged prawns from the first release in 1997 (March, GM01) differed in shape from the returns – proportionally fewer small prawns were returned than were released (Fig. 6.4). This suggests that the initial size at release influenced the probability of recapture. However, this was not the case for

the three other releases where the size distributions at-release and at-return were similar in shape.

Fitting the growth models to the tagging data showed significant differences in growth between sexes, but not between years (see also Fig. 6.5). Therefore for all subsequent analyses, data for 1997 and 1998 were aggregated into a single data set. The Fabens' model (monthly time steps) estimated the L_8 for male *P. indicus* as 33.8 mm CL, and 46.2 mm CL for females (Table 6.5). The Fabens' estimate of K was 0.011 for males and 0.0069 for females, while the best estimate of t_0 was 0.0 for both sexes (Table 6.5).

The fit to the data of to the Wang (1995) model did not improve the sum of squares significantly, which suggests that the individual variability in L_8 is low and that β does not differ significantly from zero (Table 6.5). The parameter estimates for males from the Wang model ($L_8 = 34.1$ mm CL, $K = 0.0103$) were very similar to those obtained from the Fabens' model. However, for females the Wang estimate of L_8 was larger (49.6 mm CL) and the K was smaller (0.0053) than the estimates from the Fabens' (1965) model.

From the Fabens' model, *P. indicus* grew faster at 50 days of age (males - 1.42 mm wk⁻¹; females - 1.53 mm wk⁻¹) than at either 100 days (males - 0.82 mm wk⁻¹; females - 1.09 mm wk⁻¹), or 150 days of age (males - 0.48 mm wk⁻¹; females - 0.77 mm wk⁻¹).

Table 6. 6 Estimates of growth parameters and goodness of fit for the Fabens' (1965) and Wang (1995) growth models

Parameter	Fabens' model		Wang's Model	
	Females	Males	Females	Males
K	0.0069	0.0110	0.0053	0.0103
L_8	46.24	33.81	49.64	34.05
B			-0.34	-0.06
SSQ	1802.1	1802.1	1310.0	451.2
R^2_{adj}	0.76	0.76	0.70	0.74

ESTIMATION OF MORTALITY RATES

Testing assumptions on tagging and releasing prawns

The GAM analysis of the 1997 data revealed that the probability of recapture increased with size and reached an asymptote for larger lengths (Table 6.6, Fig. 6.6). The probability of recaptures was affected significantly by date, time and sex (Table 6.6).

Table 6.7 Estimates of the scaled deviance and significance (*P*) from the Generalised Additive Model used to investigate the influence of different factors on recapture rates for data from 1997.

Factor	Df	Residual	Deviance	Chi square	<i>P</i> (Chi)
Null			3861	2949	
Date	7	139.2	3854	2810	0.000
Reward	1	0.2	3853	2810	0.667
Time	1	10.7	3852	2799	0.001
Sex	1	13.3	3851	2786	0.000
Type	1	0.5	3850	2785	0.486
Tagger	2	3.6	3848	2782	0.160
Size	3	216.2	3844	2566	0.000

When the GAM analysis was repeated for the 1998 data, size at release was not significant. This suggests that in 1998, the tagged prawns were large enough by the time fishing started that their probability of recapture was not affected by their initial tagging size. Neither tag type, nor the size of the reward affected recapture rates in 1998.

MORTALITY RATES

Size-structured model (1997 only)

The predicted number of recaptures for each cruise and sex in 1997 were close to the observed number of recaptures (Fig. 6.7). The estimated natural mortality rate was 0.05 per week. The estimate of catchability for males of 0.00026 was higher than the estimate of 0.00015 for females. This results in estimated peak weekly fishing mortality rates of 0.044 for males and 0.026 for females. The total annual fishing mortality rates for males and females were 0.36 and 0.21 in 1997. It is unclear why the recapture rates were greater for males than those for females and as a result the estimates of catchability and fishing mortality were also greater for males. These differences in recapture rates between the sexes cannot be explained by differences in size because the model takes into account size. Even if natural mortality is allowed to vary by sex in the estimation these differences between the sexes persist.

Estimates of the selectivity parameters *a* and *b* from equation 5.8 were respectively 14.0 and 0.53. The selectivity equation estimates that 50% of 26.5 mm CL *P. indicus* and 90% of 30.5 mm CL individuals are retained by commercial gear.

Non size-structured model (1997 and 1998)

The total sums of squares improved markedly as the complexity of the model increased with the addition of new catchability parameters, and the lowest sums of squares were obtained for Model option C, with 9 catchability parameters (Table 6.7). However, the sums of squares for Model D with 5 catchability parameters, were only

slightly larger than those for Model C. The improvement in the sums of squares for model A compared to model B is mainly due to better fit to the tagging data (Table 6.7). The improvement of sum of squares from model B to model C is almost exclusively due to better fit to the 1997 untagged data.

Table 6.8 Estimates for the relative sum of squares for each portion of the population for four non size-structured models. NP = nos of parameters in the model.

Model (NP)	Untagged		Tagged				Total
	1997	1998	1997 March	April	1998 February	March	
A (2)	22,388	231	10,271	29,509	4,840	1,687	68,925
B (6)	22,607	97	4,539	25,780	2,336	1,562	56,922
C (9)	13,172	102	4,113	25,209	2,026	1,707	46,330
D (5)	13,135	97	4,474	25,913	2,286	2,041	47,947

The estimates of recruitment were between three (Model A) to six times (Model B) greater in 1997 than in 1998, depending on the model used (Table 6.8). Models B, C, and D gave similar estimates in the proportional difference in recruitment between 1997 and 1998 (4.9 to 6.4 times higher in 1997), though the absolute numbers of recruits differed. The greatest difference in estimated absolute recruitment between years was found for model C when a recruitment of 77 million prawns was estimated for 1997 compared with about 15 million prawns for 1998. This is due to the larger estimate of natural mortality found for this model ($M = 0.067$ per week) than the other models. The estimated mortalities for the other models were lower than 0.044 per week (Model D, Table 6.8).

Table 6.9 Estimates of the number of recruits (millions) and natural mortality (per week) from the four non size-structured models. NP = number of parameters in the model.

Model (NP)	Recruits (millions)		Natural mortality rate (week ⁻¹)
	1997	1998	
A (2)	62.7	19.3	0.032
B (6)	72.5	11.4	0.040
C (9)	77.0	14.9	0.067
D (5)	58.0	11.8	0.044

The estimates of catchability for the untagged part of the stock were greater than those for the tagged stock for all models (Table 6.9). The estimated values for q from Models B, C (season 1 only) and D were about two times higher in 1998 than 1997, and greater for the period after the mid year closure (i.e. Season 2) than before it (Season 1) (Table 6.9). The catchabilities estimated from Models B, C and D were

about two times greater for the first tagged group (March 1997 and February 1998) than for the second tagged group (April 1997 and March 1998).

Table 6.10 Estimates of the catchability of *Penaeus indicus* from the four non size-structured models. NP = number of parameters in the model. Season 1 = April to mid-June; Season 2 = August to November. Release 1 = March 1997 or February 1998; Release 2 = April 1997 or March 1998.

Model and year (NP)	Season	Catchability ($\times 10^{-4}$)		
		Untagged	Tagged	
			Release 1	Release 2
A (2)				
Both years	1 & 2	7.00	1.23	
B (5)				
1997	1&2	6.06	2.07	0.96
1998	1&2	14.64	2.08	1.22
C (9)				
1997	1	6.45	2.69	1.01
1997	2	31.03	5.79	2.55
1998	1	11.67	2.93	1.51
D (5)				
1997	1	8.27	1.03	
1997	2	35.48	2.16	
1998	1	14.24		

DISCUSSION

RED-LEGGED BANANA PRAWN FISHERY

The reduction in fishery catch from 1,019 tonnes in 1997 to 288 tonnes in 1998 was accompanied by a reduction in effort from 1,504 nominal boat days to 812 nominal boat-days, respectively (Sharp *et al.*, 2000). The reduction in effort by the fleet probably explains our five percent tag-return rate in 1998 compared to ten percent in 1997, as fewer boats were searching in the fishery.

GROWTH

When individuals vary in their pattern of growth, the Fabens' (1965) model leads to biased estimates of L_8 and K (Hearn 1986, Wang 1995). Unfortunately, even models that acknowledge the presence of individual variability can produce biased estimates if their assumptions do not reflect the way that growth varies in natural populations. However, these same models show very little bias if the growth of individuals varies with time. In addition to problems with bias, it seems that for many data sets it is difficult to estimate the individual variance of K simultaneously with that of L_8 (Hampton 1991).

The results from fitting our data to the Wang (1995) growth model, suggest that the variability in L_8 between individual *P. indicus* is small. The unexplained variance in our fits can therefore be best associated with model error rather than with individual variability in L_8 or measurement error. The variability in L_8 for brown tiger prawns *Penaeus esculentus* is also low (Wang 1995). This contrasts with the variability in L_8 for grooved tiger prawns *P. semisulcatus*, where it was significant (Wang 1995). If the individual variability in growth for *P. indicus* is in fact low, it should be possible to accurately estimate the relative age of this species from length data. Furthermore, it suggests that the differences in length between prawns of the same sex collected at a particular time can be associated with differences in age, and thus birthdate (Die 1992b). Length data could then be transformed to relative ages and used in age-structured population models.

Our data were well suited to the Wang (1995) model because we aimed at tagging only a single cohort each time, therefore reducing the variability in age at the time of tagging. We also attempted to tag small prawns to maximise the amount of information contained in tagging data.

The fact that the Wang model did not detect significant individual variability in L_8 is surprising given that individual variability in growth seems to be clearly present in the data (Fig. 6.8). To investigate the variation in growth between individuals, we selected 77 prawns that had the same size at release (mean $CL \pm 1 SE = 30.7 \pm 1$ mm). In addition to the obvious difference in growth rate observed between males and females, there are obvious differences in their apparent growth rates (Fig. 6.8) that cannot be attributed to the time they have spent at sea. These differences in growth between individuals were particularly marked for females.

The estimated average relative age (± 1 SD) of females at the time of tagging was 153 ± 31 days, 25 days younger than that of males (178 ± 42 days). There is no evidence that male and female *P. indicus* recruit at different times to the fishing grounds or that the season of recruitment differs between the sexes. It therefore seems unlikely that the average age of male and females during the period of recruitment to the fishing grounds would differ by almost a month and that the variance in age of males should be twice that for females. This discrepancy could be explained if the assumption that t_o is the same for both males and females is not valid. We suggest that when these growth parameters are used for stock assessment purposes, t_o is adjusted so that the relative ages are comparable — for *P. indicus*, the t_o for males could be made 25 days earlier than that of females. Note that although t_o is just a parameter of the growth curve with no biological meaning, it is important to use values that will predict relative ages that are consistent with the observations. In fact, the growth of most penaeids does not start to diverge between males and females until they approach maturity (Die, unpublished data). Given that the growth rates after maturity are so different, the von Bertalanffy equation should not be used to describe growth from juveniles to senescence. It is likely that the best strategy for modelling penaeid growth is to use three equations: one for immature animals; one for mature males; and one for mature females. Many authors modelling prawn populations seem to have made the assumption that $t_o = 0$, without investigating whether the above effect was important (e.g. Die and Watson 1992, Wang and Die 1996, Watson *et al.* 1993). The importance of the effect depends on the smallest age/size considered in the modelling (the size of recruits) – the effect and possible bias is smaller for larger recruits.

The highest and lowest catches of *P. indicus* ever recorded in the Joseph Bonaparte Gulf were made during the two years of our tagging study. Our estimates of recruitment from the 4 options of the non-size structured model suggest that recruitment was 3 to 6 times higher in 1997 than in 1998 (Table 6.7). The fact that we did not find significant differences in growth between these very different recruitment years suggests that density dependent effects on growth are not important during the exploitable phase of *P. indicus* in the JBG. Furthermore, it suggests that the growth curve estimated from our study can be used to confidently represent the growth of *P. indicus* in other years. Because our data sets had very similar distributions of lengths at-release and at-recapture for the three of the four releases, we believe that the comparisons of growth curves between years are robust. Unless these conditions apply, comparisons of growth parameters between tagging data sets are unreliable (Die 1992a).

MORTALITY

Testing assumptions of tagging

We initially thought that the large and small streamer tags might have influenced recapture rates differently, through having different effects on survival, tag retention, or tag detection. However, we did not detect a significant difference in recapture rates between tag types, despite the large difference in size between the two streamer tags.

The absence of an effect due to the size of the reward on recapture rates suggests that one of the main sources of under-reporting, the size of the incentive, was not a factor during our study. Other sources of under-reporting, e.g. failing to detect tagged animals in the catch, unwillingness to collaborate with scientists because of conflict of opinions, may have affected recapture rates. However, these other sources do not necessarily bias the equal probability of recapture assumptions among tagged prawns. These sources may, however, reduce the average probability of recapture for tagged prawns and should be considered as a source of bias in the estimation of survival rates with tagging data.

The reason that length affects recapture rates is probably related to the size selectivity of commercial prawn nets and the size of the prawns at release. Small prawns have lower probability of retention by the net's codend. In the second year, the tagged prawns were probably large enough by the time fishing started to all have the same probability of recapture. This can be seen from the difference in the sizes at-release and at-recapture between the two years (Tables 6.1, 6.4). Both the released and recaptured prawns were larger in the second year, indicating that the tagged population was made up of prawns larger than the sizes that are only partially retained by the net. An alternative hypothesis is that tagging mortality is significant among small prawns. Under laboratory conditions the mortality of small tagged prawns (<20 mm carapace length) was significantly greater than for untagged prawns (Hill and Wassenberg 1985). However, results from laboratory tagging studies with *P. indicus* (Loneragan *et al.* 1997) showed that the survival of tagged and untagged prawns did not differ at sizes similar to those tagged during our field studies. However, some of the prawns tagged in March 1997 were up to 8 mm CL smaller than those used in the laboratory studies.

We do not know why recapture rates differed between the sexes. Two possibilities are suggested, morphometric differences between the two sexes, or behavioural differences that determine the prawn's availability to capture. Regardless of the reason for these differences, it forced us to estimate separate mortality rates for each sex.

Further analyses of the data to test the assumptions of the tag-release models have suggested that the difference in recapture rates between times of day and dates is a reflection of different recapture rates between batches of releases (the groups of 100 to 200 tagged prawns that were released in a given spot), and not between dates or times of the day of the releases. Tagged prawns returned to the sea within the same batch tended to remain close together. As a result, prawns of the same batch tended to be recaptured together. This is an appealing hypothesis for *P. indicus*, as they are known to aggregate naturally. Possibly the tagged prawns released in the same batch join the same aggregation and therefore remained closer to one another than to other tagged prawns from different batches. This partial mixing, however, does not necessarily preclude us from using the tagging data to estimate survival coefficients. The presence of within batch correlation will increase the standard error of survival estimates because the tagged population will in fact be made up of aggregations of tagged prawns. In future work, such within batch correlation could be incorporated in the model used to estimate survival. This would reduce the standard errors of the survival coefficients.

Estimates of mortality and catchability for stock assessment

The estimate of weekly natural mortality rate obtained with the size-structured model (0.05) was within the range of estimates obtained for the non size-structured models (0.032 – 0.067). These values equate to a range of monthly natural mortality rates between 0.13 and 0.28, similar to the range of monthly mortality rates used in a per-recruit analysis of this fishery (0.15 to 0.25, Loneragan *et al.* 1997). Our new estimates of the von Bertalanffy k for males (0.34) and females (0.21) give an average estimate for both sexes of 0.27 close to the highest value of k used by these authors (0.25).

The estimates of catchability q were much higher for the untagged than for the tagged stock. This may reflect a shortcoming of the models and not necessarily an effect of tagging. The estimates of q for the untagged stock relate only to the part of the untagged stock that was subject to fishing, and not to the entire untagged stock. Thus untagged prawns outside the area of the fishery were not incorporated in the model to predict catches. In contrast, the total initial number of tagged prawns was known, and therefore the estimates of q for tagged prawns are for the entire population of tagged prawns (not just those within the area of the fishery). If tagging had no effect on survival, the ratio of estimates of q between the tagged and untagged stocks might provide an indication of how much of the tagged stock was outside the fishing grounds. Alternative interpretations are that there was substantial mortality of tagged prawns due to the tagging procedure or that changes in behaviour of tagged prawns made them less catchable than untagged prawns. However, laboratory studies on the effects of tagging on *P. indicus* suggest that it does not effect their survival (Loneragan *et al.* 1997).

The estimates of catchability q for the tagged prawns from the size-structured (0.00026 for males, 0.00015 for females) and non size-structured models (0.00012 to 0.00058) were of the same order of magnitude. They are mostly higher than the estimate of 0.0001 previously used for *P. indicus* per-recruit models (Loneragan *et al.* 1997). The estimates of q for the untagged stock with the non size-structured models ranged from 0.0006 to 0.0035 and are much greater than the value used in the previous per-recruit modelling. They are also larger than the estimated q of 0.00024 estimated for the white banana prawns *P. merguensis* in the Gulf of Carpentaria (Somers and Wang 1997).

Care should be taken in making comparisons between the estimated catchabilities of different species because catchability is related to the nature of fishing effort, the size of the stock and its level of aggregation. Although both species of banana prawns aggregate, *P. merguensis* aggregates intensely to form “boils” that are fished by making ‘short’ trawl shots of less than 1-h (Die and Ellis 1999). Trawl shots in the red-legged banana prawn fishery of the Joseph Bonaparte Gulf are longer than 1-h, but shorter than the 3 to 4-h shots made in the tiger prawn fishery of the Gulf of Carpentaria. The densities of prawns within aggregations have been estimated for *P. merguensis* (Die and Ellis 1999), but not for *P. indicus*. The longer trawl shots for *P. indicus* suggest that their densities in aggregations are likely to be lower than those of *P. merguensis*. The *P. merguensis* stock in the Gulf of Carpentaria extends over a much larger area than the *P. indicus* stock in the JBG. It is the combination of all of these factors that explains the estimated differences in catchability.

The estimated catchabilities q from the non size-structured model differed between fishing seasons – they were higher in the second season (i.e. after the mid-season closure) than in the

first season. Since the estimated stock size was smaller during the second season, red-legged banana prawns may become more aggregated at smaller stock sizes.

Comparison of exploitation rates between red-legged and white banana prawns

The catchability estimates for red-legged banana prawns in the Joseph Bonaparte Gulf were similar in magnitude to those for white banana prawns in the Gulf of Carpentaria. The total annual effort spent in those fisheries, however is very different: around 4,200 fishing days for white banana prawns, and only 800 days for red-legged banana prawns. This implies that the total annual fishing mortality rate is five times larger for white banana prawns, than for red-legged banana prawns. The monthly mortality rate for white banana prawns estimated by Lucas *et al.* (1979) was 0.2. During April, about 3,500 fishing days are spent fishing for white banana prawns in the Gulf of Carpentaria, which according to equation 5.15, represents a fishing mortality of 0.875 and an exploitation rate ($F/(F + M)$) for this species of 0.8. This means that during the first month of the fishing season, fishing represents 80% of the total mortality suffered by white banana prawns and that 66% of the stock dies during that period. In contrast, the peak fishing effort observed for red-legged banana prawns is around 600 fishing days in the first month of the season in the JBG, which equates to a fishing mortality of 0.21 and an exploitation rate of 0.58. This means that fishing represents 58% of the total mortality suffered by red-legged banana prawns during the first month of the fishing season and that 30% of the stock dies during that period. These estimates confirm that the exploitation rate for red-legged banana prawns is much lower than that of white banana prawns, but can still be high over a short period.

CONCLUSIONS

- Von Bertalanffy growth parameters for *P. indicus* in the JBG were estimated through tagging. Estimates were different to those estimated for the same species in other areas. Surprisingly, individual variability in growth within the main fished cohort was estimated to be low, suggesting that length is a good predictor of age for this species. This supports the use of length data for the purposes of conditioning age-structured stock assessment models for this species. It is recommended, however, that when these models are used, the age scaling parameter t_0 is adjusted so that male and female prawns have a similar age at the time they recruit to the fishery. Growth did not differ between years the two years of this study, despite large differences in the estimated recruitment between years. This suggests that the estimated growth rates could be applied in future assessment models and therefore that there is no need to re-estimate growth in the near future. It may be important, however to check if cohorts born at substantially different times of the year also have the same growth rates.
- Recapture rates were estimated to vary as a function of the characteristics of the tagged animals (size, sex), and the conditions at release for each batch of tagged animals (location, date, time) but not as a function of the tag-recapture procedure (tag type, size of reward). Variations due to size and sex can be controlled through experimental design by selecting animals during tagging, or accounted for

in the estimation model. Although we do have an explanation for the differences between sizes (gear selectivity), we do not know why recapture rates differed between males and females. The reasons for this difference e.g. differences in morphometrics, gear selectivity or behaviour between the sexes, should be explored. Variations in recapture rate between batches of tagged animals are difficult to control but generate substantial variation in recapture rates. Controlling some of the conditions may reduce the variance in the estimation of recapture rates. However, the variation may represent real differences in the fate of prawns located in different areas, therefore it may represent real natural variability. In the later case it is important that such variability is taken into account in the estimation and assessment process, and that it is not ignored by overly controlled tagging experiments.

- Estimates of natural mortality rates remain uncertain, but within the range of the values used previously in the assessment of this species. Estimates of catchability differ greatly between tagged and untagged prawns, but this may be the result of shortcomings of the modelling and not of real differences between tagged and untagged prawns. This could result from the fact that the initial size of the tagged population is known and that of the untagged population is unknown. Estimates of the catchability for the untagged population may be biased and this should be further investigated.
- Fishing mortality rates and exploitation rates for *P. indicus* are lower than those for *P. merguensis* in the Gulf of Carpentaria. It is not known, however, whether the exploitation rates for *P. indicus* are sustainable or if they are negatively affecting the recruitment of young red-legged banana prawns. It is therefore essential for future research to investigate the long term impact of fishing on the productivity of the *P. indicus* stock in the JBG.

In summary this research was very valuable for providing better estimates of the population parameters that form the basis of stock assessments of *P. indicus*. Estimates derived from this study show that growth rates and catchability parameters used by Loneragan et al (1997) in their evaluation of fishing closures were too low, and highlights the need for repeating their analysis with the new parameters (Chapter 8).

