Is the inshore area a spatial refuge for commercial prawns in the NPF? At-sea research to develop a new method of evaluating catch rates of banana and tiger prawns.

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CHAPTER 1: OVERVIEW

FRDC 2002/014: Is the inshore area a spatial refuge for commercial prawns in the NPF? At-sea research to develop a new method of evaluating catch rates of banana and tiger prawns.

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1.1 Objectives

1. To quantify the spatial dynamics of common banana and tiger prawns between the inshore and offshore components of their range,

2. To establish the relationship between catchability and biomass, and

3. To determine an at-sea predictor of prawn catch and use this information to provide management advice

1.2 Non-technical summary

1.2.1 Synopsis of report

This report addresses key issues with regard to the management of banana and tiger prawns in the Northern Prawn Fishery. These are to:

1.   quantify the spatial dynamics of common banana and tiger prawns between the inshore and offshore components of their range and discuss the implications for management (Chapter 3),

2.   assess whether the classic spawning index derived using total survey catches needs to be replaced by more detailed oceanographic and larval modelling (i.e. to identify the effective spawning population) that may produce a better index of spawning success (Chapter 4),

3.   assess whether high rainfall years at times produce years of high banana prawn catch because (a) more prawns move offshore and become available for capture (Chapter 3 and 5) or (b) more nutrients are flushed downriver producing an increase in the prawn population (Chapter 3 and 5), and

4.   whether there is a density-dependent relationship between catchability and abundance of banana prawns (Chapter 6).

The different research approaches described in this report all found that overall patterns of prawn catches, whether spatial or temporal, were different between the regions studied in this report (Weipa, Karumba, Mornington). Patterns of inter-annual variation were not synchronous across the regions. These regional and inter-annual differences in environment, population dynamics and fishery are very significant and clearly need to be taken into account in the assessment approach, management and future research. It is clear that management should consider, especially for banana prawns, the regional dynamics of each area. However, the scale of the NPF is such that that it may not be practical to deal with each area individually.

When considering the relationship between catch rate and population density for banana prawns, there were occasional years (differing among regions) that deviated from the standard assumption that catch rates decrease during the fishing season in proportion to the decrease in stock biomass. There is the risk of over- or under-predicting the population status during and at the end of the season depending on the shape of this relationship. More often than not, when there was sufficient statistical evidence to reject this assumption, the catch rates increased with decreasing biomass. In these years, there is a grave risk of over-predicting the population when in fact it has been almost completely depleted. Furthermore, it seemed impossible to predict beforehand which years would be susceptible to over-optimistic management.

One needs good spatial and temporal data to extrapolate spatio-temporally. This seems obvious, but even gaps of one or two months between surveys were difficult to interpolate. Clearly, two surveys a year such as the current series for NPF monitoring would not be sufficient for interpolating spatio-temporally but this should not detract from their value as they are essential for independent estimates of stock and recruitment.

Even more importantly, there are extremely large differences between the species: where they live spatially, when they move offshore and inshore, and how far they need to move inshore for successful recruitment to the estuaries. *P. esculentus* (brown tiger prawn) adults are particularly poorly placed in the Albatross Bay region for successful delivery of post-larvae to nursery habitat in the estuaries. This may well account for this species not being a significant component of commercial catch in this region.

There is no actual river flow data presently being collected in the Gulf of Carpentaria. This is still important information to the understanding of banana prawns in some areas. Most of the rainfall data are sourced far from the river mouths and may have little relationship with what prawns in the estuaries are actually experiencing. This project started collecting salinity data (as it is a good surrogate for emigration – see Chapter 5) in the estuaries in Albatross Bay and the Norman River and should be continued by the NPF long-term monitoring program. In future, this data may be a useful surrogate for river flow data.

None of the surveys using commercial trawlers provide data on the close inshore component of the prawn population. This means that it is difficult to categorically answer the question of whether a good commercial catch year corresponds to high productivity or simply high catchability. However, in Queensland, data from an estuarine beam trawl fishery was more useful in discussing this question (Tanimoto *et al* 2006 referred to in Chapter 4).

Below are summaries of each chapter.