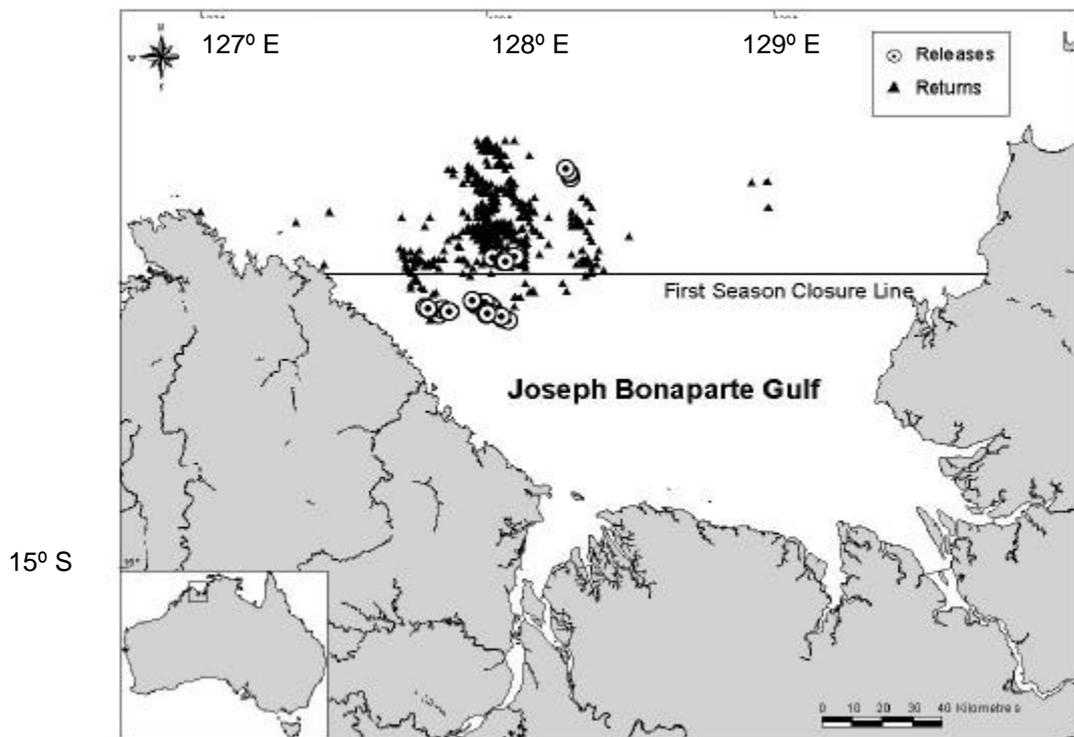
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(a) 1997



(b) 1998

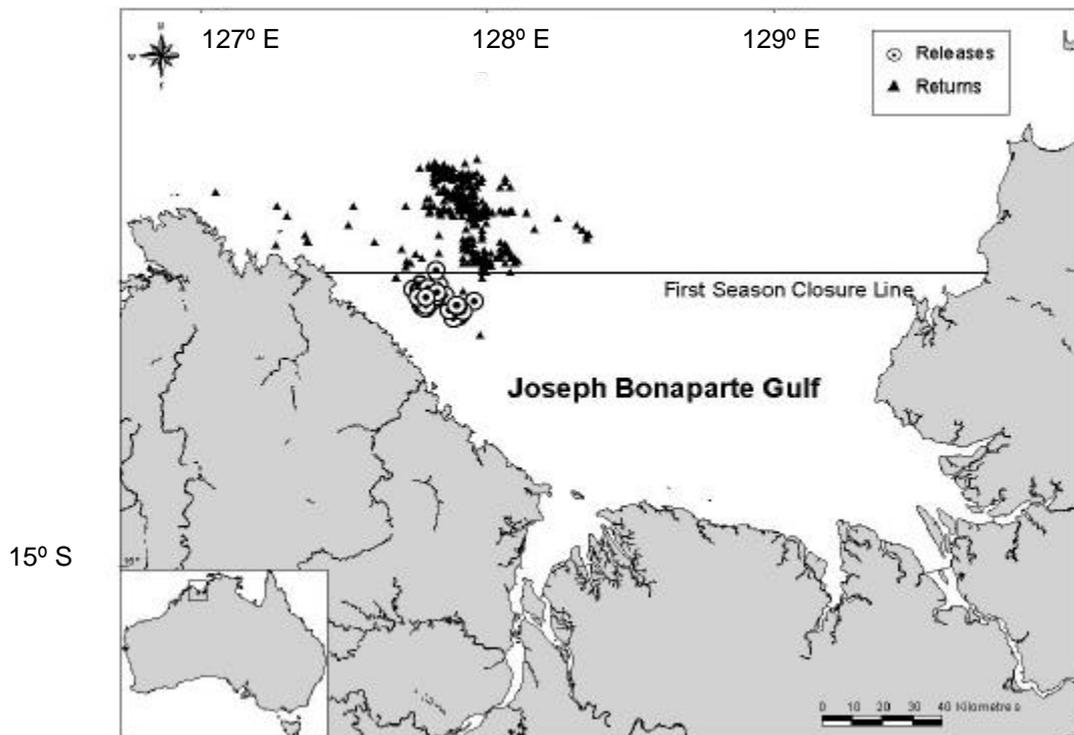


Figure 6.1 The locations of tagged prawn release and recapture sites in (a) 1997 and (b) 1998.

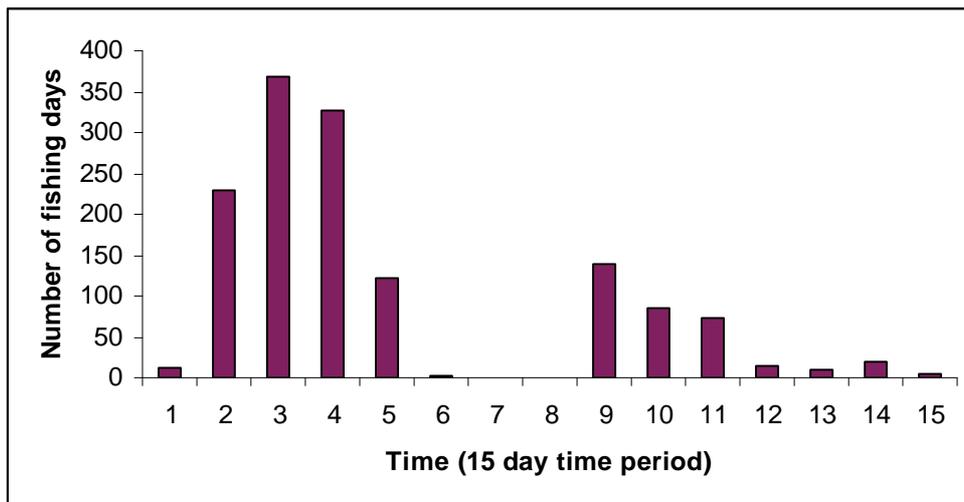


Figure 6.2 Fishing effort (number of fishing days where more than 50% of the catch was banana prawns, or there was no catch) in the JBG during 1997, immediately after the release of tagged prawns in March. Time is represented in 15 day intervals. Time 1 starts on April 1 and Time 9 on August 1.

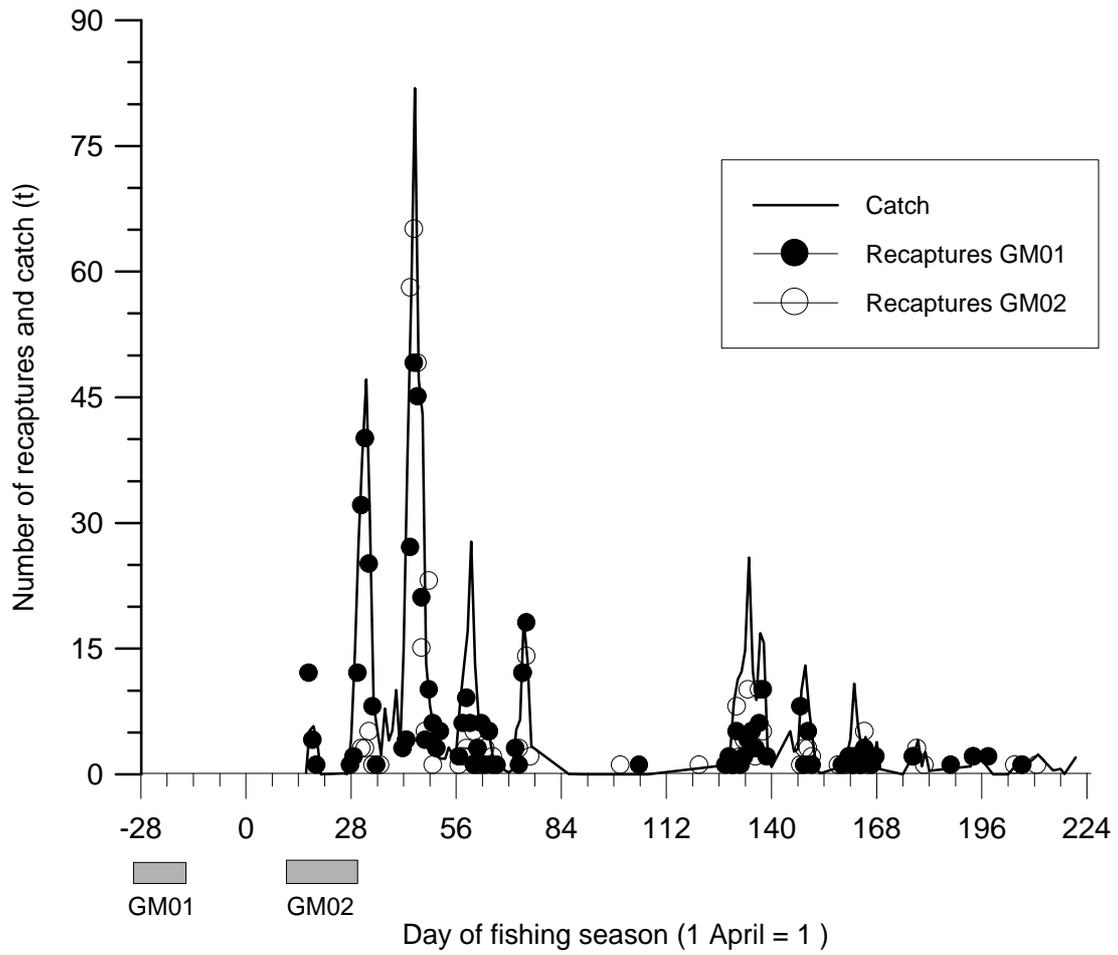


Figure 6.3 Number of recaptures from tag-releases in March (GM01) and April (GM02), and total catch of the fleet during 1997.

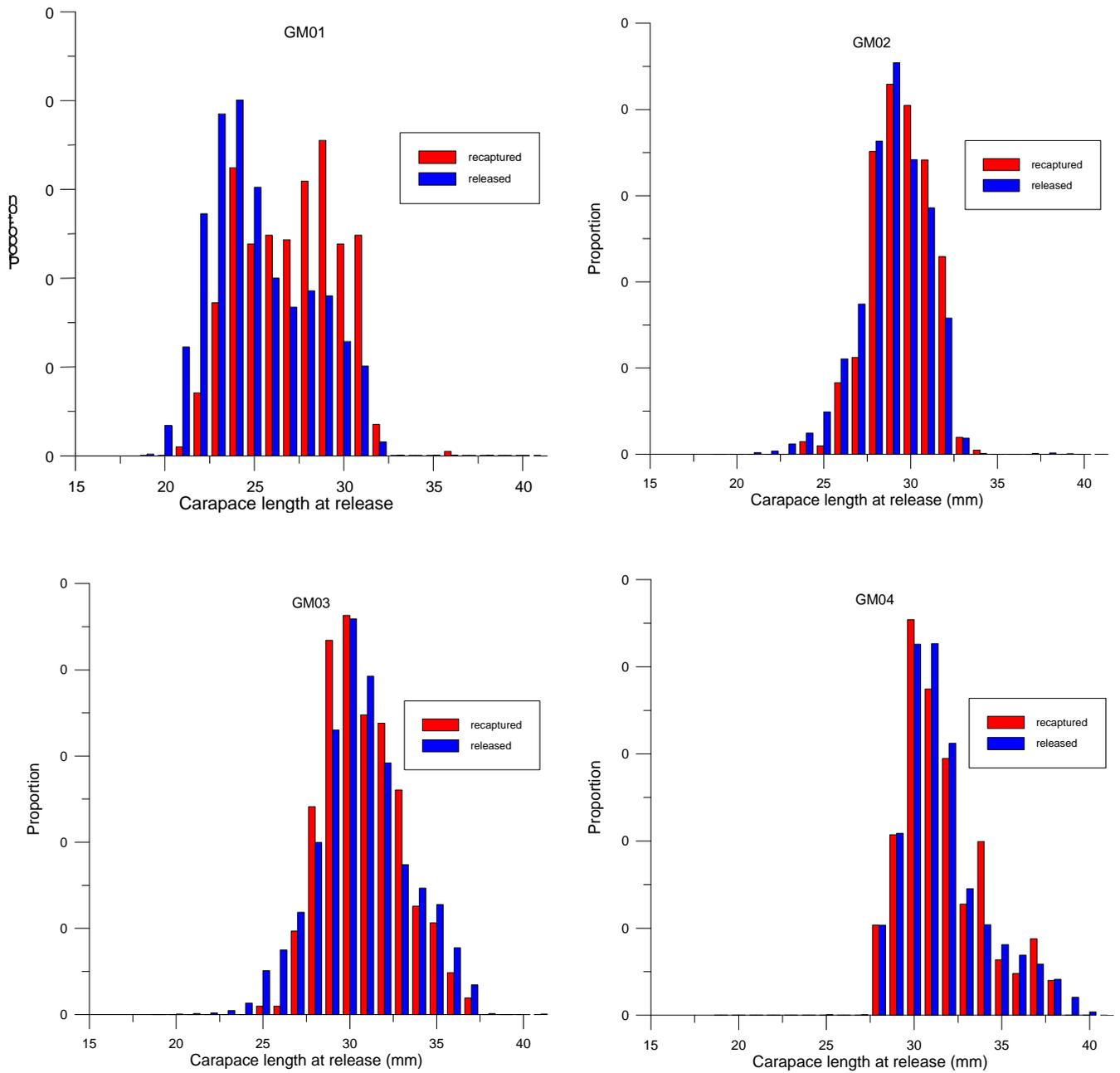


Figure 6.4 Size frequency distribution of tagged animals at release and at return. GM01 – GM04 represent each of the four tagging cruises. GM01 = March 1997; GM02 = April 1997; GM03 = February 1998; GM04 = March 1998.

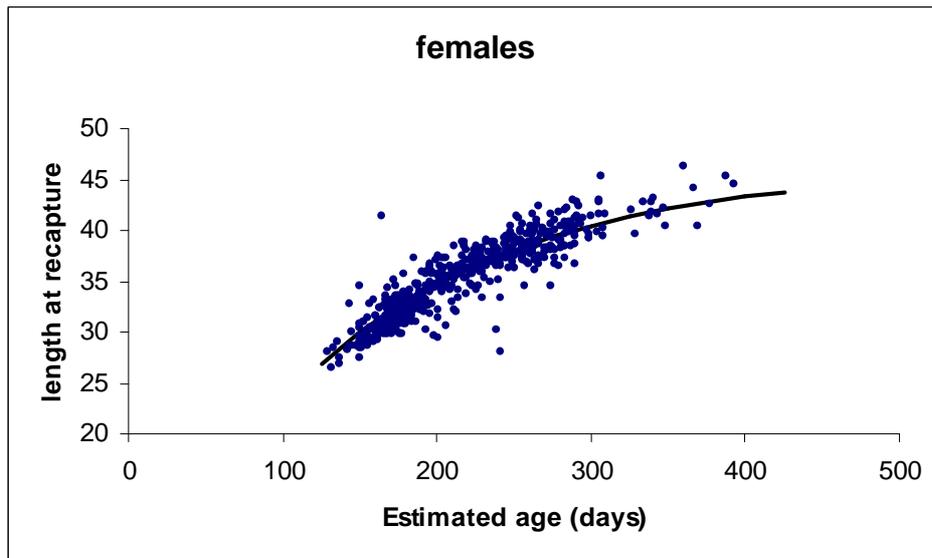
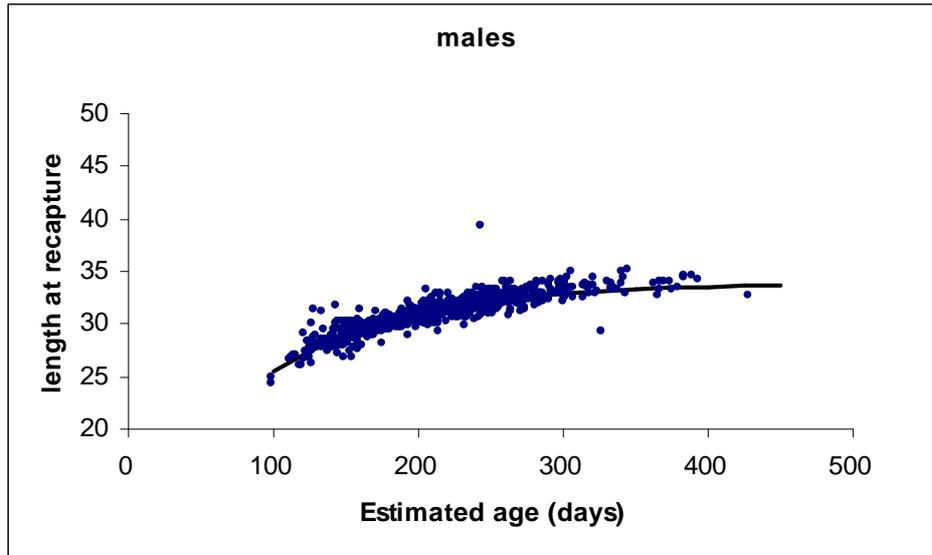


Figure 6.5 The fit of growth models to tagging data for *P. indicus* for tag returns in the Joseph Bonaparte Gulf. The solid line is the predicted growth curve and the points are our observations. The estimated age at recapture was calculated as the sum of the age at tagging plus the time at liberty, as suggested in Die (1992b).

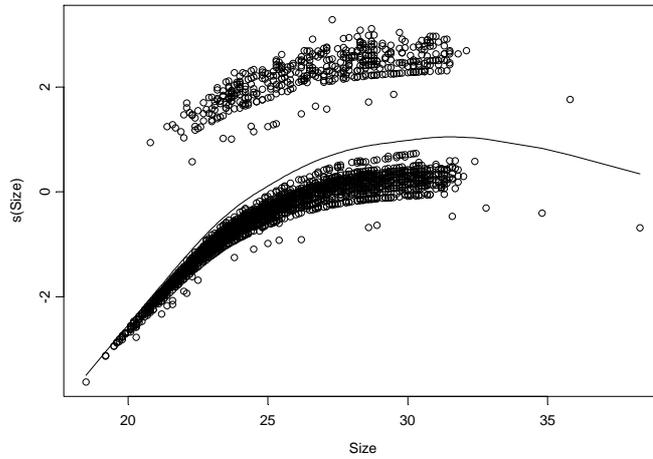


Figure 6.6 The estimated effect of size on the probability of recapture (solid line). Also shown are the expected probabilities of recapture for all observations (circles). Both probabilities are normalised to the intercept of the GAM model.

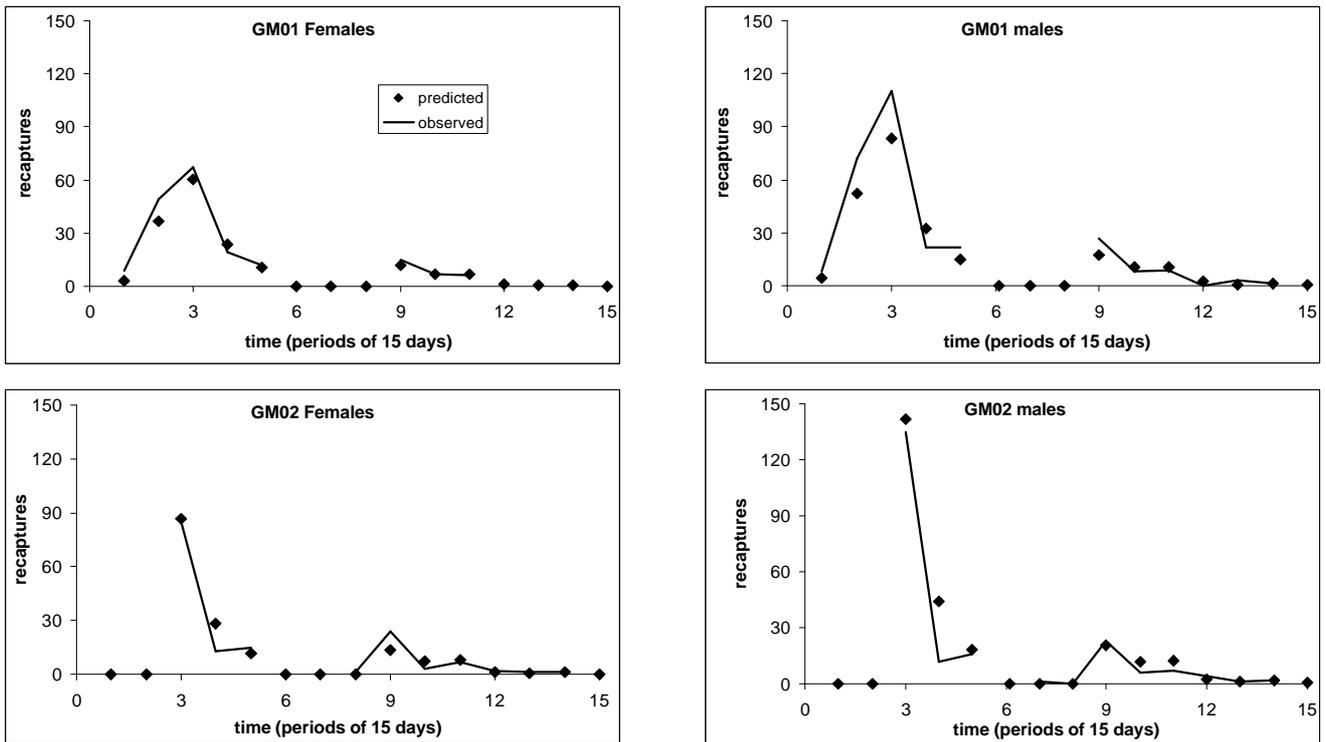


Figure 6.7 Number of recaptures observed per 15 day time period (diamonds) in 1997 and predicted number of recaptures (lines) from population model. Each panel correspond to a different cruise and sex. GM01 = prawns released in March 1997; GM02 = prawns released in April 1997.

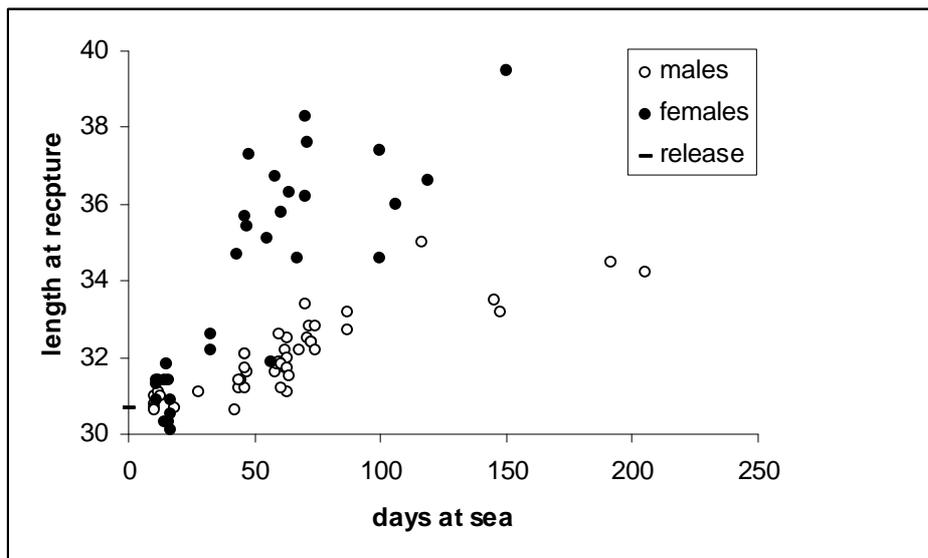


Figure 6.8 Variability in length at recapture among 75 tagged prawns that had the same length at release (mean carapace length = 30.7 ± 1 mm) and were recaptured at different times.

7. CHAPTER SEVEN: MIGRATION AND MOVEMENT OF RED-LEGGED BANANA PRAWNS IN THE JOSEPH BONAPARTE GULF

(Authors: RA Kenyon, DJ Die, NR Loneragan)

Note that this work has been published in the following paper:

Kenyon, R.A., D.J. Die and N.R. Loneragan. (2000). Preliminary analyses of migration and movement of adult, red-legged banana prawns in Joseph Bonaparte Gulf, northern Australia. *In: Hancock, D.A., D.C. Smith and J.D. Koehn (eds) Fish Movement and Migration*. Australian Society for Fish Biology Workshop Proceedings, Bendigo, Victoria, September 1999. Australian Society for Fish Biology, Sydney

INTRODUCTION

Red-legged banana prawns form about 10% of the catch of the Northern Prawn Fishery (NPF) and they have been fished regularly since the early 1980's with fishing effort and catch increasing markedly (Robins and Somers, 1994). Currently, the catch fluctuates between about 200 tonnes and 1000 tonnes per year. During this time, overall effort has increased from <20 boat days prior to 1980 to about 1000 to 1500 boat days since 1993 (Taylor and Die, 1999). Since fishing closures have been imposed in the NPF, the pattern of fishing effort in the JBG has shifted from September to December (1981-1984), through June to September in 1985 and 1986, to effort being highest in May-June and October-November since 1988 (Robins and Somers, 1994; Loneragan *et al.*, 1997).

Presently, fishing in the NPF extends over two parts of the year - the first season begins in April and ends in mid-June; the second season begins in early August and ends in November. During the first season, a fishing closure is in place in JBG, south of 13° 57' S, to prevent fishing on recent recruits to the offshore region. Due to the large tide range in JBG (up to 7m), *P. indicus* are fished on the neap tides, when tidal currents are least. Thus, over a tide cycle, fishing effort is high on the late spring-neap, neap and early neap-spring tides, and low to non-existent at other times when the fleet moves to fishing grounds north of Melville Island and Port Essington, outside the JBG.

In 1997 and 1998, a tag-release-recapture experiment was undertaken in Joseph Bonaparte Gulf to evaluate the status of the *P. indicus* population by determining the natural and fishing mortality, as well as determining growth and movement of *P. indicus* in the Gulf. The tag-release-recapture experiment has been described previously in this report. This chapter uses the tag-return data to determine the movement of tagged *P. indicus* in JBG, and to assess whether there is any evidence of an inshore movement of large prawns to areas south of the seasonal closure line in JBG, where they cannot be fished until August.

MATERIALS AND METHODS

The tagging, release and recapture of the prawns have been described elsewhere in the document, they will not be repeated here.

ANALYSIS OF PRAWN MOVEMENT

To accommodate the nature of fishing operations as driven by tidal cycles, the fishing season (the possible time span over which tagged prawns could be recaptured) was divided into fishing periods (Table 7.1). Fishing periods were referenced to the neap tides, including the week before and the week after the neap when most fishing occurred. Fewer boats fished in JBG during 1998 and they caught fewer tagged prawns, so only the first half of the fishing season was divided into fishing periods. Changes in the movement of prawns during the year were analysed using these reference fishing periods.

Table 7.1 Fishing Periods used in the analysis of movements of tagged prawns.

Fishing period	1997	1998
1	01 April to 16 April	27 April to 10 May
2	17 April to 27 April	11 May to 27 May
3	28 April to 10 May	28 May to 15 June
4	11 May to 24 May	16 June to 31 October
5	25 May to 08 June	
6	09 June to 21 June	
	Seasonal Closure	
9	22 July to 06 August	
10	07 August to 22 August	
11	23 August to 05 September	
12	06 September to 18 September	
13	19 September to 02 October	
14	03 October to 17 October	

Tagging did not provide information on the short-term movements that the prawns made during their time at liberty; we only gained a record of the net vector of movement by a prawn from release to recapture. To describe movement, the net vectors were classified within 16 classes corresponding to the arcs of a circle, each

class representing 22.5° (Table 7.2). The arcs were centred on prominent compass points, e.g. north-north-east, south-east or west-south-west. The total number of prawns that moved within each arc was calculated for each fishing period.

ANOVA analysis

A two-way ANOVA was used to compare the mean direction of movement by tagged prawns between fishing periods and months of tagging (1997 and 1998 were analysed separately). Only those fishing periods with adequate numbers of recaptures (>50) were included in the analyses. Thus, for 1997, fishing periods 2, 3, 4, 5 and 9 were analysed. For 1998, fishing periods 1, 2, and 3 were analysed. In 1997, only those prawns released in the southern section of the fishing grounds were included in the analysis as their movement was not consistent with those released in the northeast.

We analysed differences in the direction of movement of tagged prawns by standardising the direction of prawn movements around the mean direction of movement (X_o). We calculated the mean direction of prawn movement following the method of Mardia (1972). Once the mean direction was calculated, all movement was standardised relative to this mean direction.

Table 7.2 The 16 arcs of a circle, based on compass points, used to interpret the direction of movement of tagged prawns.

	Centre point (degrees)	Least angle (degrees)	Greatest angle (degrees)
North	0	348.75	11.25
North-north-east	22.5	11.25	33.75
North-east	45	33.75	56.25
East-north-east	67.5	56.25	78.75
East	90	78.75	101.25
East-south-east	112.5	101.25	123.75
South east	135	123.75	146.25
South-south-east	157.5	146.25	168.75
South	180	168.75	191.25
South-south-west	202.5	191.25	213.75
South-west	225	213.75	236.25
West-south-west	247.5	236.25	258.75
West	270	258.75	281.25
West-north-west	292.5	281.25	303.75
North-west	315	303.75	326.25
North-north-west	337.5	326.25	348.75

We made all the directions travelled by prawns to be within the range of +180 to -180 from the mean direction. This process sets a normal distribution around zero degrees for the analysis.

We used the formula below to calculate the standardised direction (X_t') from the observed direction (X_t):-

i.e if $X_t < X_o$, then $X_t' = - (X_o - X_t)$; as well,

if $X_t < (X_o + 180)$, then $X_t' = (X_t - X_o)$; and

if $X_t > X_o + 180$, then $X_t' = (X_t - 360 - X_o)$.

Categorical Models

We also used Log-linear categorical analysis models to investigate the relationship between fishing effort and the catch of tagged prawns within the fishing grounds. We grouped recaptures and effort into 12 x 12 minute fishing grids (144 square nautical miles), and by the fishing period defined in Table 7.2.

We then tested the following hypotheses:

(1) **That there is complete mixing of tagged prawns within the fishery:** The hypothesis is that recapture probabilities for any given grid for each fishing period are proportional to the fishing effort in that fishing period.

The predicted number of recaptured prawns R_{ij} in fishing period i and grid j are:

$$R_{ij} = \frac{f_{ij}}{\sum_i f_{ij}} \sum_i r_{ij} \quad (7.1)$$

where f_{ij} is the fishing effort and r_{ij} is the observed number of recaptured prawns.

(2) **That the probability of recapture is independent of the fishery:** The hypothesis is that recapture probability for any given grid is constant, independent of fishing effort and fishing period.

Under this hypothesis, the predicted number of recaptured prawns R_{ij} in fishing period i and grid j are:

$$R_{ij} = \frac{\sum_i r_{ij} \sum_j r_{ij}}{\sum_j \sum_i r_{ij}} \quad (7.2)$$

where f_{ij} is the fishing effort and r_{ij} is the observed number of recaptured prawns.

RESULTS

PRAWN MOVEMENT BY COMPASS POINTS

1997

During the first two fishing periods, all recaptured prawns had moved in a north-north-westerly to east-north-easterly direction from their release point. During all of the fishing periods before the mid-season closure (One to Five), only two prawns out of the total of 601 recaptures had moved in a direction with any southerly-component. However, during fishing periods Three to Five, prawns were caught in a wider arc (180°), from due west, through due north, to due east.

This result is confounded by the fact that during April, May and June, no recaptures could occur south of many of the release points due to the fishing closure south of $13^\circ 57' S$. Prawns that may have moved south would not have been detected. Thus, few prawns being recaptured south of their release points are to be expected. Even those prawns that were released a short distance north of the closure line had little chance of recapture to the south of their release point.

However, during the second half of the fishing season (after the lifting of the seasonal closure), most tagged prawns still were caught to the north of their release point, although quite a few had moved west, north-west and east. Only 9 prawns out of 148 (6 %) had moved in a direction with any southerly-component; for example some had moved south and southwest.

In contrast to prawns released in the southern section of the fishing ground, those prawns released in the northern section did move in directions with a southerly-component. Throughout the fishing season, 47 prawns (63 % of recaptures) moved in the 135° arc from west-south-west to east-south-east. Some had also moved due west, west-north-west and northwest. Also in contrast to those that were released in the southern section of the fishing ground, none had moved in the 90° arc from due north to due east.

1998

In 1998, during the first half of the fishing season (fishing periods One to Three), the majority of recaptures (94 %) had moved north in a 90° arc from due north to due east. Six percent moved in the arc from north-north-west to due west. However, as all of the prawns were released south of the first-season closure line, no recaptures could occur south of the line, as no fishing occurred south of the closure line during the first half of the season. Thus, prawn movement to the south could not be detected.

Only 16 recaptures in total were made in the second half of the fishing season, after the lifting of the seasonal closure. However, of those 16 prawns, 63% had moved in an arc from north-north-west to due west, compared to 6% (one prawn) that had moved in a 90° arc from due north to due east. Thirty one percent had moved in a direction with some southerly-component.

STATISTICAL ANALYSIS OF DIRECTIONAL PRAWN MOVEMENT

During 1997, the mean direction of movement of tagged prawns recaptured during the second fishing period was north (10.2°); 9.4° for those released during March, and 18.7° for those released during April/May (Table 7.3). This direction of movement differed significantly from those during all other fishing periods (Tables 7.3 and 7.5). During fishing periods 3, 4, 5 and 9, tagged prawns moved in a north-north-westerly direction (-14.2° to -20.7°) and their mean direction of movement did not differ significantly between each of the fishing periods (Table 7.3).

Table 7.3 The direction (degrees from 180 to +180 , with 0 being North) and distance (nautical mile) of movement of tagged prawns released and recaptured in Joseph Bonaparte Gulf in 1997. Numbers in parentheses are the recaptures in each fishing period.

	March		April/May		Total	
	Direction (degrees)	Distance (km)	Direction (degrees)	Distance (km)	Direction (degrees)	Distance (km)
Period 2 (134)	$9.4^\circ \pm 1.67$	44.8 ± 1.39	$18.7^\circ \pm 7.39$	12.2 ± 0.35	$10.2^\circ \pm 1.66$	41.9 ± 1.50
Period 3 (334)	$-2.0^\circ \pm 2.20$	42.8 ± 1.28	$-30.2^\circ \pm 3.53$	16.9 ± 1.06	$-15.3^\circ \pm 2.17$	30.6 ± 1.09
Period 4 (61)	$-9.4^\circ \pm 4.00$	40.2 ± 2.59	$-43.7^\circ \pm 13.2$	27.1 ± 2.87	$-20.7^\circ \pm 5.43$	35.9 ± 2.11
Period 5 (60)	$1.3^\circ \pm 5.03$	32.2 ± 1.56	$-33.3^\circ \pm 8.24$	13.7 ± 1.96	$-14.2^\circ \pm 5.10$	23.9 ± 1.70
Period 9 (80)	$-5.0^\circ \pm 4.48$	33.4 ± 1.46	$-33.2^\circ \pm 7.62$	22.2 ± 1.76	$-19.1^\circ \pm 4.67$	27.8 ± 1.30
Total (669)	$0.6^\circ \pm 1.31$	40.4 ± 0.74	$-29.8^\circ \pm 2.90$	19.1 ± 0.76		

The mean direction of prawn movement differed significantly between the two months of tagging. Tagged prawns released during March moved in a northerly direction (0.6°), while those released during April/May moved in a north-north-westerly direction (-29.8° , Table 7.3).

During 1998, the mean direction of prawn movement differed significantly for the recaptures from each fishing period (Tables 7.4 and 7.5). Those recaptures taken during fishing period One had moved in a north-north-easterly direction (21.6°), while those taken during fishing period Two moved north (4° , Table 7.4). Prawns caught during fishing period Three had also moved north (10°), however, their mean direction of movement was sufficiently different to those taken in fishing period Two to be significant ($p < 0.05$).

Table 7.4 The direction (degrees from 180 to +180 , with 0 being North) and distance (nautical mile) of movement of tagged prawns released and recaptured in Joseph Bonaparte Gulf in 1998. Numbers in parentheses are the recaptures in each fishing period.

	February		March		Total	
	Direction (degrees)	Distance (km)	Direction (degrees)	Distance (km)	Direction (degrees)	Distance (km)
Period 1 (201)	13.5°±2.50	31.7 ± 1.13	34.8°±2.95	29.8 ± 1.28	21.6°±2.04	30.9 ± 0.85
Period 2 (124)	-1.0°±2.77	44.7 ± 1.06	8.3°±2.66	42.8 ± 1.15	4.0°±1.96	43.7 ± 0.80
Period 3 (123)	2.6.°±2.81	43.0 ± 2.67	14.9°±2.84	38.2 ± 1.15	10.1°±2.11	40.0 ± 1.26
Total (448)	7.7°±1.68	36.7 ± 0.93	19.8°±1.80	35.4 ± 0.80		

Table 7.5 Mean square and significance levels for an ANOVA analysis of the direction on movement of tagged prawns released during two tagging-cruises in each of 1997 and 1998, in Joseph Bonaparte Gulf . The analysis for 1997 only included fishing periods 3,4,5 and 9. When period 2 was included, the treatment “fishing period” became significant, but the ANOVA was unbalanced.

	1997		1998	
	Mean square	(d.f)	Mean square	(d.f)
Tagging cruise	112381 ***	(1)	16536 ***	(1)
Fishing period	805	(4)	12808 ***	(2)
Interaction	1195	(4)	5948 ***	(2)
Error	1202	(659)	600	(442)

In 1998, the mean direction of prawn movement differed significantly between the two tagging cruises. Tagged prawns released during February moved in a northerly direction (7.7°), while those released during March moved in a north-north-easterly direction (19.8°) (Table 7.4).

The mean distance that tagged prawns moved was about 40 km, except those released during April/May in 1997. The prawns released during April/May were released further north than others and they moved an average of about 20 km.

MIXING OF TAGGED PRAWNS AND INDEPENDENCE OF RECAPTURE

The analyses using categorical models shows that the recapture probabilities for any given grid for each fishing period were not proportional to the fishing effort in that fishing period ($\chi^2_{80} = 10,849$, $p < 0.001$). As well, they showed that the recapture probability for any given grid was not constant and therefore, that it was affected by fishing period ($\chi^2_{30} = 5,761$, $p < 0.001$).

DISCUSSION

DIRECTION OF MOVEMENT OF ADULT *P. INDICUS*

In 1997 and 1998, the number of tagged prawns that were recaptured differed markedly because fewer boats fished in JBG during 1998 and these boats started fishing much later in the year. As a result, the fishing periods used in our analyses are not strictly comparable from one year to the next. However, a consistent trend in prawn movement is evident in both years. During both years, 100 % and 94%, respectively, of the tagged prawns that were recaptured during the first weeks of fishing (fishing period 1 and 2 in 1997, April 1 to 27; and fishing period 1 in 1998, April 27 to May 10) had moved in an arc from east-north-east to north. During the remainder of the fishing seasons of both years, significant numbers of prawns had moved more north, through to the northwest. In 1997, their westward movement was more pronounced.

In the second half of the fishing season, after the fishing closure was lifted and recaptures south of the line were possible, only six percent of tagged prawns were recaptured in a position to the south of their release position. Thus, the prawns that were released in the southern portion of the fishing grounds largely moved north and their movement suggests that *P. indicus* continue to migrate north to deeper offshore waters (70-80 m), usually less than about 60 km, and that they don't return inshore. However, some individuals moved further afield towards Lesueur Island (13° 49.2' S, 127° 16.2' E) and Cape Londonderry (13° 44.4' S, 126° 57.6' E).

Juvenile *P. indicus* are found in extensive inshore mangrove habitats of Cambridge Gulf and the eastern Joseph Bonaparte Gulf (CSIRO Marine Research, unpublished data), south of 14° 45' S, 128° 15' E and 14° 34.8' S, 129° 19.8' E, respectively (Figs. 7.1 and 7.2). Emigrating juveniles and sub-adults must move from these inshore habitats 200-300 kilometres to the north and north west to the offshore fishing grounds. They seem to move rapidly across shallower (30-40 m), sandy substrates to the south and east of the area where prawns were tagged in 1997 and 1998. This conclusion is inferred from two sources – little fishing effort occurs in this region during the period when the areas are open to fishing (Figs. 7.1 and 7.2), and – regular trawling of these areas during the tagging cruises in an attempt to find prawns to tag

resulted in no catches of *P. indicus* (R. Kenyon, personal observation). They move beyond the 45 m depth contour into the region where we found them in sufficient numbers to tag for this study.

As no fishing occurred south of the closure line from April to June each year, it is possible that many prawns moved southward. They would not have been detected until during the second half of the fishing season. However, southward movement seems unlikely as:-

- large numbers of tagged prawns were not caught south of the closure line during the second half of the fishing season,
- of those tagged prawns caught after the seasonal closure was lifted, most had moved in a northerly direction, and
- during fishing periods 1 and 2, over 90% of tagged prawns had moved in a relatively restricted arc from east-north-east to north. Few had moved eastward or westward.
- A difference in habitat to the south of the areas where prawns were tagged and released may also support the contention that *P. indicus* does not return inshore. South of the release area, water depth decreases from 45-50 m to about 30-40 m and the substrates change from mud to sandy substrates.

By contrast, a significant percentage of those prawns released in the northern portion of the fishing grounds moved south and west. This result suggests that initially *P. indicus* move north into the “fishing ground”, but don’t necessarily continue to move in a northern direction. The release sites in the northern portion of the fishing grounds were about 50 km northeast of the main area of releases. By chance, 50 km is similar to the average distance that tagged prawns moved northward during this study. Thus, it would seem that those tagged prawns released in the north were released towards the “natural” northern extent of their range, which matches the northern boundary of high commercial catches (Figs. 7.1 and 7.2). Consequently, most of the prawns that were released to the north of the fishing ground did not move further north; they moved in a more random way. Although some of these prawns moved in west-north-west to north-north-west directions, none moved in the 90° arc from due north to due east, despite an easterly component of movement being common for tagged prawns released in the southern portion of the fishing ground. Of course, some tagged prawns moved greater distances than average and ranged further north, east and west. Their distribution matches the distribution of low commercial catches (Figs. 7.1 and 7.2). Less fishing effort in areas of lower catch may confound our estimates of movement and the incidence of recaptures in relation to effort is currently being investigated further.

The predominant northward movement of tagged prawns does not support the existence of a strong inshore migration of *P. indicus* to shallower waters during the fishing season. However, *P. indicus* probably move toward the western portion of the fishing grounds later in the year, as shown by tagged prawn recaptures being made to the north-west of release points in the latter fishing periods (after a longer period at liberty), compared to recaptures made to the north-east early on. The lack of a return

migration suggests that the current spatial seasonal closure, which prevents fishers from accessing the shallow water prawn stocks during April to June, is not reducing their access to the adult population that is already resident in the offshore fishery. The shallow-water stock is made up of a high proportion of recent recruits to the fishery.

PRAWN MIXING AND INDEPENDENCE OF RECAPTURE

In both years, the tagged prawns from the two months of tagging moved in different directions and were not recaptured in the same area at the same time. This result implies that the prawns released during the two cruises each year may have different migration patterns, or that the time delay between tagging cruises results in incomplete mixing of the prawns that were tagged on each cruise, and a staggered pattern of movement between the two cruises. The prawns were released at two times to facilitate the estimation of natural and fishing mortality, however, their movement in different directions confounds the issue.

Recapture locations are not just a result of fishing effort. At some locations the number of tagged prawns recaptured was greater than what would have been expected from the distribution of fishing effort. In other locations, the number of tagged prawns that were recaptured was smaller than what would have been expected from the distribution of fishing effort. This result implies that tagged prawns were not fully mixed with the rest of the fished population. The distribution of tagged prawns was more localised than the distribution of the prawn population that was fished by the fleet. Prawns probably recruit to the fishery over a broader front than the area in which we tagged and released prawns. Thus, as the tagged prawns initially moved north-north-east, they probably mixed with the wild population to the north, but not to the west or east. More detailed analyses of recaptures in relation to fishing effort and time at liberty will provide a full account of prawn movement.

Despite the tagged-prawn release sites being chosen for a study of natural and fishing mortality, and despite the restricted range of prawn movements that can be monitored from limited release areas, the information gained on the movement of the recaptured prawns has provided an insight into the effectiveness of the seasonal spatial closure in JBG. Small adult prawns are found south of the closure line, and there is no evidence of a strong inshore migration by large individuals during the first half of the fishing season, thus, the closure does not prevent access to prawn stocks.