1.2.2 Spatio-temporal modelling of banana and tiger prawns (Weipa, Karumba and Mornington Island)

Modern statistical modelling (generalised additive models) was used to explore factors impacting migratory patterns and therefore the spatial and temporal patterns of penaeid prawns in Albatross Bay, Karumba and Mornington Island. The data used rests heavily on survey data collected in previous years but also uses survey data collected over a two-year period within this project.

The general migration patterns of, particularly, banana prawns, when plotted spatially over time, clearly show:

1. the offshore movement of recruits at the start of the year,

2. the reduction of densities after the fishery is opened, and

3. the movement of adults back inshore towards the end of the year.

There are indications that at the end of the year, higher than normal densities of animals inshore do not always lead to high levels of postlarval and juvenile prawns subsequently. In other words, high density of inshore spawners, by itself, is not enough to guarantee good recruitment of young to the inshore nursery areas. The results of the analyses carried out shows that there are certainly spawners in the inshore waters at the time of the year when critical spawning happens, although there is little evidence of major congregations of prawns in these inshore regions compared to the more offshore areas.

Rainfall variables are significant in many of the models describing distribution of prawn catch rates for several species and areas. However, in some cases it is difficult to understand the biological mechanism underlying the relationships described by the models.

Depth was also found to be an important predictor for all species and location combinations, although the use of sediment-type predictors such as percentage mud was problematic.

The within-year pattern was modelled using *sin* and *cos* harmonic terms, whereas the between-year patterns was modelled using harmonic terms and interactions with the year term. For data sets with good within and between-year temporal coverage (e.g. Albatross Bay), these terms are excellent at capturing the periodic nature of prawn behaviour. In the Karumba region, however, the interaction of year and the periodic terms could not be included due to low between-year coverage. In Mornington, the temporal coverage was the poorest both within and between-years which did not allow for the use of any periodic terms.

Spatial extrapolation was found to be problematic using these general additive models. It is not advisable to extrapolate for any model, but in particular models that include smooth terms or tensor product smooth terms. On the other hand, these models interpolate well between points.

1.2.3 Effective population size of banana and tiger prawns (Weipa)

A fundamental feature of stock assessment models is the stock-recruitment relationship, which has proven highly variable in many commercial fisheries. In Australia's Northern Prawn Fishery, the short lifecycle of the prawns and the spring pulse in spawning should result in a well-defined stock-recruitment relationship.

However, this has proven particularly elusive for the common banana prawn, *P. merguiensis*. One explanation may be that only a subset of the spawning stock contributes effectively to next year's recruits.

It is known that postlarvae are transported from offshore spawning areas to coastal nursery habitat by rising in the water column on flood tides and remaining on the bottom otherwise, but only when they find themselves in water shallower than a transition depth. In deeper water they exhibit a diurnal vertical migration unrelated to tides that generally leaves them offshore outside the 'advection envelope'.

Offshore trawl surveys of three commercial species (*P. merguiensis*, *P. semisulcatus* and *P. esculentus*) were used to model density of nauplii and then linked to a larval advection model coupled with location-based survival and travel time to (a) determine the locations where spawning is most effective and (b) estimate the total number of month-old postlarvae arriving in estuaries of Albatross Bay.

The effect of two transition depths (7m and 15m) has been compared on the number of postlarvae that successfully settle and the effects vary considerably among the three species due to the differences in spatial distribution of adult spawners.

The peak density of *P. merguiensis* in shallow waters (<10m) ensures successful advection of larvae in Albatross Bay at both transition depths, producing 300-400 small juveniles per spawner. In contrast, the offshore peaks in spawner density of both *P. semisulcatus* and *P. esculentus* imply that far fewer larvae reach the estuaries (ratios of ~70 and ~30 respectively for 15m transition depth). The numbers drop to a tenth of this for the 7m transition depth, which may partly explain the relative abundance of these species in the Albatross Bay region.

For the period 1986-1992, the new effective spawner index was compared with density of small juvenile *P. semisulcatus* and *P. merguiensis* juveniles in nursery habitat. The new index appears to set an upper limit on recruitment to nursery habitat, but other environmental factors not incorporated in the model appear to reduce the actual number arriving and settling.