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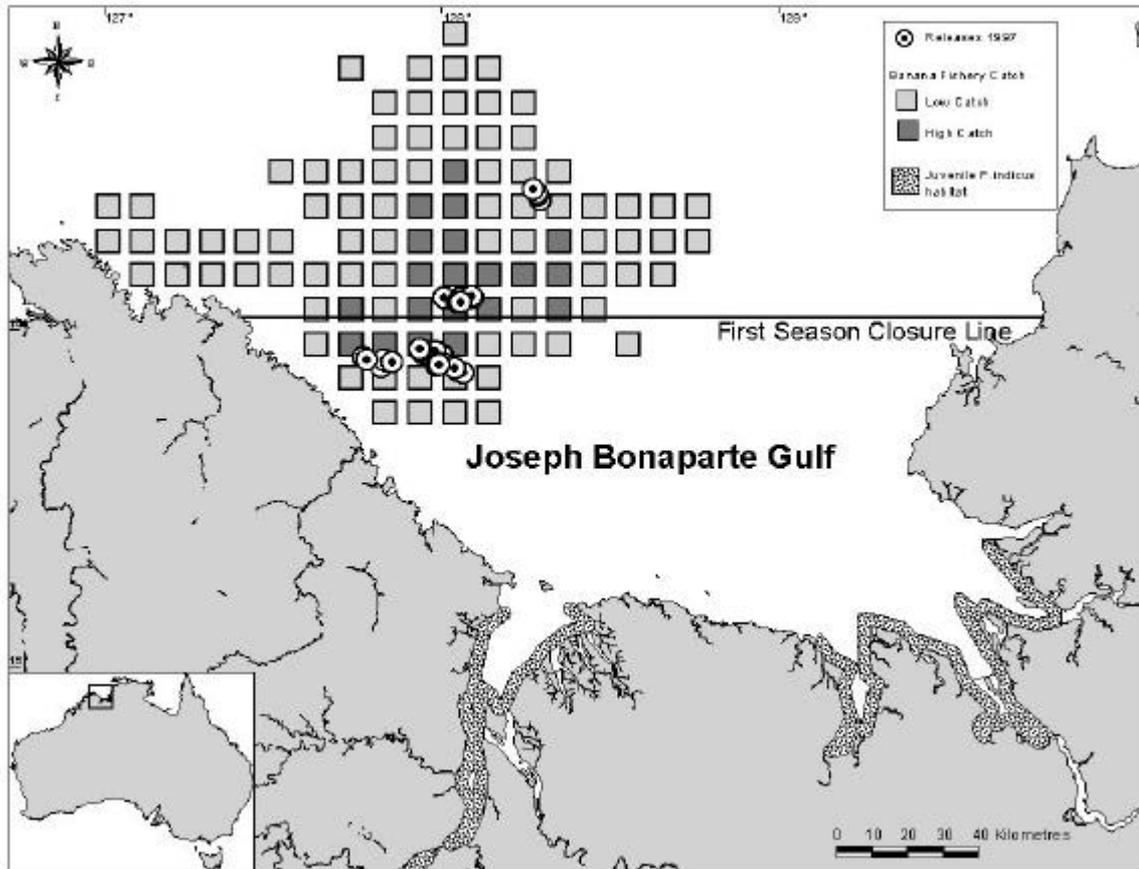


Figure 7.1 Map of the Joseph Bonaparte Gulf, northwestern Australia showing the location of the release sites for tagged prawns (*Penaeus indicus*) in 1997 and the distribution of fishing catches over 10 years from 1988 to 1998. The stippled area on the coast shows the location of mangrove-lined creeks and rivers that are the juvenile habitat for *Penaeus indicus*. (The catch distribution is from grids where at least 5 vessels fished for at least ten vessel-days over the 10 years, to protect the anonymity of fishing vessels.)

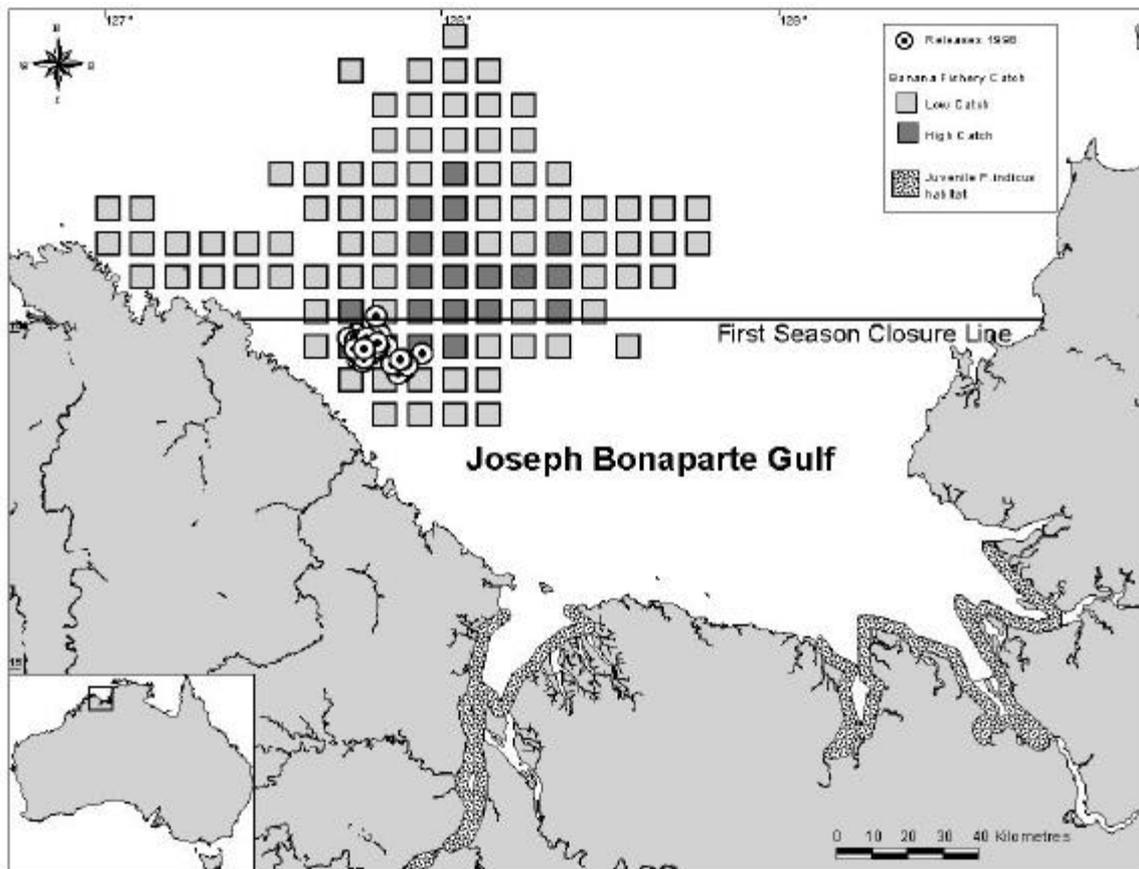


Figure 7.2 Map of the Joseph Bonaparte Gulf, north-western Australia showing the location of the release sites for tagged prawns (*Penaeus indicus*) in 1998 and the distribution of fishing catches over 10 years from 1988 to 1998. The stippled area on the coast shows the location of mangrove-lined creeks and rivers that are the juvenile habitat for *Penaeus indicus*. (The catch distribution is from grids where at least 5 vessels fished for at least ten vessel-days over the 10 years, to protect the anonymity of fishing vessels.)



8. CHAPTER EIGHT: STATUS OF STOCKS

(Authors: NR Loneragan, DJ Die)

INTRODUCTION

Initially the JBG fishery developed as an alternative to fishing in the Gulf of Carpentaria: during years of poor catches in the Gulf of Carpentaria, more fishing effort was applied in the JBG. In the early years most effort was concentrated at the end of the year (Chapter 5). In recent years, however, in addition to being more heavily fished in years of poor catches elsewhere, JBG stocks are fished earlier in the season by a consistent number of boats, regardless of catches elsewhere in the NPF.

A preliminary model for the red-legged banana prawn fishery in the JBG was developed to evaluate the impacts of changes in the pattern of fishing effort on the yield and spawning biomass of red-legged banana prawns (Loneragan *et al.* 1997). However, many of the parameter estimates used in this model were taken from literature values for other species in different regions (particularly the white banana prawns *P. merguensis*).

The estimates of population parameters obtained from the tag-release and recapture studies in Chapter 5 allow us to revise the previous per-recruit analyses and the assessment of different patterns of fishing effort on yield, value and egg-production that were carried out by Loneragan *et al.* (1997).

METHODS

We followed the methods used by Loneragan *et al.* (1997). In their analyses, they documented how parameter uncertainty affected the per-recruit estimates. We have not attempted to repeat such analyses here. The current analysis only attempts to re-estimate the base model by using the new set of “best” parameter values obtained in Chapter 5. To estimate per-recruit values we used the SIMSYS software (Watson *et al.* 1996a), also used by Loneragan *et al.* (1997). To make the two base models comparable, recruitment was adjusted so that annual yields were around 800 tonnes.

The SYMSIS model was developed to evaluate seasonal closures in tropical penaeid fisheries (Watson *et al.* 1996a). It is based on a per-recruit model that requires the input of parameters for growth, recruitment, mortality and fishing effort. SIMSYS models complex recruitment and seasonal fishing effort patterns, and systematically evaluates different seasonal closures, or different seasonal patterns of fishing effort.

The time step selected for the model was one month and 3 generations of 12 months each were used to estimate the equilibrium per-recruit values.

POPULATION PARAMETERS

The value for the monthly Von Bertalanffy growth rate (k) estimated from the tagging study in Chapter 5 was slightly higher than the highest value of k investigated by Loneragan *et al.* (1997) (Table 8.1). The value of catchability estimated from the current study was about 10 times higher than the previous value (Table 8.1). The estimated monthly natural mortality rate was within the range of previously used values (Table 8.1).

The length-weight relationship for male and female red leg banana prawns were those developed by Loneragan *et al.* (1997) in their analysis of data collected by NT Fisheries:

Females Weight (g) = 0.000889 CL (mm)^{2.914}
 Males Weight (g) = 0.000372 CL (mm)^{3.197}
 (Buckworth, NTDPIF, unpublished data).

Table 8.1 Parameter values used in the current study and those used by Loneragan *et al.* for the SIMSYS per-recruit analyses of different seasonal patterns of fishing (1997).

Parameter	Study	
	Current stu	Loneragan <i>et al.</i> 1997
M – monthly natural mortality rate	0.20	0.15, 0.20 and 0.25
q – catchability	0.001	0.0001
k – monthly Von Bertalanffy k	0.27	0.15, 0.20 and 0.25
Length at 50% selection	26.5	21.5
Slope of selectivity curve	0.53	0.3

a) Recruitment

The seasonal pattern of recruitment was the same as that used by Loneragan *et al.* (1997) who used the length frequency data from NT Fisheries. Data were standardised to represent relative abundance by using the catch (in numbers) per unit of fishing effort from the commercial fishery. The total number of recruits for each month, sex and age was estimated from the “maximum of minima” method (Watson *et al.* 1996b). The main assumption of this method is that there is at least one month of the year where no recruits enter the fishery. Length frequencies for months where no data were available (December, January, February) were interpolated from the length frequencies in November and March. The same assumption was made for the other two months (April and August) without length frequency data. This assumption equates to a broad, single peak recruitment pattern for red-leg banana prawns.

Our lack of length frequency data at the beginning of the year means that we cannot dismiss the possibility that recruitment only occurs for three months (February to April).

b) Seasonal pattern of fishing

The seasonal pattern of fishing effort was estimated for three different periods: 1981-84, 1985-86 and 1988-1995. The year 1987 was considered to be a transitional year between different closure regimes and was not evaluated. The average monthly percentage of effort was calculated for each of the three different periods and used to distribute the 1,000 boat-days that, on average, the red-leg fishery receives every year.

c) Reproduction

Loneragan *et al.* (1997) used data from NT Fisheries to estimate the proportion of females that were mature for each 1 mm size group in each month, following the model of Restrepo and Watson (1991). They found that the data formed two distinct groups: April - September when the proportion of mature females is low; and October - March when it is high. The data were grouped according to these two periods and we obtained the following relationships:

$$\begin{array}{ll} \text{Apr. - Sep.} & \text{Proportion mature} = 0.37 / (1 + e^{10.8 - 0.3 \text{ CL}}) \\ \text{Oct. - Mar.} & \text{Proportion mature} = 0.66 / (1 + e^{10.8 - 0.3 \text{ CL}}) \end{array}$$

The model fitted assumed only that the asymptote of the proportion mature changes during the season. This is similar to the approach taken by Restrepo and Watson (1991) for *P. esculentus* in the Torres Strait.

There is no information on the number of eggs produced by female red-legged banana prawns. The fecundity relationship for *P. esculentus* (Restrepo and Watson 1991) was therefore used as an approximation.

d) Price

We used a price of \$10 per kg for all red-leg banana prawns with a carapace length of 25 mm or larger, and \$0 for smaller prawns (prawns weighing 11 g, thus belonging to the 40 count per pound size category).

Parameter uncertainty and sensitivity analysis

Loneragan *et al.* 1997 investigated the sensitivity of the results to changes in values of growth (i.e. the *k* parameter), natural mortality, total annual fishing effort, and the pattern of recruitment through an analysis of extreme values. All the analyses were done by assuming that uncertainty in a parameter was independent of the other parameters, except for natural mortality and growth, which were assumed to be positively correlated. No sensitivity analysis was completed in the current study.

All comparisons were made by using the same level of annual fishing effort but only changing the seasonal pattern of this effort.

RESULTS

The qualitative results of the base model with the new parameters are similar to those reported by Loneragan *et al.* (1997) (Table 8.2). Thus, the current fishing effort pattern, although quite different from that of 1985-1986 produces almost the same estimates of yield-per-recruit, value-per-recruit and egg-per-recruit. In the earliest years of the fishery (1981 – 1984), fishing occurred throughout the year. The yield- and value-per-recruit were lower but the eggs-per-recruit were higher than those for more recent years, as also reported by Loneragan *et al.* (1997). The relative improvements in yield- and value-per-recruit resulting from this switch in seasonal effort pattern estimated in the current study was about 25% compared with an estimate of 20% for the previous study.

Table 8.2 Yield-, value- and egg- production for red-legged banana prawns during 3 historical periods of the fishery in the Joseph Bonaparte Gulf: 1981-84; 1985-86; 1988-1995, estimated from SIMSYS. Estimates are those using the parameters estimated in the current study (Chapter 5) and those from the base model of Loneragan *et al.* 1997. The effort was 1, 000 boat days for all analyses.

Study and Pattern of fishing	Estimates of		
	Yield (Kg)	Value (1,000 \$)	Eggs (millions)
Current study ($M = 0.20, k = 0.27$)			
81-84	703,514	7,004	14,393
85-86	882,776	8,825	11,416
88-95	873,943	8,724	11,510
Loneragan <i>et al.</i> 1997 ($M = 0.20, k = 0.20$)			
81-84	703,060	6,937	155,437
85-86	833,922	8,317	152,797
88-95	822,034	8,090	152,859

The largest difference between the two base models is in the amount of recruitment required to produce the current yields. In the previous base model 1,000 million recruits were required to support such yields whereas the current base model suggests only 166 million are required. The new estimate compares well with the 60 to 80 million 5 month old recruits estimated for 1997 with the non-size structured model (Chapter 6, Table 6.8). As a consequence, the estimated egg production from the current model is also about 10 to 15 times lower than from the previous model (Table 8.2).

This result is probably the most significant finding from the current analysis. It suggests that Loneragan *et al.* (1997) had assumed that the stock that supported the JBG fishery was about seven times larger than the current analyses suggest. From the short time series available for this fishery, it is not possible to infer trends in recruitment and whether recruitment is affected by the size of the spawning stock or fishing mortality. The effect of fishing upon subsequent

recruitment, however, cannot be dismissed and should be investigated in the future, specially given the high exploitation rates now estimated for this stock.

Sensitivity of the results

The sensitivity analysis completed by Loneragan *et al.* (1997) found that the results were sensitive to the values of mortality and growth, but not to the annual level of fishing effort. They also pointed out that the seasonal pattern of recruitment used in the analysis is highly uncertain because of the lack of length frequency samples between December and February. It is therefore important to obtain more information about recruitment.

DISCUSSION

Even though in terms of per-recruit values, the current analyses do not differ much from those of Loneragan *et al.* (1997), the estimates of population size differ by 10 to 15 fold. The estimated number of recruits from both Chapter 6 and from SIMSYS using the new parameter values suggest that the red-legged banana prawn fishery in the Joseph Bonaparte Gulf is sustained by a much smaller stock than that envisaged by Loneragan *et al.* (1997). Unfortunately, because the JBG is a relatively young fishery, we cannot yet make comments on the relationship between spawning stock size and recruitment. However, our results imply that the stock is much smaller than previously assessed and thus may not be as resilient to exploitation as previously thought. The fact is that whereas Loneragan *et al.* (1997) estimated that the annual fishing mortality rate was around 0.1, the data collected during our tagging studies suggest that it is ten times higher, about 1.0. This latter value is still low in comparison to the annual natural mortality rate (M) of 2.4, but is now within the same order of magnitude as M .

The implications from the previous per-recruit analyses suggested that management could focus on maximising the yield or the value from a single cohort and ignore the effects of fishing on recruitment. Our current results suggest otherwise. Although it is still useful to attempt to maximise yield and value though an appropriate seasonal closure, the impact of fishing on the spawning stock can no longer be discounted i.e. we now have to consider that fishing might reduce spawning stock to such low levels that recruitment is also reduced. There is no evidence that this is now the case, but given the current higher estimates of fishing mortality and lower estimates of population size, it is a scenario that cannot be dismissed.

How can the effects of fishing on the spawning stock and subsequent recruitment of red-legged banana prawns in the JBG be tested? We believe that the tagging experiments in Chapter 6 were an effective tool to estimate population size and recruitment, but they are costly. A feasible alternative is to use the information on catch and effort from the logbooks to estimate population size and fishing mortality, combined with commercial size information from the landings returns to estimate the proportion of recruits and spawners in the population at different times of year. These data sources could be used with a model similar to that presented in Chapter 6 to produce estimates of population size and recruitment so that hypotheses about stock recruitment relationships can be tested.

Unfortunately the hypothesis testing proposed above may take years to be achieved, because of the number of years of data required. Managers should not wait until then to make decisions on the appropriateness of current fishing practices. The precautionary principle calls for caution in managing resources when information is insufficient to define optimum levels of fishing mortality. We therefore recommend that NORMAC adopts a cautious approach in the management of red-legged banana stocks. Specifically we recommend that NORMAC adopts measures so that effective fishing effort does not increase any further in the JBG fishery. We particularly recommend that NORMAC continues to make sure that measures aimed at protecting other prawn stocks do not lead to increases in effort on the red-legged banana prawn fishery. Given the changes in the fishing pattern in JBG in the recent past (Chapter 6), it seems likely that the pattern of fishing or the number of boats fishing JBG could easily change again, possibly putting increased fishing pressure on the stock.

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Manson, F.J., Loneragan, N.R., McLeod, I.M. and Kenyon, R.A. (2001). Assessing techniques for estimating the extent of juvenile prawn habitats: topographic maps, aerial photographs and Landsat TM imagery. *Marine and Freshwater Research* **52**: 787-792.

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Appendix 1.

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Volume 50, 1999
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Corrigendum

Volume 50, Number 7

Simple morphometric characters, confirmed by gel electrophoresis, separate small juvenile banana prawns (*Penaeus indicus* and *P. merguensis*)

R. C. Pendrey, N. R. Loneragan, R. A. Kenyon and D. J. Vance.

p. 679. Table 1, line 3 (first tooth to ant. peduncle), where ‘anterior’ is entered under *P. indicus* and ‘posterior’ under *P. merguensis*. ‘Anterior’ and ‘posterior’ should be reversed. However, the text throughout the paper is correct. Hence, Table 1 should read as follows:

Table 1. Summary of morphological measurements of juvenile banana prawns from the Joseph Bonaparte Gulf, identified by gel electrophoresis

L_1 , distance from anterior-most dorsal rostral tooth (termed first tooth) to tip of rostrum; $L_{1,2}$, distance between first and second dorsal rostral teeth

Character	Species		<i>n</i> (<i>P. indicus</i> , <i>P. merguensis</i>)
	<i>P. indicus</i>	<i>P. merguensis</i>	
$L_1:L_{1,2}$	3.16 ± 0.82	1.56 ± 0.084	59, 36
First tooth to ventral teeth	2–5 (mode 3–4)	2–5 (mode 3–4)	59, 36
First tooth to ant. peduncle	posterior	anterior	59, 36
No. dorsal teeth behind eye	5: 4.5%	5: 93.9%	89, 49
	6: 95.5%	6: 6.1%	
Mean carapace length (mm)	8.2 ± 0.22	5.3 ± 0.27	89, 49
Carapace length (mm)	3.1–16.5	3.4–13.1	89, 49

Simple morphometric characters, confirmed by gel electrophoresis, separate small juvenile banana prawns (*Penaeus indicus* and *P. merguensis*)

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Abstract. The juveniles of red-legged banana prawns *Penaeus indicus* and white banana prawns *P. merguensis* are difficult to distinguish. Gel electrophoresis, with the enzyme malate dehydrogenase, clearly separated into species both large and small prawns. Four morphological characters were measured from juvenile prawns (identified using electrophoresis): three of these provided reliable separation into species. The mean ratio of the distance from the anterior-most dorsal rostral tooth (first tooth) to the tip of the rostrum (L_1) to the distance between this tooth and the second tooth ($L_{1,2}$) was higher for *P. indicus* (3.16) than *P. merguensis* (1.56). All juvenile *P. indicus* had the first tooth posterior to the antennular peduncle, while it was anterior for all *P. merguensis*. More than 90% of *P. indicus* had six rostral teeth behind the eye, while over 90% of *P. merguensis* had five teeth behind the eye. Damage to the rostrum prevented measurements of the position of the first tooth in 20 to 30% of juvenile prawns. Combining the measurements of the ratio of $L_1 : L_{1,2}$ and the count of the number of rostral teeth behind the eye meant that all prawns could be unambiguously identified.

Introduction

Red-legged banana prawns *Penaeus indicus* and white banana prawns *P. merguensis* are important commercial species throughout the Indo–West Pacific region, including Australia. In Australia, *P. indicus* is restricted to more northern tropical waters (north of 15°S), whereas *P. merguensis* extends south to Shark Bay on the west coast (~26°S) and into northern New South Wales (~30°S) on the east coast (Grey *et al.* 1983). The juvenile stages of *P. merguensis*, which have been well studied in Australia, are mostly found along mangrove-lined mud-banks (e.g. Haywood and Staples 1993; Vance *et al.* 1998). However, little is known of the biology or the nursery habitats of *P. indicus* in this region.

The adults of these two banana prawns can be distinguished on the basis of morphological characters (Chong and Sasekumar 1982; Grey *et al.* 1983). Although work in India (Muthu and Rao 1973) and Malaysia (Chong and Sasekumar 1982) has suggested that the juveniles can also be identified from their morphological characters, there are limitations to these studies: the Indian study did not clearly identify the sources of the two species; and the Malaysian study did not examine small *P. indicus* (≤ 10 mm carapace length, CL). In the estuaries of northern Australia, most juvenile *P. merguensis* are < 10 mm CL and have not developed the distinguishing morphological features of the much larger sub-adult prawns.

We used gel electrophoresis (Lavery and Staples 1990) to separate the small juveniles of *P. indicus* from *P. merguensis* and then determined whether it was possible to separate the juveniles by easily measured morphometric characters.

Materials and methods

Collection of known large prawns for electrophoresis

For the initial testing of enzyme systems, identified sub-adult and adult banana prawns were collected: *Penaeus indicus* ($n = 111$) from trawls in the Joseph Bonaparte Gulf of northern Western Australia in February 1997 (14°S, 128°E); and *P. merguensis* ($n = 117$) purchased from beam-trawl fishers in the Brisbane River (26°S, 152°E) in February 1998.

The adults of *P. indicus* and *P. merguensis* were distinguished by the presence of a distinct gastro–orbital ridge in *P. indicus* and its absence in *P. merguensis*, and a higher rostral crest for *P. merguensis* (following Grey *et al.* 1983). The mean carapace lengths (± 1 s.e.) were 39.8 ± 0.52 mm for *P. indicus* and 18.7 ± 0.37 mm for *P. merguensis*.

Collection of small prawns for electrophoresis and morphometrics

In total, 218 unidentified juvenile banana prawns were collected in beam-trawls in the rivers of the Joseph Bonaparte Gulf between October and December 1997. Prawns were collected from the Kumberbar Creek, Victoria River and Forsyth River in the eastern Joseph Bonaparte Gulf (14°50'S, 129°30'E), the Lyne River in the Cambridge Gulf of the central Joseph Bonaparte Gulf (14°50'S, 128°5'E), and the Berkeley River of the western Joseph Bonaparte Gulf (14°25'S, 127°40'E). Juveniles were placed on ice, frozen and transported to the laboratory for gel electrophoresis (using the system established for the adult prawns) and morphological measurements.

Gel electrophoresis

The malate dehydrogenase enzyme system was tested for separating *P. indicus* and *P. merguensis*. Tail-muscle tissue was homogenized in one drop of electrode buffer solution (0.05 M Tris–malate, pH 7.5). The homogenate from the tissue extracts was placed on a cellulose acetate gel plate, the electrophoresis chamber was filled with electrode buffer and the gel was placed in a refrigerator at 5°C. Power was applied (15–20 mA, 220–240V) to the gels for ~60 min before the gels were transferred on to a glass, blotted and stained with a solution of staining buffer (Tris–HCl, pH 8), 1.0 M malate solution, methyl thiazolyl blue, phenazine methosulfate, nicotinamide

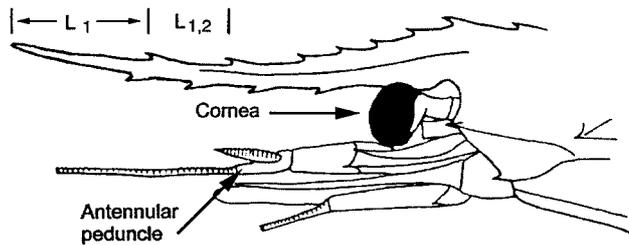


Fig. 1. Morphometric features measured in juvenile banana prawns collected from the Joseph Bonaparte Gulf of northern Australia. L_1 , distance from anterior-most dorsal rostral tooth (termed the first tooth) to tip of the rostrum; $L_{1,2}$, distance between first and second dorsal rostral teeth.

adenine dinucleotide and liquid agar (Richardson *et al.* 1986). The plates were left to develop in the dark for 5–10 min at $\sim 23^\circ\text{C}$. Samples of tissue homogenate from known (i.e. identified larger prawns) *P. indicus* and *P. merguensis* were run on each plate as a reference point.

Morphometric characters

The number and position of the dorsal rostral teeth have been used to identify the juveniles of *P. merguensis* and *P. indicus* (Muthu and Rao 1973; Chong and Sasekumar 1982). The following features of the dorsal rostral teeth (Fig. 1) were recorded:

- Distance between the anterior-most dorsal rostral tooth (hereinafter referred to as the first tooth) and the tip of the rostrum (L_1): distance between the first and second dorsal rostral tooth ($L_{1,2}$). This ratio, $L_1:L_{1,2}$, was denoted $L_i:L_{ap}$ by Chong and Sasekumar (1982).
- Position of the first tooth relative to the ventral teeth, e.g. first tooth between ventral teeth 3 and 4.
- Position of the first tooth in relation to the antennular peduncle (i.e. anterior or posterior to the peduncle), and
- Number of dorsal rostral teeth behind the eye (i.e. the anterior edge of the cornea).

Where possible, the above four characters were measured on all the juvenile prawns before samples from each prawn were run for gel electrophoresis to establish their identity to species. Because of damage to the carapace and rostrum, morphometric measurements were made on only 138 of the 218 juvenile prawns, and all four measurements could be made on only 95 of these prawns. The results from the gel electrophoresis were used to classify the juvenile prawns as *P. indicus* or *P. merguensis*, and mean or modal values were calculated for each of the morphometric characters.

Results and discussion

Gel electrophoresis

Only two fast heterozygotes (0.8%), both *Penaeus merguensis*, for malate dehydrogenase (MDH) were found in the total of 228 sub-adult and adult prawns (Fig. 2). The allozymes from *P. merguensis* travelled further (i.e. ran faster) than those for *P. indicus* (Fig. 2).

The MDH allozyme patterns were expressed strongly and clearly in the juvenile prawns, and the allozyme patterns of homozygous and fast heterozygotes for juveniles were the same as for the adults (Fig. 2). Two fast heterozygous juvenile *P. merguensis* were found in the total of 218 juveniles (0.9%). Morphometric analysis confirmed that these individuals were *P. merguensis* (see below). A second very fast heterozygous pattern, not present in the larger prawns, was found

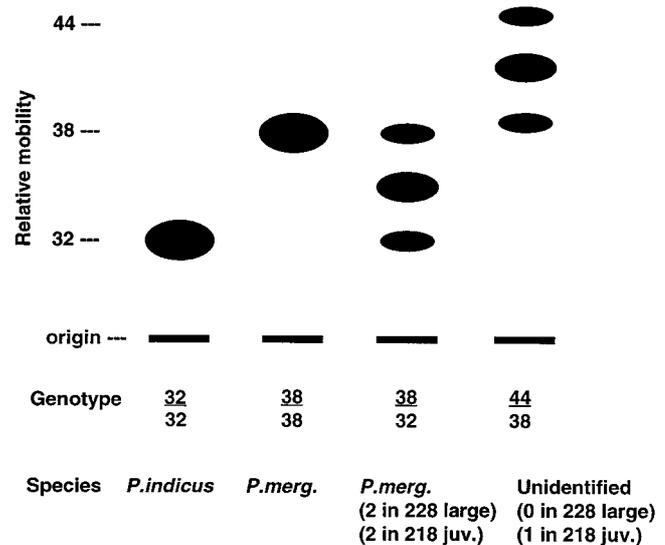


Fig. 2. Diagrammatic representation of banding patterns for malate dehydrogenase allozymes in *Penaeus indicus* and *P. merguensis* (*P. merg.*). Juv., juveniles.

in one unidentified juvenile prawn (Fig. 2). The allozyme results from both large and juvenile prawns show that the MDH system clearly separates *P. indicus* from *P. merguensis* in over 99% of individuals. All four of the fast heterozygotes were *P. merguensis* and only one very fast heterozygote (0.2%) could not be identified.

Morphometrics

The distance from the first tooth to the end of the rostrum was much longer for *P. indicus* than for *P. merguensis*, and hence the ratio $L_1:L_{1,2}$ was higher for *P. indicus* (3.16) than *P. merguensis* (1.56) (Table 1). Only 5 *P. indicus* had $L_1:L_{1,2}$ values that overlapped with those of *P. merguensis*, and 6 *P. merguensis* values overlapped with those of *P. indicus*.

The mean values of $L_1:L_{1,2}$ were also higher for larger juvenile *P. indicus* (2.32) than *P. merguensis* (0.9 to 1.0) from Selangor waters in Malaysia (Chong and Sasekumar 1982). The modes for the $L_1:L_{1,2}$ ratio from the Kakinda region of India show a similar difference between species, with modal values of 2 to 3.4 for *P. indicus* and 0.5 to 1.4 for *P. merguensis* (Muthu and Rao 1973).

In the present study, the modal position of the first tooth was between the 3rd and 4th ventral teeth (Table 1) and there was no clear difference in position between species. The species separated more clearly on position in the Indian study: the modal position for *P. merguensis* was between the 3rd and 4th ventral teeth, and for *P. indicus* between the 4th and 5th ventral teeth. The separation between species was clearer for larger (>50 mm total length, ~ 14 mm CL) than smaller prawns in Indian waters.

The first tooth was posterior to the antennular peduncle for all *P. indicus* and anterior for all *P. merguensis* in the

Table 1. Summary of morphological measurements of juvenile banana prawns from the Joseph Bonaparte Gulf, identified by gel electrophoresis L_1 , distance from anterior-most dorsal rostral tooth (termed first tooth) to tip of rostrum; $L_{1,2}$, distance between first and second dorsal rostral teeth

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First tooth to ant. peduncle	anterior	posterior	59, 36
No. dorsal teeth behind eye	5: 4.5%	5: 93.9%	89, 49
	6: 95.5%	6: 6.1%	
Mean carapace length (mm)	8.2 ± 0.22	5.3 ± 0.27	89, 49
Carapace length (mm)	3.1–16.5	3.4–13.1	89, 49

present study (Table 1). Similar results were reported for these species in Malaysia (Chong and Sasekumar 1982) and India, except that the first tooth was posterior to the peduncle in about 80% of the smaller *P. indicus* from India (Muthu and Rao 1973).

The number of dorsal rostral teeth behind the eye was a good character for separating the species in the present study, with >90% of *P. merguensis* having five teeth in this position (Table 1). In contrast, >90% of *P. indicus* had six teeth behind the eye (Table 1). Although similar results were found for *P. merguensis* and *P. indicus* in Malaysia and India, there was more overlap between species in the number of teeth behind the cornea than found in the present study. The proportion of *P. merguensis* with six teeth behind the cornea increased above 15 mm CL in Malaysian waters (Chong and Sasekumar 1982).

The other important white prawn in the south-east Asian region, *P. penicillatus*, is not found in Australian waters (Dall *et al.* 1990), and separated from *P. merguensis* in Malaysia solely on the ratio of $L_1:L_{1,2}$ (Chong and Sasekumar 1982). However, *P. penicillatus* can be separated from *P. merguensis* and *P. indicus* by gel electrophoresis using the peptidase (glycyl–leucine) enzyme system (Lavery, personal communication).

The lengths of the dactylus and propodus of the third maxilliped, the presence of setae on the maxilliped of males and the numbers and distribution of chromatophores have also been used to separate *P. merguensis*, *P. indicus* and *P. penicillatus* (Muthu and Rao 1973; Chong and Sasekumar 1982). However, these characters are more time-consuming to measure than the four rostral characters that we used.

The position of the first tooth in relation to the antennular peduncle and the ratio $L_1:L_{1,2}$ have provided good separation of juvenile *P. indicus* and *P. merguensis* in Australia, India and Malaysia. In Malaysia, the ratio of $L_1:L_{1,2}$ remains a consistent feature as the prawns increase in size. Because of damage to the fragile rostral tips of the small juvenile prawns, these two features could not be measured in ~30% of the

individuals from Australia. However, the number of rostral teeth behind the anterior margin of the cornea could be counted on more juvenile prawns. When the number of rostral teeth behind the cornea was used in combination with the position of the first tooth, all prawns could be assigned correctly to species. Results from India and Malaysia suggest that the number of teeth behind the cornea is less reliable for larger juvenile prawns and, hence, care must be taken in using this feature to separate larger juveniles.

Acknowledgments

We thank Colin Cant, David Hawke and Sally of the *Gwendoline May* for helping to collect adult *P. indicus* in the Joseph Bonaparte Gulf and Neil Montgomery, Larni Montgomery and Des of the *Makaira II* for help in collecting juvenile prawns. John Salini provided advice on electrophoresis and comments on the manuscript. Chris Jackson and Vivienne Mawson also gave helpful comments on the manuscript. The Fisheries Research and Development Corporation of Australia (FRDC 97/105) and the CSIRO Division of Marine Research funded this project.

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Manuscript received 29 March 1999; revised and accepted 24 June 1999

Appendix 2.

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Assessing techniques for estimating the extent of mangroves: topographic maps, aerial photographs and Landsat TM images

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Abstract. Coastal habitats are critical to the sustained production of many fisheries. It is important, therefore, that fishery managers obtain accurate estimates of the extent of these habitats. This study investigated three methods of estimating the linear extent and area of mangroves (commercially available topographic data, aerial photographs and Landsat Thematic Mapper satellite imagery) in two regions in northern Australia: the Joseph Bonaparte Gulf (in particular, the Berkeley and Lyne Rivers) with typically narrow fringes of mangroves (<50 m wide), and the Embley River on Cape York Peninsula, with much broader mangrove stands (50–1000 m wide). Ground-truthing verified that aerial photographs provided the most accurate estimates of extents of mangroves in all rivers, because of their high spatial resolution (2 m). Landsat Thematic Mapper imagery gave good estimates of the area of habitats, but, because of the 30 m pixel resolution, it underestimated the linear extent in places where the mangrove fringe was narrow. Topographic data gave good estimates of the extent of mangroves where the forests were more extensive and less linear in shape, but were very poor otherwise at this scale. These findings have implications for the use of remote sensing techniques in ecological studies in these regions.

Introduction

Mangrove habitats directly support many estuarine and offshore fisheries by providing food, shelter, breeding grounds and nursery areas. For a number of fisheries, a positive relationship has been found between the extent of coastal habitats and offshore fishery production (e.g. Turner 1977; Staples *et al.* 1985). Determining the extent of coastal habitats is therefore important for understanding changes in fisheries production and for fisheries management. However, some fisheries extend over vast areas, making it difficult, labour-intensive and expensive to map the adjacent coastal habitats.

Remote sensing can be used to map coastal habitats and it is often an easier and cheaper alternative to ground-survey methods of mapping, particularly in remote or inaccessible regions (e.g. Aschbacher *et al.* 1995; Laba *et al.* 1997; Mumby *et al.* 1999). A variety of remote sensors and image-processing methods can be used; their advantages and disadvantages are site-specific and vary with the requirements of the project. For example, the choice of using either aerial photography or satellite imagery involves a trade-off between the high spatial resolution obtained from aerial photography, and the large coverage area and high spectral resolution available from satellite imagery (Green *et al.* 1998; Mumby *et al.* 1999).

In this paper, we report on our mapping of the coastal ecosystems around the Berkeley and Lyne Rivers in Joseph

Bonaparte Gulf (JBG; Fig. 1), and the Embley River on the western side of Cape York Peninsula (Fig. 2). These regions lie within Australia's Northern Prawn Fishery, and their mangrove ecosystems act as critical nursery grounds for banana prawns (*Penaeus merguianus* and *P. indicus*), one of the main components of this fishery. The mangroves in Joseph Bonaparte Gulf typically grow as a relatively thin band of vegetation lining the coast, whereas those in the Embley River form broad forests. We used three data sources – commercially available digitized topographic data, aerial photographs and Landsat Thematic Mapper (TM) satellite imagery – to estimate the area and linear extent of the mangroves. The three methods are compared and the accuracy of each method is discussed.

Methods

Study sites

We selected two rivers that run into Joseph Bonaparte Gulf (Fig. 1): the Berkeley River and the Lyne River. This is a remote and undeveloped region. The nearest town is Wyndham (population 900), ~130 km south-east of the Berkeley River and 70 km south of the Lyne River. Along the banks of both rivers, the mangroves form narrow fringes, generally <30 m wide, with few areas reaching 100 m in width. The two rivers have a similar species composition of mangroves, dominated by *Rhizophora stylosa*, *Avicennia marina* and *Sonneratia* sp. (Manson, personal observation).

Our results have been compared with those from the Embley River in the north-eastern Gulf of Carpentaria (Fig. 2, results reported by Long *et al.* 1992). This system is less isolated than those of the JBG, with the town of Weipa (population ~3000) near its mouth (Fig. 2).

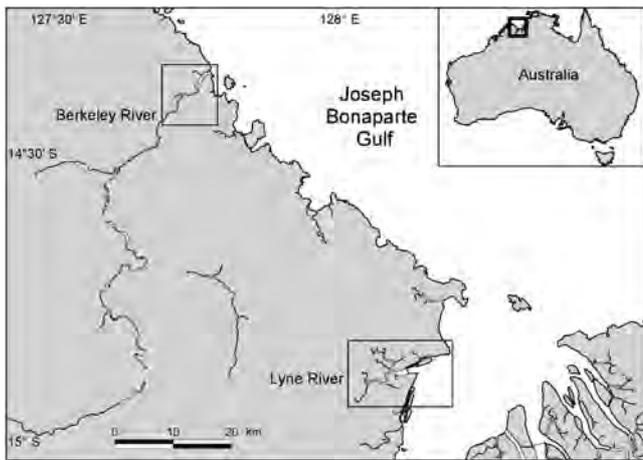


Fig. 1. Study sites in the Berkeley and Lyne rivers, in Joseph Bonaparte Gulf, north-western Australia. Boxes show where the areas and linear extents of mangroves were estimated.

The mangroves lining this river grow in much broader stands than those in the JBG, with the width of the forest ranging from ~50 m to >1000 m. The most common mangrove species here are *R. stylosa*, *A. marina* and *Ceriops* sp. (Long *et al.* 1992).

Topographic data

The topographic data were obtained from the Australian Surveying and Land Information Group (AUSLIG) Topographic 1:250 000 database, released in January 1994. This database was digitized primarily from the 1:250 000 National Topographic Map Series, which was completed

in 1988, and based on aerial photographs of variable age and scale. The database defines coastal habitats including mangroves, saltflats, swamps, lakes and land subject to flooding.

Aerial photographs

Black-and-white aerial photographs of the coastal region of western Joseph Bonaparte Gulf were obtained from the Western Australian Department of Conservation and Land Management. The photographs were taken between 1 and 3 August 1994. Colour photographs of the Embley River, taken on 25 September 1989, were obtained from the Queensland Beach Protection Authority.

The aerial photographs were taken at a scale of 1:50 000 and scanned at 400 dpi, giving 2 m ground resolution. They were imported to the image analysis software ERDAS Imagine 8.3 (ERDAS Inc. 1997), on which they were georectified against control points on the AUSLIG data and selected ground control sites. Fifty-six ground control points were taken in the Berkeley River, and 36 in the Lyne River. These points were selected to be recognizable from the aerial photographs (e.g. prominent rock features), and to be as widespread as possible throughout the image, to improve the accuracy of the georectification. Positional errors were introduced during the georectification process because the Global Positioning System (GPS) used to record ground control points may have inaccuracies of up to 100 m due to the selective availability of the satellite. However, the accuracy of recording ground control points was improved to within 30 m by averaging over five readings. Differential GPS, which gives much higher levels of accuracy, was not available because of the remoteness of the region and the limited time in the field, making it impossible to set up a base station. Further error may have been derived from the difficulties encountered in selecting identifiable and precise ground control points in such a remote region.

The scanned images were enhanced and classified with ERDAS Imagine 8.3 software. We carried out a texture analysis on each image, based on low-pass focal windows of 3 × 3, 5 × 5 and 7 × 7 pixels,

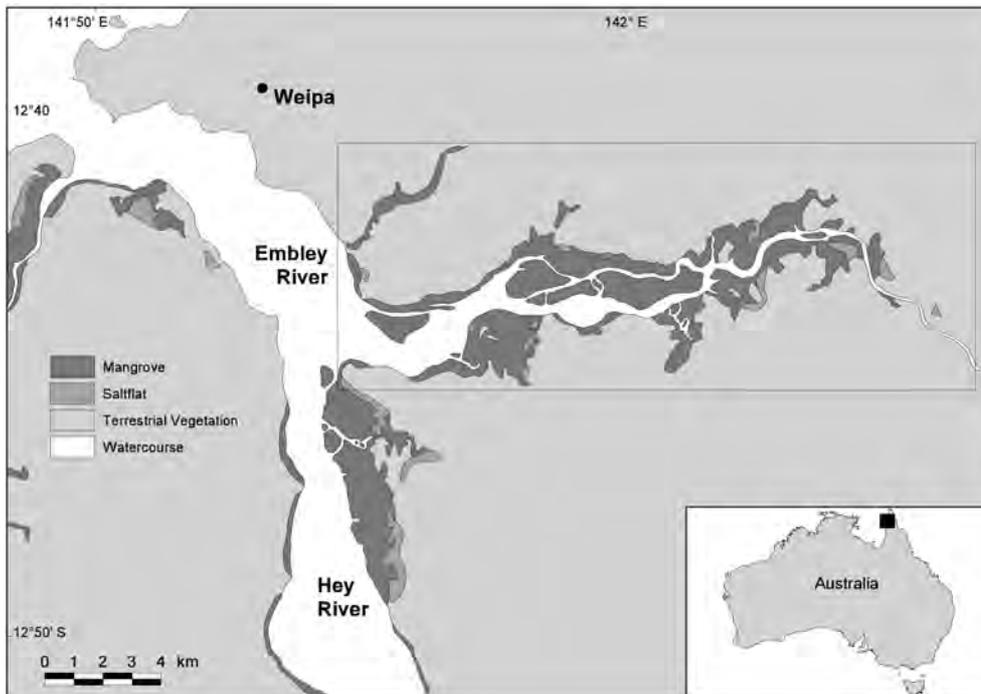


Fig. 2. Study site in the Embley River, north-eastern Australia. The box shows where the area and linear extent of mangroves were estimated. Waterbody features from the AUSLIG dataset are shown.

followed by a principal component analysis with three principal components. This process added further dimensions to the data, by incorporating a measure of the texture of the land cover types, thereby facilitating the subsequent classification process. The resulting images were classified by an unsupervised isodata-clustering classification, to produce four classes, defined as mangrove, saltflat, river and terrestrial vegetation. Ground-truthing was carried out at two mangrove sites in each of the Berkeley and Lyne rivers in December 1998, and used to visually confirm the accuracy of the classifications. At each site, between 20 and 26 marks were taken ~100 m apart, around both the landward and seaward edges of the mangrove stands.

Landsat TM

A Landsat-5 TM window processed to Level 8 (map oriented; systematic corrected; two-dimensional resampling to align with map grid AMG52, Datum AGD66) was acquired for the JBG region. The image was captured on 11 July 1994, which coincides closely with the date of the aerial photographs. The pixel resolution of the image was 30 m. Bands 1-5 and 7 were used in the analysis, because these are considered the most useful for vegetation mapping (Kay *et al.* 1991).

The Landsat TM image was spectrally enhanced with a Tasseled Cap transformation (Crist and Kauth 1986), a technique that optimizes the visualization of vegetation information (ERDAS Inc. 1997). An unsupervised isodata-clustering classification was then carried out, resulting in 24 classes, and the mangrove class was confirmed by visual comparison with the aerial photographs and the ground-truth data.

The area of mangroves in the Embley River was previously estimated from a Landsat TM image by Long *et al.* (1992). Their analysis did not include an estimate of the linear extent of mangroves in the Embley River, or any assessment of the accuracy of their classification.

Estimation of area and linear extent of mangroves

The areas and linear extents of mangroves were calculated with ArcView 3.0a GIS software. The areas of the mangroves were calculated (km²) with an Avenue script (T. Taranto, CSIRO, unpublished data). Linear extents were calculated in ArcInfo by converting the mangrove polygons to arcs, selecting those arcs bound on one side by water and on the other by mangrove, and calculating the length of these interfaces in kilometres with an Avenue script (Taranto, unpublished data). The Landsat TM image of the Embley River could not be used to calculate linear extent because it was not available to us in digital format.

Comparison of methods

We compared the accuracy of the classifications of mangroves in the three rivers with error matrices (Congalton 1991). Firstly, the three coverages for the Berkeley and Lyne rivers (AUSLIG, aerial photographs and Landsat TM), and the two available coverages for the Embley River (AUSLIG and aerial photographs) were converted to raster grids with 10 m pixels (ArcView Spatial Analyst). The AUSLIG and Landsat TM grids were then cross-tabulated with the aerial photograph grids. The aerial photographs were taken as the reference data in the error matrix because ground-truthing showed that this was the most accurate of the three techniques (see below). It should be remembered, therefore, that this gives a relative, rather than an absolute, accuracy. The number of pixels in the AUSLIG coverages and the Landsat TM classifications that were (a) correctly classified as mangrove (b) misidentified as mangrove (error of commission) or (c) undetected as mangrove (error of omission) were calculated as a proportion of the total number of mangrove pixels in the aerial photographs. The accuracy assessments obtained from this type of error matrix are a combination of both attribute accuracy (accuracy of

the classification of features) and positional accuracy (accuracy of georectification).

Results

Area

For both the Berkeley and Lyne rivers, the areas of mangroves estimated from the aerial photography and Landsat methods were within 0.5 km² of each other (Table 1), despite the much lower resolution of the Landsat TM image (30 m) compared with the aerial photographs (2 m). In contrast, the areas of mangroves calculated from the AUSLIG data were much less than those calculated by the other techniques (Table 1). However, in the Embley River, estimates by all three techniques were within 5 km² of each other (Table 1).

Linear extent

In the JBG, the linear extents of mangroves estimated from the AUSLIG data were only 14% (Berkeley River) and 22% (Lyne River) of those estimated from the aerial photographs (Table 1). Although the Landsat imagery gave higher linear estimates than AUSLIG, they were only 49% (Berkeley River) and 41% (Lyne River) of the extents estimated from the aerial photographs. In the Embley River, the linear extent of mangroves estimated from the aerial photograph classification was 117 km, compared with 81.2 km (69%) estimated from the AUSLIG dataset.

Comparison of methods

In the Berkeley River, the proportion of correctly classified mangrove pixels relative to the aerial photographs was low for both the AUSLIG data (11.3%) and the Landsat TM classification (27.9%, Table 2). For the AUSLIG data, the proportion of pixels of undetected mangroves was high (88.7%), and the proportion of misidentified mangroves was 42.5%. For the Landsat TM classification, the proportions of

Table 1. Estimates of area and linear extent of mangrove habitats in the Berkeley, Lyne and Embley Rivers from the Australian Land Information Group (AUSLIG) topographic data, aerial photograph classifications and Landsat Thematic Mapper (TM) classifications
NA, digital format not available

River	Aerial photographs	AUSLIG	Landsat TM
Area (km ²)			
Berkeley	1.31	0.72	1.53
Lyne	18.05	4.98	17.51
Embley	30.20	29.70	25.50
Linear extent (km)			
Berkeley	36.45	5.04	17.76
Lyne	124.18	27.78	50.31
Embley	117.00	81.20	NA

Table 2. Proportion (as a percentage of the number of mangrove pixels) of 10 m pixels in the AUSLIG data and Landsat TM classification that were classified correctly, misidentified as mangroves, or undetected as mangroves

Data in digital format were not available to complete this analysis for Landsat TM in the Embley River

River and Technique	Correct (%)	Misidentified as mangroves (%)	Undetected as mangroves (%)
Berkeley			
AUSLIG	11.3	42.5	88.7
Landsat TM	27.9	85.7	72.1
Lyne			
AUSLIG	12.7	14.9	87.3
Landsat TM	46.6	50.6	53.4
Embley			
AUSLIG	81.1	21.6	18.9

misidentified pixels (85.7%) and undetected pixels (72%) were both high. Most errors in classification, in both the AUSLIG and Landsat TM, were derived from poor discrimination between mangroves and terrestrial vegetation and, to a lesser extent, between mangroves and the river.

Similarly, in the Lyne River, the proportion of correctly classified mangrove pixels in the AUSLIG data was low (12.7%), with a large proportion of mangrove pixels going undetected (87.3%). However, a higher proportion of mangrove pixels was correctly identified by the Landsat image (46.6%) than by the AUSLIG data. Similar proportions of pixels were in the remaining categories — misidentified as mangroves (50.6%) and undetected mangroves (53.4%) — suggesting that the source of error was positional rather than due to classification errors. The positional errors are in the order of up to 60 m between the aerial photographs and Landsat TM, and up to 150 m between these two and the AUSLIG data. This will clearly account for a large but unquantifiable part of the discrepancy in the accuracy assessment. In future work, this positional error should be reduced because of the removal of selective availability on satellites in June 2000, which has greatly improved the accuracy of GPS.

In contrast to the JBG, in the Embley River the number of correctly classified pixels in the AUSLIG data was high (81.1%), and the number of misidentified and undetected pixels was low (21.6% and 18.9% respectively; Table 2). This parallels the results for the estimation of extent of mangroves in the Embley River (Table 1), where the AUSLIG data gave relatively good estimates of mangrove extent in this river.

Discussion

The capabilities of different techniques for mapping coastal habitats have been directly compared in few studies (e.g. Green *et al.* 1998; Mumby *et al.* 1999). In our study of three small (<200 km²) remote regions in northern Australia, the

accuracy of aerial photography relative to the other techniques can be attributed to its higher resolution, which allows fine-scale, detailed mapping of small areas of vegetation. The photographs used in this study had a pixel resolution of 2 m. This enabled even the narrow mangrove fringes and small mangrove stands, typical of the Joseph Bonaparte Gulf region, to be identified (Fig. 3b). In contrast, the Landsat TM image had a pixel resolution of 30 m, and the AUSLIG mapping had a scale of 1:250 000.

Over large areas, aerial photography is more expensive per square kilometre than satellite imagery, because the many photographs required for full coverage increase the cost of both acquisition and processing (Mumby *et al.* 1999). For example, mapping the entire extent of the Northern Prawn Fishery, covering 6000 km of coastline, would require an enormous number of photographs. However, our study areas were covered by one photograph (Berkeley River), five photographs (Lyne River) and four photographs (Embley River), which made aerial photography a cost-effective option at this scale.

The AUSLIG database is intended for use at a scale of 1:250 000, and its positional accuracy is such that 90% of features fall within 250 m of their mapped location. We concluded that the AUSLIG data can reliably identify mangrove stands of ≥ 50 m wide, but cannot consistently identify those <50 m wide (Fig. 3a). The mangrove fringes along the rivers of northern Australia are generally narrow — less than 30 m in many cases. Consequently, the AUSLIG data underestimated both the area and the linear extent of mangroves in the JBG. The very high proportion of incorrectly classified pixels found in the accuracy assessment (Table 2) reflects both the lack of accuracy in identifying mangroves, and also poor spatial accuracy at this scale. The estimates from the AUSLIG data were much more accurate for the Embley River (Table 1, Table 2), where the mangroves form more extensive, less linear forests than those in the JBG.

Landsat TM imagery, with its 30 m pixel resolution, has a lower resolution than aerial photography, and does not provide as much detail of coastal habitats (Fig. 3c). One of the problems with comparing images from different sources can be low spatial accuracy because of the difficulties in georectification in very remote and inaccessible regions. There are very few features that can be readily and accurately identified in such regions. Despite this, the overall estimates of the area of mangroves we obtained from the Landsat TM images were similar to those from the aerial photographs (Table 1), suggesting that this would be a useful technique for broad-scale habitat mapping.

Landsat TM is frequently used to map vegetation because it has good spectral resolution and relatively good spatial resolution and its images can cover large areas (Green *et al.* 1996). A spatial resolution of 30 m provides good discrimination of vegetation types on the broad-scale,

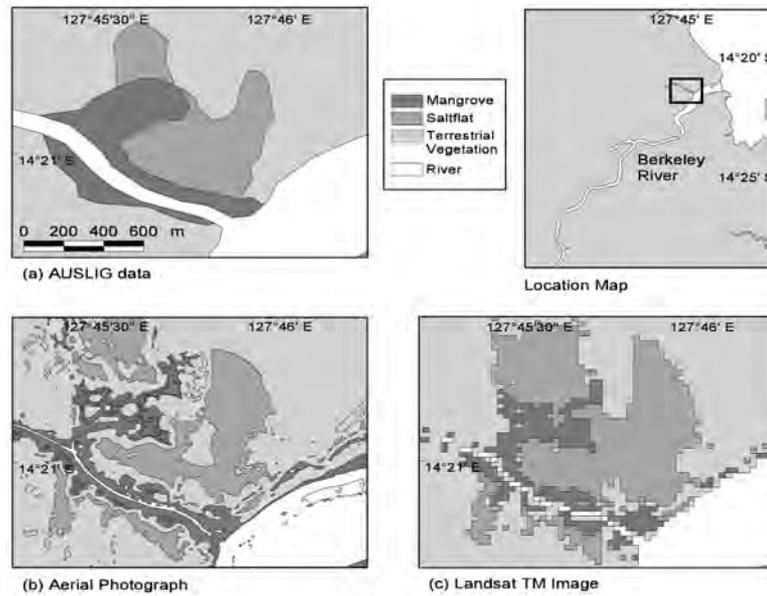


Fig. 3. A comparison of the three mapping techniques. The land-cover types (mangroves, saltflat, river and terrestrial vegetation) are shown for a side creek of the Berkeley River: (a) topographic data (AUSLIG) (b) classification of an aerial photograph (c) classification of a Landsat TM image.

but not at the scale required to detect narrow fringing mangroves. When Ong *et al.* (1992) mapped mangrove forests in Malaysia, they concluded that for a mangrove patch to be identified by Landsat TM it must have an area of at least 0.5 ha (0.005 km²). Our work confirms that Landsat TM has limitations when one dimension of the habitat being mapped is close to its spatial resolution, and suggests that mangrove fringes of 30 m width or less will only be partly detected by Landsat TM, and that a stand at least 50 m across is required for more reliable identification. The main benefit of using Landsat TM is that a single scene covers an area of 185 km by 185 km (i.e. 34 225 km²), making it suitable for the study of large areas such as the Northern Prawn Fishery.

Our study demonstrates the importance of selecting the appropriate mapping technique relative to the scale of the region of interest. It also demonstrates the difficulties of achieving high spatial accuracies in remote and inaccessible regions. We have shown that topographic maps at scales of 1:250 000 or coarser can grossly underestimate the area and linear extent of mangroves, particularly in localities such as northern Australia, where rivers are typically lined by a narrow fringe of mangroves. This could have serious implications for ecological studies, such as those that attempt to model the relationship between habitat area and the productivity of commercial fisheries. However, since the AUSLIG dataset is relatively cheap (AU\$50 per tile per theme), and is simple and quick to use, these maps are

certainly still useful for obtaining a first-pass view of an area, before using higher-resolution techniques, such as aerial photography and Landsat TM imagery. These latter are readily available, and can achieve far better estimates of habitat extent, and would improve the accuracy of the ecological models. The use of aerial photographs for fine-scale studies, and of Landsat TM or other satellite imagery over larger areas, provides the most cost-effective approach to accurate habitat mapping.

Acknowledgments

This study was funded by the Australian Fisheries Research and Development Corporation (FRDC 97/105). We thank Mick Haywood, Tim Skewes, Stuart Phinn and Vivienne Mawson for their constructive comments on the manuscript. We thank Tom Taranto for providing the Avenue scripts to estimate area and linear extent of mangroves.

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Manuscript received 6 April 2000; revised 15 September, accepted 13 November 2000

Appendix 3.

Venables, Bill – Composition of juvenile banana prawns in the JBG.

1 Composition of juvenile banana prawns in the JBG

Bill Venables, 3 May 2001

The problem considered here is to model the proportion of *Penaeus indicus* juveniles in combined *P. indicus* and *P. merguensis* trawl samples taken in the Joseph Bonaparte Gulf, as a function of external determining variables. These variables included location, temperature, salinity, turbidity, climatic conditions and various other site and weather variables detailed elsewhere.

1.1 Form of the model

The sampling unit is the trawl and the response will take the form of a ratio:

$$P = \frac{\text{Number of } P. \textit{ indicus} \textit{ juveniles}}{\text{Total number of Banana prawn juveniles in the trawl}} = \frac{N}{T}$$

Our first aim is to model the behaviour of the proportions, P , as a function of the determining variables. For this purpose we will condition on the total number of juveniles, T . A second problem to be considered later is to model the behaviour of the total number of juveniles itself as a function of the determining variables.

Although the response is a ratio of frequencies, it is unlikely (and unreasonable to expect) that these will behave like binomial proportions, since the assumption of independence between juveniles is not credible. However it is reasonable to assume that the behaviour of these proportions will, like binomial proportions, have a variance depending on the true (mean) proportion and will be zero if the true proportion is 0 or 1 and maximum if the true proportion is $1/2$. According to statistical convention we will denote the true (or expected) proportion by m : $E[P] = m$, and we assume that the distribution of P is determined by its mean, m , and a scale parameter, f . Rather than make an explicit distributional assumption our analysis will be based on a quasi-likelihood generalized linear model (see (McCullagh and Nelder 1989)) with the following properties:

- $\log \frac{m}{1-m} = b_0 + s_1(x_1) + \dots + s_p(x_p)$, where x_1, x_2, \dots, x_p are the determining variables and s_1, s_2, \dots, s_p are flexible smooth functions for which we choose a spline family. This is usually called a logistic link function.
- $\text{Var}[P] = \frac{m(1-m)}{T/f}$, where T is the total number of juveniles and f is the scale parameter. This guarantees that if the true proportion is near 0 or 1 the variance of the sample proportion is slow. Also, the larger the total number of juveniles in the sample the more accurate is the sample proportion as an estimate of the true proportion.

The component functions, s_i , will show the effect of the determining variable, x_i , on the true proportion (through its logistic transform), assuming no interactions. Care is needed to ensure the determining variables are chosen so that significant interactions between them are unlikely.

This is a generalized linear model; it differs from a generalized additive model only in that the component functions are explicit spline functions rather than smoothing splines (or their allies), which have to be estimated using penalized maximum likelihood. This simplifies the inference without losing too much flexibility.

1.2 Model fitting results

It is important to choose the terms in the generalized linear model carefully: if unimportant terms are left in the model it will reproduce not only the signal but the randomness in the training data, which in turn will be transmitted into predictions from the model. On the other hand, if the model is pruned too severely and important terms are left out, predictions will be biased.

Some indication of the proportions is given in Figure 1, which shows the actual proportions of *P. indicus* observed the 162 stations (trawls) where at least some banana prawns were sampled. The proportions presented in this figure are based on widely different numbers of animals and so have variable accuracy. Nevertheless it is clear that the stations with high proportions of *P. indicus* are concentrated near the mouths of the larger rivers and in the south-west of the JBG.

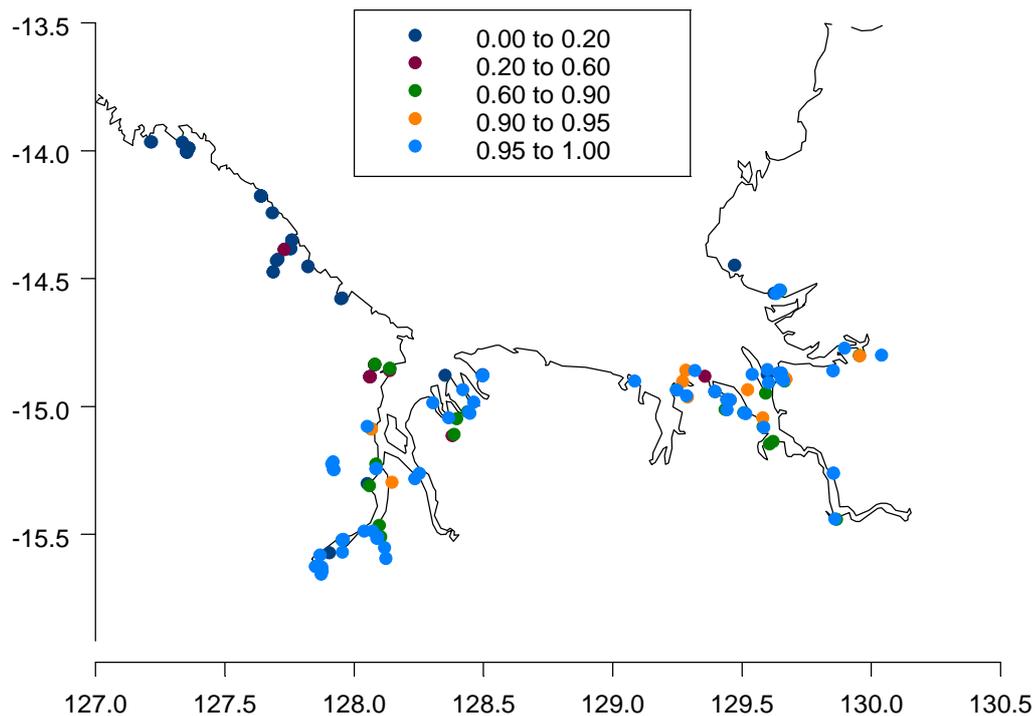


Figure 1: Stations classified by the raw proportions of *P. indicus*

Of the available determining variables we have considered the following reduced set as potential predictors: *Temperature*, *Salinity*, *Secchi* depth, *Pelite* (mud) in the substrate, *Mangroves* (presence or absence), and two location variables. The two location variables were not latitude and longitude but a coordinate system tilted at 45° so one axis, *NWSE*, runs from south-east to north-west and the other, *SWNE*,

runs from south-west to north-east. Since the orientation of the major coastal system for our purposes is along the *NWSE* axis, this choice of system minimises the necessity for inclusion of interacting terms. We anticipate that the orthogonal axis, *SWNE*, will play little part in the model.

It is clear from the observed proportions shown in Figure 1 that the term in *NWSE* will be necessary, although from a biological point-of-view it is not a very satisfactory explanatory variable as it corresponds to no topographic or physical feature of the landscape. At best we can assume that it is a surrogate for other, unmeasured explanatory variables that would be more generally applicable. We include it in our model, however, to check if other explanatory variables have additional explanatory power. We will investigate later possible explanations for feature variables for which the *NWSE* variable may be surrogate.

The continuous predictors were included in the model, as we have said above, as spline terms with an equivalent of 4 degrees of freedom each. This appears to allow the terms to have adequate flexibility, while at the same time producing a reasonable stable model.

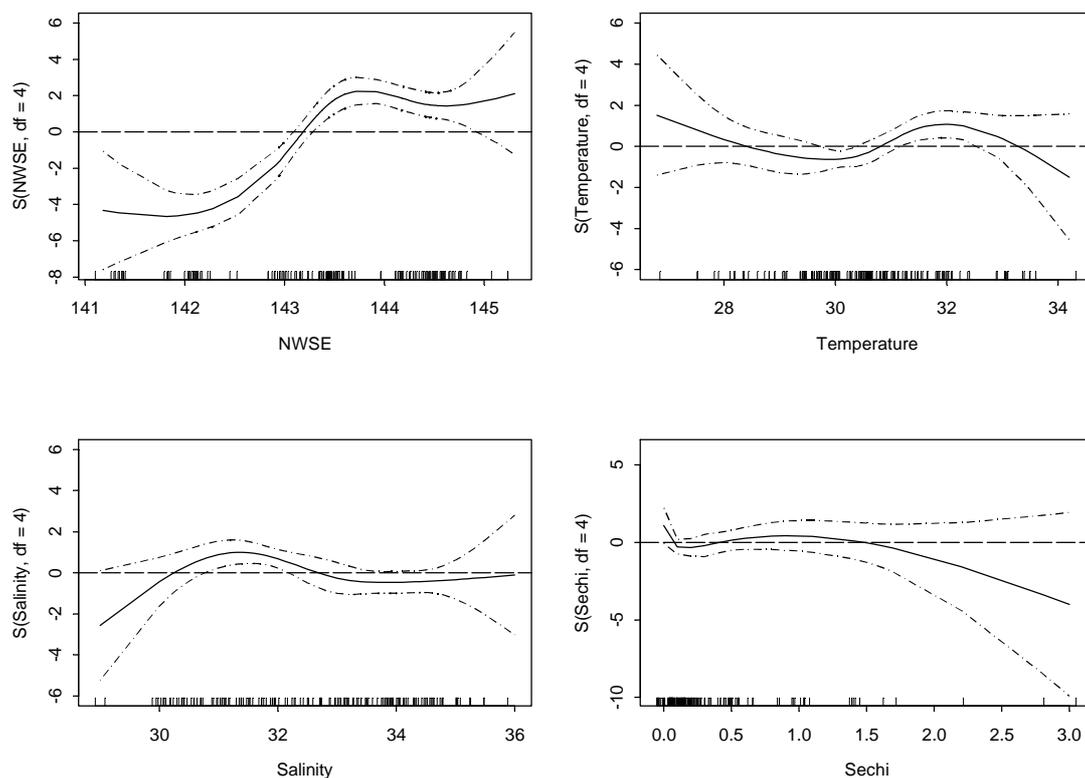


Figure 2: Additive components for the logistic transform of the model proportions

Salinity has been modified for modelling purposes. Two stations were far enough inland for the salinity to be very low. These greatly influence the modelling process and distort the graphical representation of the component. In the fitted model if the salinity is less than 29 units we replace it by 29. At low salinities the proportion of *P. indicus* is essentially zero in any case and this modification does not materially affect the model in any other way.

The first panel in Figure 2 shows the increase in proportions as the location moves from NW to SE. This is the dominant effect. The second panel shows that possibly *P. indicus* has a preferred temperature range, but the effect is smaller. The third panel shows again that possibly there is a preferred salinity range, with a range in the less saline water preferred. The final panel shows the contribution of Sechi depth. This component is only barely significant, though it shows the animals prefer more turbid water. We return to this component below.

The following table shows the approximate significance of each term in the final model in the sense of giving the importance of its contribution additional to all other terms. This is an approximate F-statistic only as no exact theory of testing is available for quasi-likelihood models (See (McCullagh and Nelder1989))

Table 1: Significance of terms included in the model

Component	Degrees of freedom	F statistic	P value
$s_4(NWSE)$	4, 145	36.733	0.000
$s_4(\text{Temperature})$	4, 145	3.590	0.008
$s_4(\text{Salinity})$	4, 145	4.063	0.004
$s_4(\text{Sechi})$	4, 145	2.291	0.062

The estimate of the scaling parameter was:

$$\hat{j} = 18.138$$

This implies that the variation in the proportions is like binomial variation but with a clump of about 18 animals corresponding to an independent trial of the Bernoulli process.

We can gain some idea of how well the model is accounting for the observed proportions by comparing a similar plot to Figure 1 using the model proportions. This is shown in Figure 3 below.

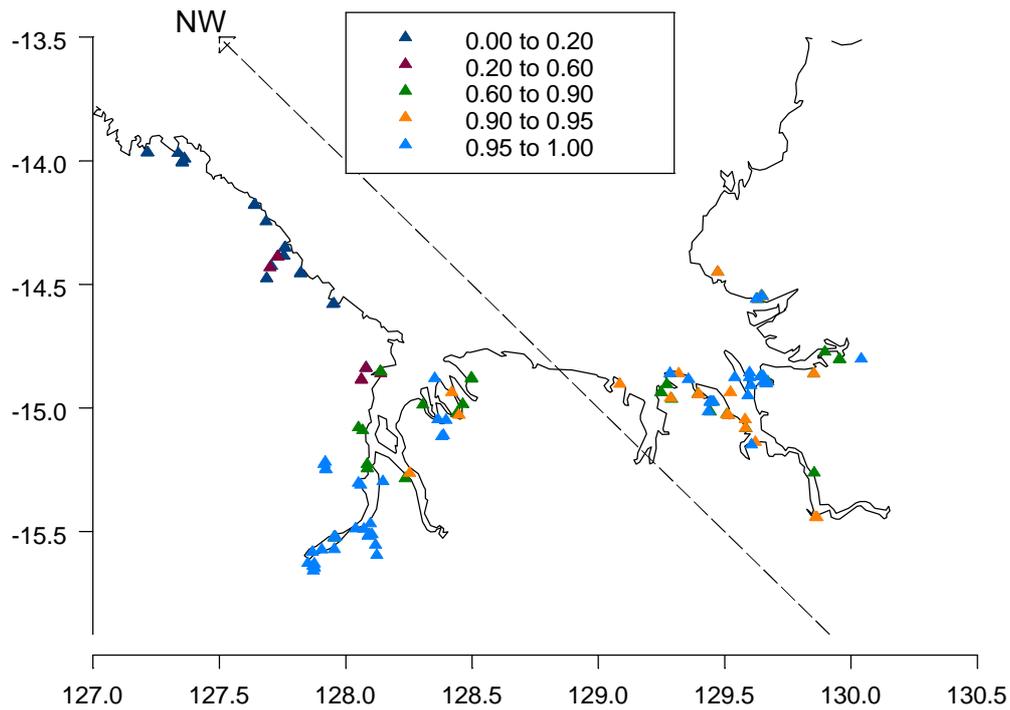


Figure 3: Proportions of *P. indicus* estimated from fitted model

Another way to compare model with data is to tabulate the stations in accordance with the way their actual and model-based estimates agree. We use the same five categories as above. The frequencies are shown in Table 2 below.

Table 2: Comparison of actual and model-based estimates of proportions of *P. indicus*

		Model-based estimates of proportions of <i>P. indicus</i>				
		0.00-0.20	0.20-0.60	0.60-0.90	0.90-0.95	0.95-1.00
Observed proportions of <i>P. indicus</i>	0.00-0.20	32	5	2	1	5
	0.20-0.60	0	6	0	1	3
	0.60-0.90	1	1	9	6	10
	0.90-0.95	0	0	5	3	4
	0.95-1.00	0	0	23	15	30

There is a clear separation of regions with very low proportions from those where it is very high, but the fit of the model is possibly not good enough apart from some interpretative purposes. Accurate prediction seems not to be possible. Note, also, that this table is based on observed proportions based on numbers of individuals that differ very widely. This difference in accuracy makes interpretation difficult.

1.3 A possible surrogate corresponding to the NWSE location variable

Figure 4 shows a plot of Secchi depth against the coordinate in the NWSE axis. Clearly the SE corner of the JBG has a much lower Secchi depth than the more NE

parts, and more *consistently* low. The line on the graph is a lowess smoother which suggests that the median level decreases almost linearly as the location moves SE until the mouth of the Ord river when it essentially flattens out. The main feature of the plot, though, is the large difference in variance along the line.

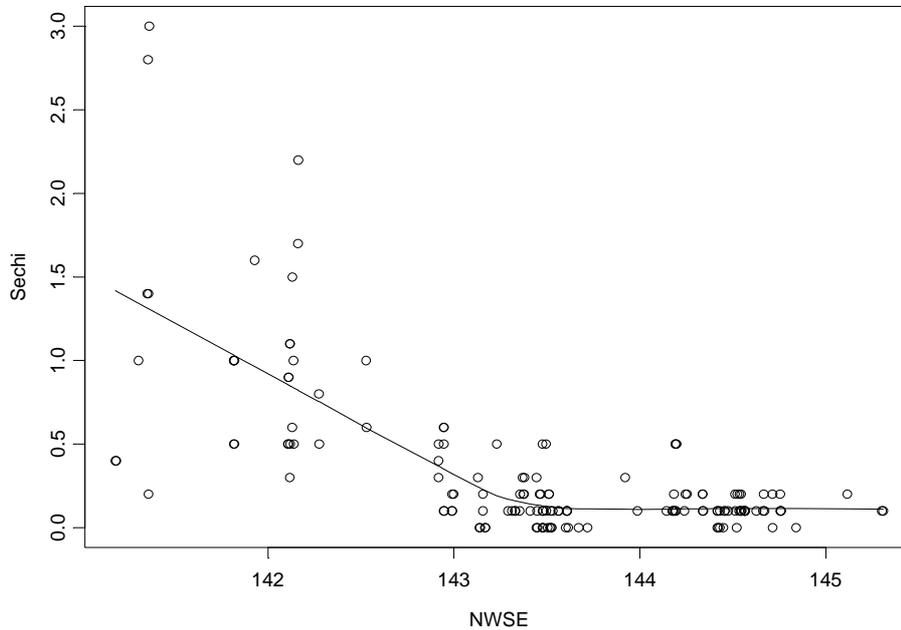


Figure 4: Plot of Secchi depth against its coordinate on the NWSE axis

If the data is smoothed in two directions using both latitude and longitude the smooth curve shown in this diagram is very little different. This suggests to us that the NWSE axis is a good surrogate for the consistent mean turbidity in the area. In the SE corner not only is the Secchi depth low (and hence turbidity high) but this is consistently the case in all neighbouring regions. Outside the SE corner there are large variations in turbidity. This high variance in the predictor in parts of the range may well explain why it does not act as well as the NWSE predictor, especially if high spatial variation is also accompanied by high temporal variation. The animals may require consistently high turbidity, not just temporary high turbidity. Notice, also, that where the lowess smoother flattens out roughly corresponds to the point where the NWSE component also levels off.

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Appendix 4.

Venables, Bill - Notes on the total number of prawns in trawl samples from the JBG.

2 Notes on the Total Number of Prawns in Trawl Samples from the JBG

Bill Venables, 3 May 2001

1 Data

There were 229 shots in the data I have, 162 had some prawns present and 67 had none. Figure 1 shows a frequency diagram for the numbers of prawns per shot, but accumulating all shots with more than 200 prawns in the 200 category. The actual maximum number of prawns found was 1280.

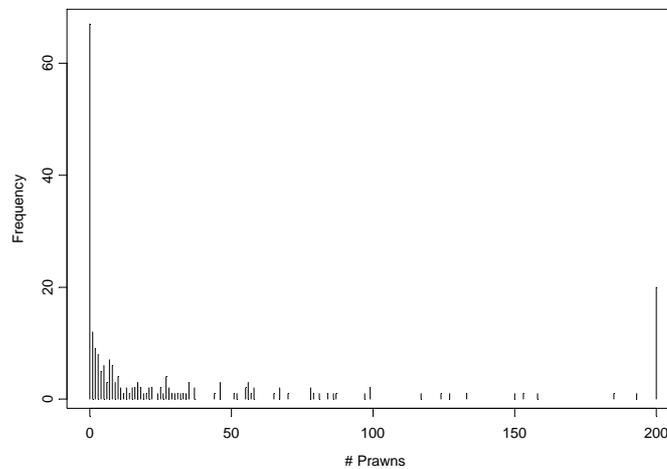


Figure 1: Censored frequency diagram for numbers of prawns per shot

This suggested to me a two-phase approach, namely estimate the probability of finding *any* prawns in the shot first and later estimate the numbers of prawns found possibly given that there were some.

2 Logistic regression models for presence of any prawns

A natural tool to use to estimate the probability of finding any prawns under the conditions existing in the survey is logistic regression. If p is the probability of finding any prawns in a shot, logistic regressions models the relationship between p and the determining variables as:

$$\log \frac{p}{1-p} = b_0 + b_1 x_1 + L + b_k x_k$$

where the b_j s are regression coefficients and the x_j s are the determining variables. We will generally use spline bases to allow a flexible contribution from each of the determining variables, which amounts to using a whole group of linear terms for one genuine predictor variable and rating the term not by coefficients but by a plot of the

contribution of the whole composite term to the logistic transform of the probability. It is therefore more natural to think of the model as having the form:

$$\log \frac{p}{1-p} = b_0 + S_1(x_1) + L + S_k(x_k)$$

where the $S_j(x)$ terms are called the *partial contributions* to the logistic transform.

The determining variables we considered for this model are as follows:

- **Temperature**,
- **Salinity** (with a few sporadic values less than 29 promoted to 29 to guard against undue influence of outlying points in the determining variables),
- **Pelite** (as a percentage of the sediment sample),
- **Cloud cover**,
- **Sechi depth**,
- **Sediment** (a categorical variable with three levels: mud (152 stations), intermediate (33 stations) and sand (44 stations)),
- **Water Type** (a categorical variable with three levels: Coastal (29 stations), Creek (100 stations) and River (100 stations)),
- **Salt Flat** (a categorical variable with two levels: No (115 stations) and Yes (114 stations)).
- **Distance travelled by the trawl itself**.
- **Location** along a Northwest-Southeast axis as a surrogate for other unmeasured determining variables (as in companion paper on composition).

The initial model used natural splines for continuous variables with 4 degrees of freedom (except for Cloud which had too few distinct values and so the spline term had three degrees of freedom) and separate constants for each level of the categorical variables.

Pruning the model by maximising the Akaike Information Criterion (AIC) led to a reduced variables regression retaining only *Salinity*, *Cloud*, *Sediment* and *Pelite*. The significance of each of these terms is shown in Table 1.

Term	df	Deviance	p-value
<i>ns(max(Salinity, 29),4)</i>	4	25.90538	0.00003
<i>ns(Cloud,3)</i>	3	12.28874	0.00646
<i>Sediment</i>	2	32.46126	0.00000
<i>ns(Sechi,4)</i>	4	21.88625	0.00021

Table 1: Contributions of each remaining term to the pruned logistic regression model

The four partial contributions to the regression model are shown in Figure 2. It seems clear that the animals are most likely to be found in turbid water (low Sechi depth)

with muddy sediments and high salinity on a cloudy day, but the standard error lines on the graphs warn that the picture is not strikingly clear for much of the range.

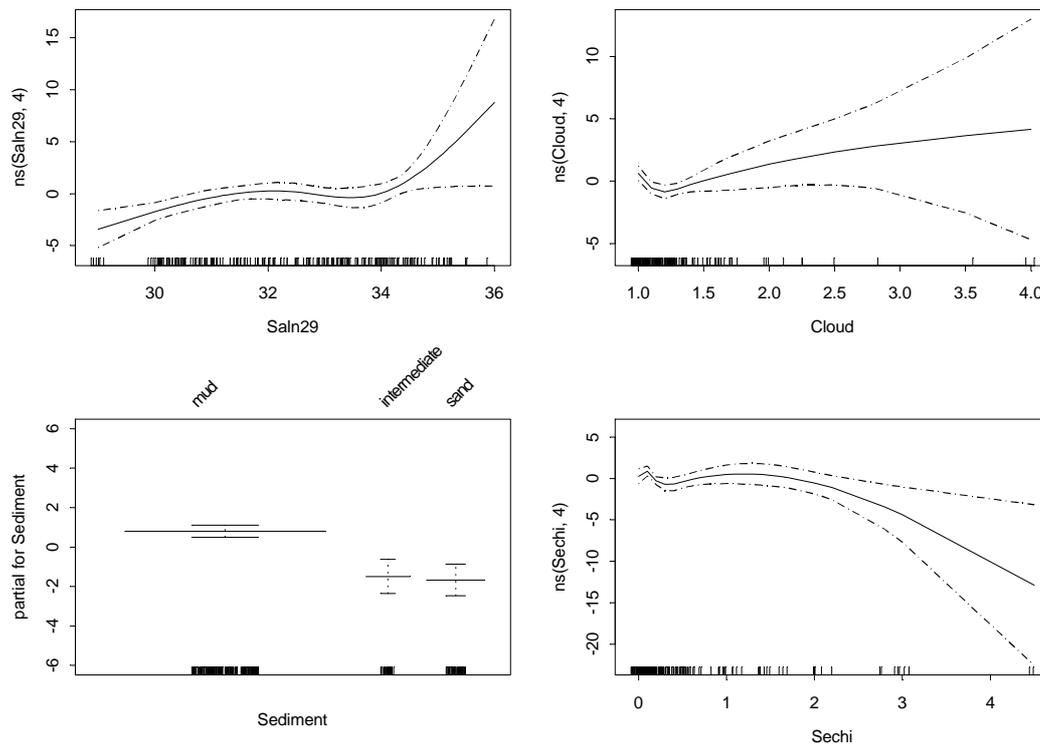


Figure 2: Partial contributions of each term to the pruned logistic regression

3 Presence of *P. indicus*

The data set has 129 stations where *P. indicus* were caught and 100 where the species was not. We can repeat the above analysis checking for the presence or otherwise of *P. indicus* only. Using the same suite of candidate predictors, more remain as significant contributors to the model. Table 2 shows the terms in the final model. Note that the first term, a spline term in the NW-SE axis location, is a surrogate for unmeasured variables that themselves are progressively distributed along this axis. The interesting point to notice is that the remaining terms are all significant *separately* and *in addition* to this location term, suggesting that they have some biological significance.

Term	df	Deviance	p-value
<i>ns(NW-SE, 6)</i>	6	18.1337	0.0059
<i>ns(Temp, 4)</i>	4	13.8309	0.0079
<i>ns(Cloud, 3)</i>	3	10.4028	0.0154
<i>ns(Saln29, 4)</i>	4	18.2579	0.0011
<i>ns(Sechi, 4)</i>	4	14.6427	0.0055
<i>Sediment</i>	2	28.9737	0.0000

Table 2: Remaining contributions to the model predicting the presence of *P. indicus*

Figure 3 shows the partial contributions of each variable to the fitted model.

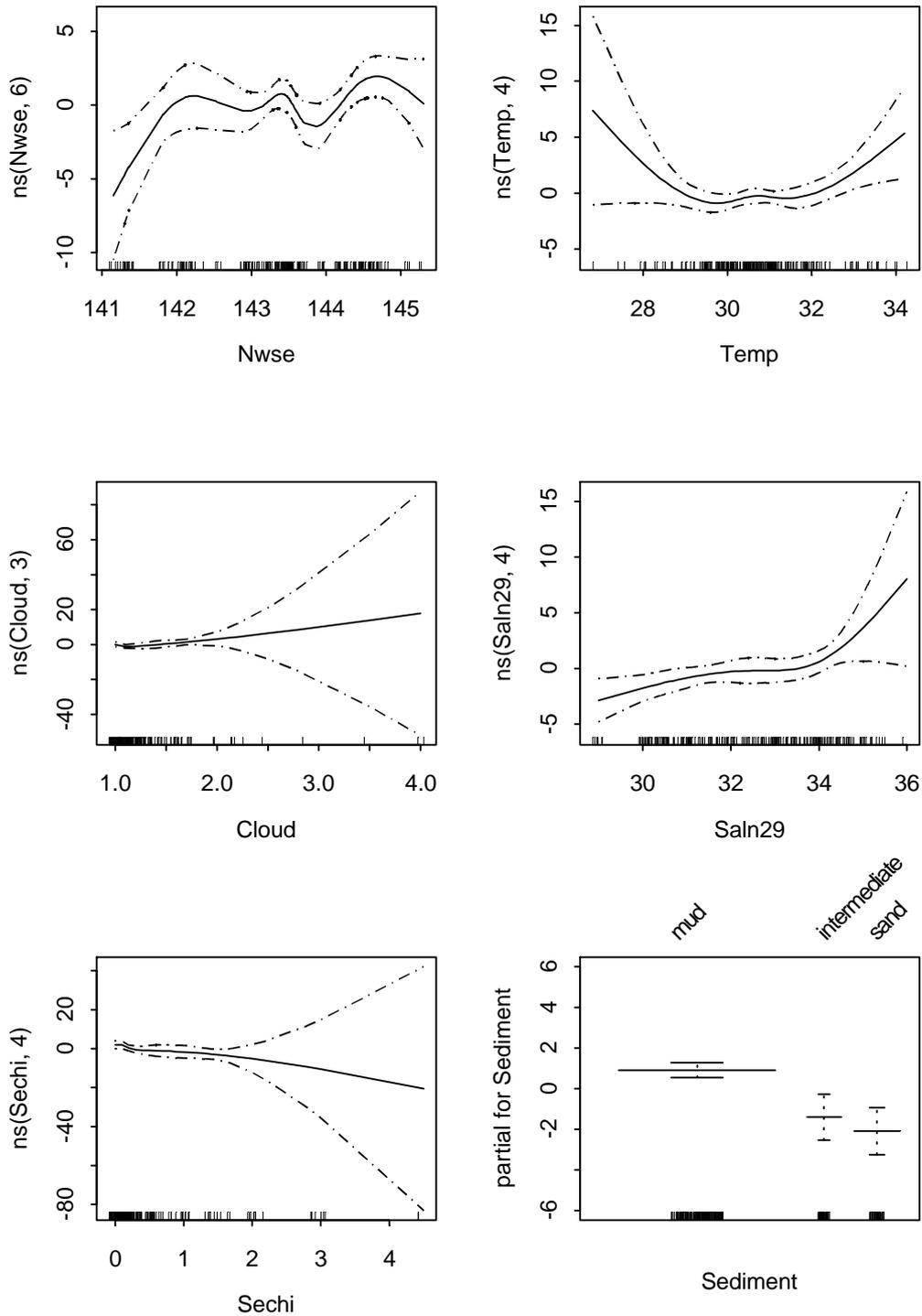


Figure 3: Partial contributions to the linear predictor for the *P. indicus* presence model

The diagrams in Figure 4 show the stations arranged in groups so that the predicted probability of finding *P. indicus* is steadily increasing. This give some indication that the probability is not dominated by the NW-SE location variable.

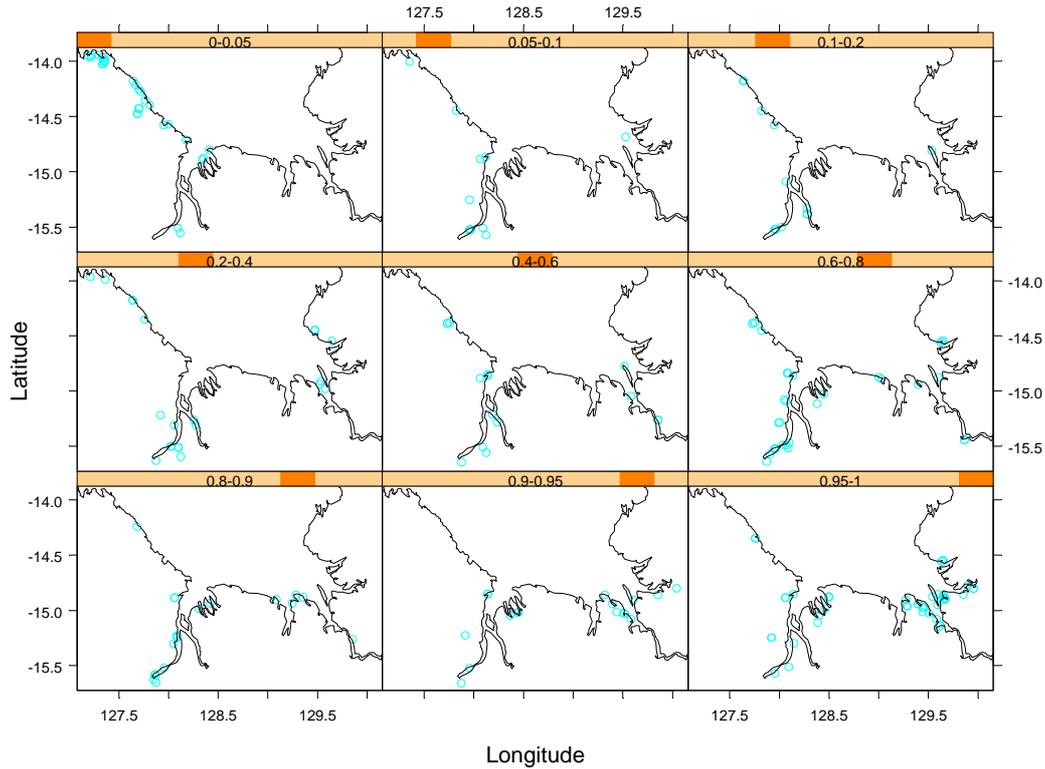


Figure 4: Spatial dispositions of stations according to the probability of finding *P. indicus*

4 Presence of *P. merguensis*

The data set has 107 stations where *P. merguensis* were caught and 122 where the species was not. A similar analysis to assess how the probability of finding *P. merguensis* varies with predictor variables reveals a simpler model with a stronger dependence on the NW-SE location variable. The terms remaining in the pruned model are shown in Table 3.

Term	Df	Deviance	Pr(Chi)
<i>ns(NW-SE, 6)</i>	6	26.3378	0.0002
<i>ns(Sechi, 4)</i>	4	13.8510	0.0078
<i>Sediment</i>	2	10.9978	0.0041
<i>Water Type</i>	2	6.4482	0.0398

Table 3: Significant terms in the model for predicting presence of *P. merguensis*

The terms themselves are shown graphically in Figure 5. The spatial disposition of the stations arranged according to an increasing chance of finding *P. merguensis* is shown in Figure 6.

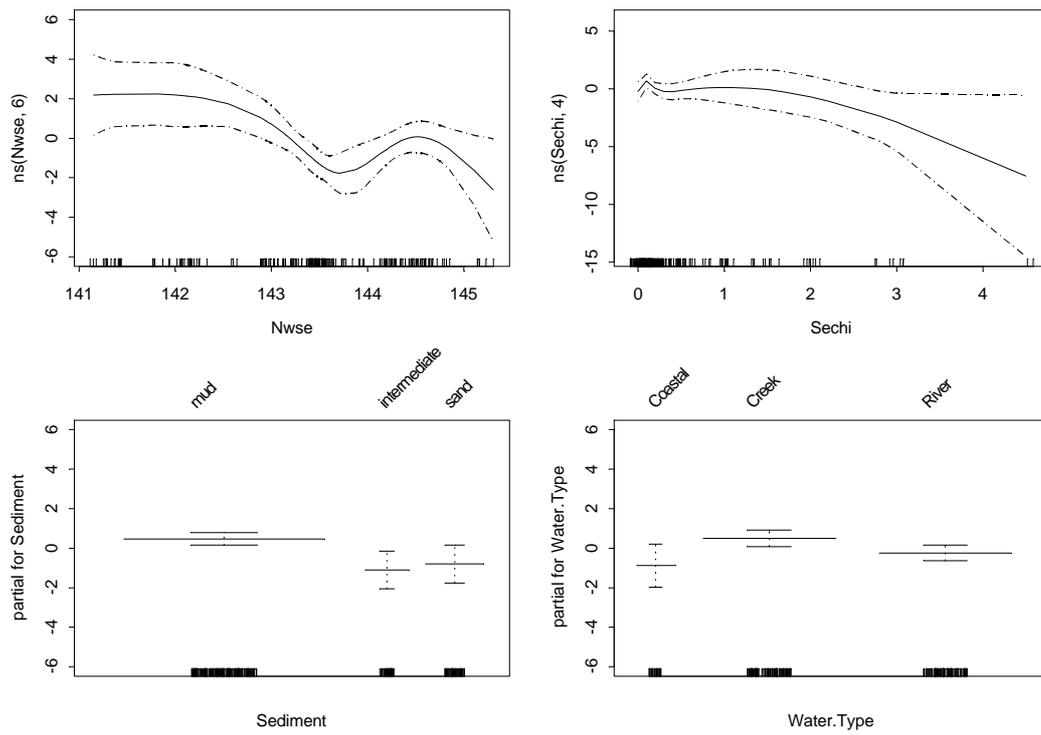


Figure 5: Partial contributions to the model predicting presence of *P. merguensis*.

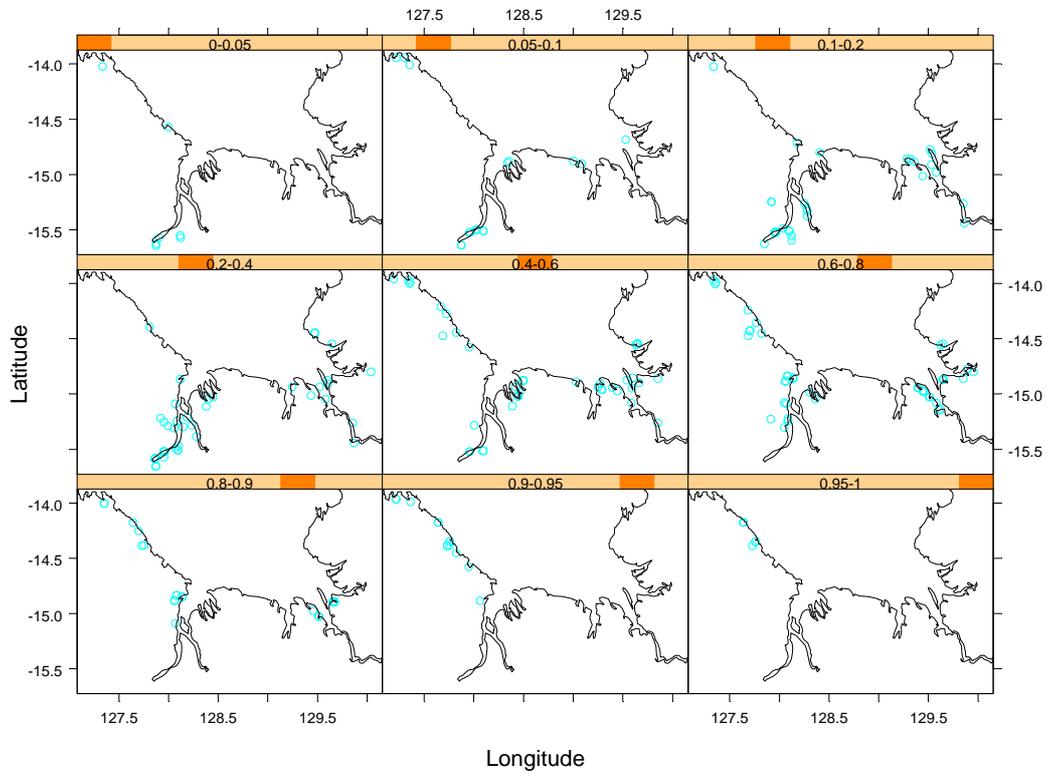


Figure 6: Spatial disposition of stations according to the probability of finding *P. merguensis*

5 Density of prawns caught

In this section we attempt to explore by standard modelling techniques the total number of prawns caught per metre of trawl distance, either of *P. merguensis* or *P. indicus*, separately. We use two different modelling techniques, namely a generalised linear model with a quasi-likelihood error structure, log link and variance proportional to the mean and secondly a tree-based model that seeks to find the major drivers of prawn density using recursive partitioning of the data.

5.1 Density of *P. indicus* using a parametric model

We will consider a quasi-likelihood generalized linear model with log link and variance function proportional to the mean. The response will be

$$\frac{\text{No. of } P. \text{ indicus}}{\text{Distance travelled in the trawl}}$$

Under some optimistic assumptions this variable could be approximately proportional to a Poisson random variable, suggesting a variance proportional to the mean.

Using the same suite of variables as possible predictors as we used in the previous case of predicting the probability of finding the species, the terms shown in Table 4 appear to carry useful information.

Term	df	Deviance	F Value	Significance
<i>ns(NW-SE, 4)</i>	4	154.6478	6.7587	0.0000
<i>ns(Sechi, 4)</i>	4	238.3981	10.4189	0.0000
<i>ns(Cloud, 3)</i>	3	74.6338	4.3491	0.0053
<i>Water Type</i>	2	351.1422	30.6926	0.0000

Table 4: Significance of terms in a quasi-likelihood GLM for the number of *P. indicus*

As with many quasi-likelihood models the significance of each term has to be treated with some caution. There seems little doubt that these terms do have some predictive capacity in this context, but it is by no means always clear how this is achieved. About the only really clear message is that the density of animals in the creeks is higher than in either the river or coastal regions. Graphical representations of the partial contributions of these terms to the linear predictor are given in Figure 8. However the capacity of the model to predict with any accuracy is quite limited. Figure 7 shows the actual density of *P. indicus* in trawls plotted against the predicted density of animals in counts/metre from the model. Clearly there is some ability for the model to select the trawls that will have the larger density but accurate prediction seems not to be possible.

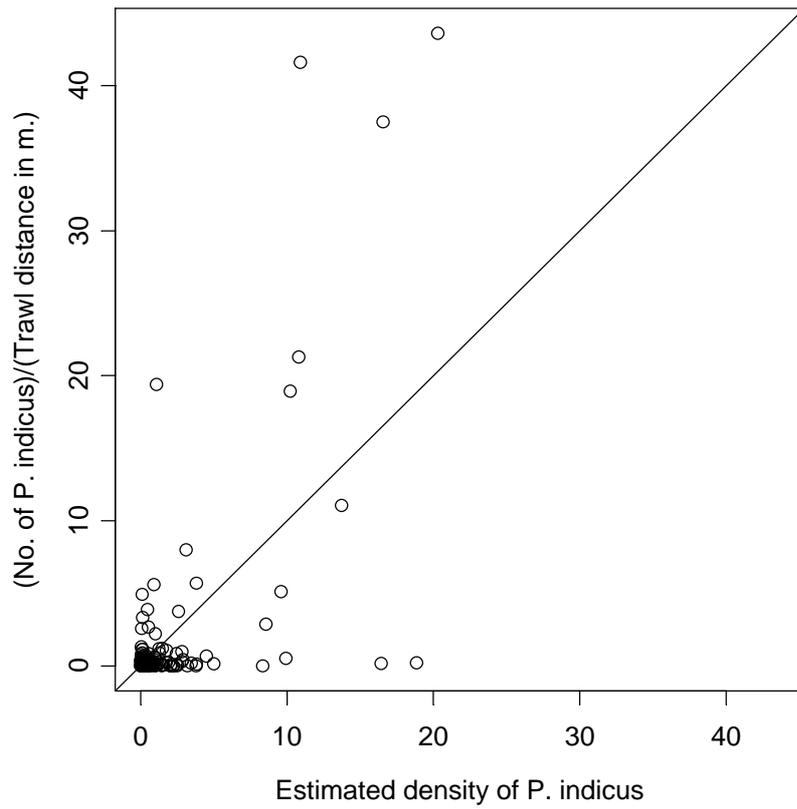


Figure 7: Actual versus predicted densities of *P. indicus*

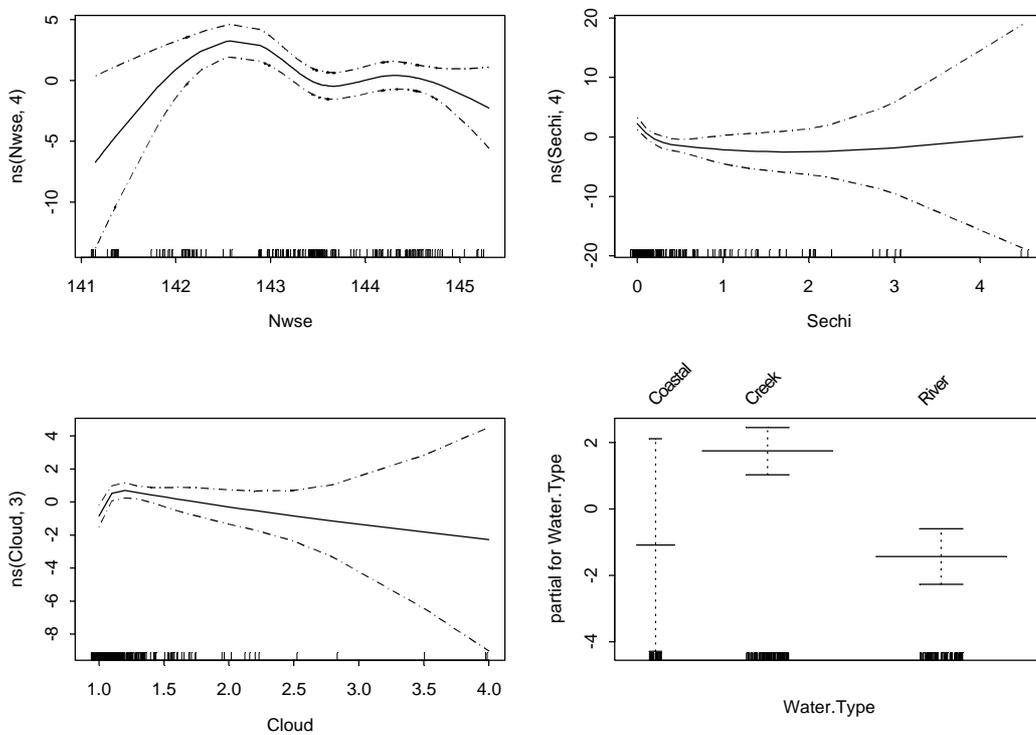


Figure 8: Partial contribution of terms to the predictive model for the density of *P. indicus*

5.2 Density of *P. indicus* using a tree-based model

A simpler approach to predicting density is to use the idea of recursively partitioning the data and producing a binary tree predictive device of the same style as botanical keys. The data is partitioned into increasingly homogeneous groups with respect to density by a binary splitting on the most effective determining variable, at the most effective place, at each recursive stage. For more details see, for example, (Venables & Ripley, 1999), Chapter 10, and references therein. After an initial tree is formed cross validation techniques are used to see the degree of complexity in the tree is warranted. The tree is then optimally pruned to the degree of complexity suggested by the cross validation so that it is neither too simple (which would result in seriously biased predictions) or too complex (which would result in the errors in the training set being reproduced in the predictions).

The standard procedure applied in this instance to the same response variable yields a tree of 5 or 6 terminal nodes. We have selected the one with 5 terminal nodes and the diagram is shown in Figure 9.

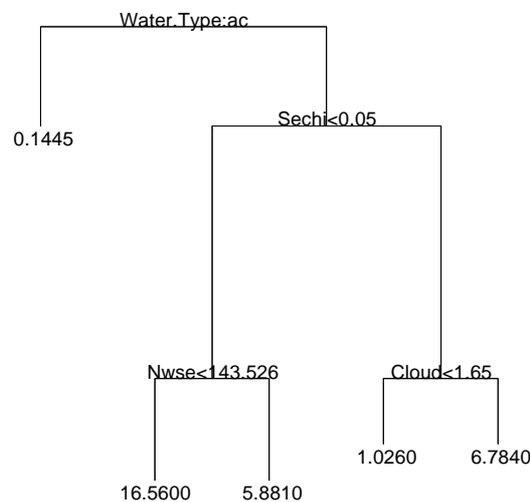


Figure 9: Pruned tree diagram for predicting density of *P. indicus*

Note that the same four variables are chosen as in the parametric model. The first split is on water type, with the river and coastal zone trawls going to the left and the creeks to the right to be further subdivided. The creek trawls are then subdivided on Sechi depth and each group further subdivided on a separate variable.

Again the predictive capacity of this model is not great, but it does suggest that these variables at least have some interpretative value.

5.3 Density of *P. merguensis*

Our study of *P. merguensis* density will exactly parallel the analysis presented above for *P. indicus*. A quasi-likelihood parametric model suggests a more complex picture than for *P. indicus* but with a greater reliance on the NW-SE location variable surrogate. The terms remaining in the parsimonious model and their significance are shown in Table 5. Similar qualifications apply to the significance column in this case as applied for the previous one. Nevertheless it seems clear that these terms do have some predictive capacity for the distribution of density. Graphical representations of the terms are shown in Figure 10.

Term	df	Deviance	F-Value	Significance
<i>ns(Sechi,4)</i>	4	29.4738	4.0210	0.0037
<i>ns(Temp,4)</i>	4	25.5776	3.4895	0.0088
<i>Sediment</i>	2	13.3564	3.6444	0.0278
<i>Water Type</i>	2	42.5568	11.6118	0.0000
<i>ns(Saln29,4)</i>	4	35.4971	4.8428	0.0009
<i>ns(NW-SE,4)</i>	4	242.0877	33.0273	0.0000

Table 5: Terms in the predictive model for density of *P. merguensis* and their significance

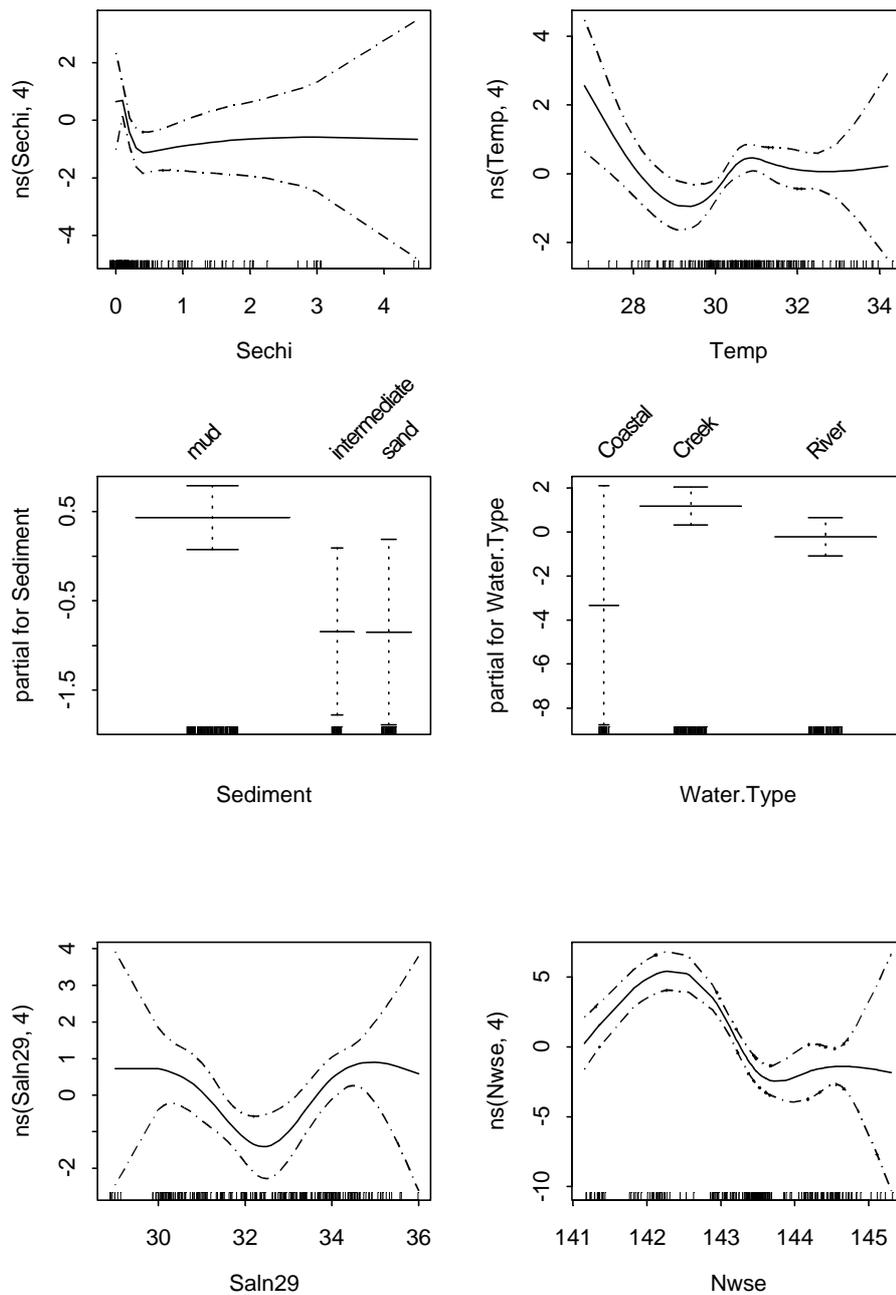


Figure 10: Partial contributions of terms to the predictive model for density of *P. merguensis*

5.4 Density of *P. meguiensis* by tree models

The same tree construction and pruning process suggests that in this case whether or not the tree model idea works at all is somewhat problematical. The tree of 4 terminal nodes shown in Figure 11 must therefore remain somewhat speculative. Nevertheless it does select from the main variables suggested by the parametric model and in roughly the same order. The heights of the vertical bars in these diagrams are proportional to the effectiveness of the splits in reducing the residual sums of squares. In this case it is interesting to note that the most effective split in this sense is on cloud cover, but only for the creek trawls in the north-western part of the sample range.

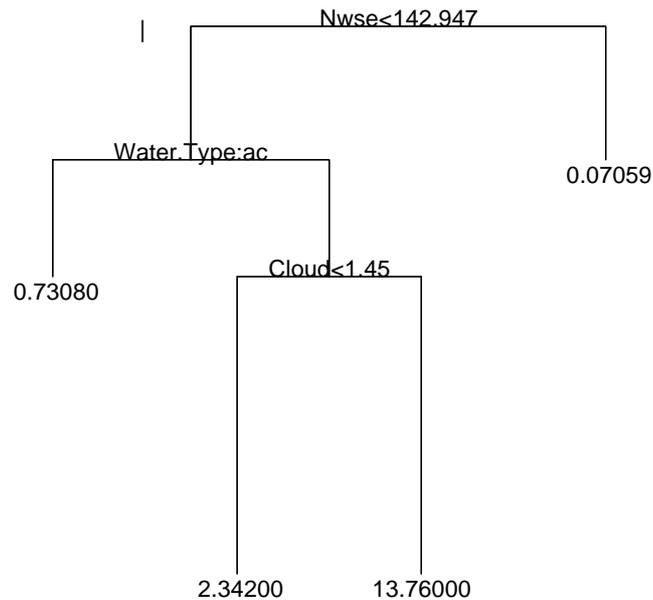


Figure 11: Tree-based model for density of *P. meguiensis*

Reference List

Venables, W. N. and Ripley, B. D. (1999) *Modern Applied Statistics with S-PLUS (3rd Edition)*. New York: Springer-Verlag.