Effective spawner population size is an important factor to consider when comparing recruitment success based on spawning density, but clearly is not the sole factor that contributed to recruitment success. This research is essentially a first step in examining the relationship between spawning stock size and recruitment, with a long way to go before we are in a position to develop a specific stock-recruitment relationship for either *P. merguiensis* or *P. semisulcatus* in the Albatross Bay region using these methods.

1.2.4 Offshore availability of banana prawns to fishing vs. rainfall and salinity (Weipa, Karumba and Mornington Island)

The banana prawn fishery in the Gulf of Carpentaria occurs in April/May each year and targets mainly prawns that have newly recruited to the fishing grounds from inshore areas. Although much spawning does occur in April/May, most of the spawning that gives rise to larvae that will produce next year's population actually occurs later in the year (August – October). Therefore, the critical spawning population of *Penaeus merguiensis* in the Gulf is composed mainly of prawns that are not caught by the commercial fishery earlier in the year. An important question for managers of the fishery to answer is: what proportion of the total prawn population

each year is actually caught by the fishing fleet, and consequently, what proportion is left to produce next year's crop?

A corollary of this question is then: what proportion of the prawn population remains inshore of the commercial fishing grounds each year, safe from commercial fishing, and does the proportion vary from year to year in response to rainfall or salinity changes?

In this project it was not possible to survey as close to the coastline as would have been liked due to limitations imposed by the size of the commercial fishing vessels used for the surveys. However, it was possible to undertake analysis of the available survey data to get some indication of any trends in distribution of the prawns related to rainfall and salinity for the corresponding years.

Based on the data available, one can conclude that there seems to be no relationship between rainfall or salinity, and the inshore/offshore dispersion of *Penaeus merguiensis* at Weipa or Karumba. This conclusion is strongest for Weipa, where there is nine years of data to analyze. This conclusion seems consistent with earlier studies of environment and commercial catch at Weipa (Vance et al. 1985, Vance et al. 2003). This is the best result for Weipa management as it means that a higher catch year is not likely to represent higher availability of banana prawns (and therefore higher fishing mortality) than would otherwise be assumed in standard stock assessment models.

Unfortunately, in Karumba, the region where the relationship between rainfall and juvenile prawn emigration is strongest, the results need to be treated with much more caution. In Karumba, we only had four years of data to use in the analysis. Also the variation in rainfall over the three years of the current project has been quite low and there has also not been great variation in survey catches.

Inspection of annual commercial catches of *Penaeus merguiensis* in the Karumba region emphasizes that the results need to be treated with caution. This fishing ground is characterized by large year-to-year fluctuations in banana prawn commercial catches. The years of high catch tend to be associated with high rainfall. However, there is almost always a year of relatively low catch following a good catch year. The reason for these very low catch years may be, at least in part, a result of a lower spawning stock in the previous year, because the high rainfall meant that a larger proportion of the population was available for capture by the fishery.

1.2.5 Density-dependent catchability

Banana prawns, *Penaeus merguiensis*, in the Gulf of Carpentaria, Australia typically form dense aggregations during a fishing season. It has been speculated that catchability decreases significantly as the fishing season progresses and stock size decreases. We used commercial catch effort data from 1987 to 2004 for three stocks in the Gulf to investigate whether density-dependent catchability exists in this species of aggregating penaeid. We developed two stochastic models based on an improved depletion method, one assuming a linear relationship between catchability and abundance and the other assuming a nonlinear power function between catchability and abundance. A stock-specific annual catchability coefficient, initial biomass, and a shape parameter of the power function were estimated using maximum likelihood or hierarchical Bayesian approach (for density independent catchability models). For the majority of the datasets, the two models result in similar estimates. Although a weak but statistically significant density-dependent catchability, either positive or negative,

was detected in about one fifth of the datasets, there is no clear pattern that points to positive density-dependence as suggested by previous studies. With all years and stocks combined, the density-dependent parameter in the second model has an overall mean of -0.03 and a standard deviation of 0.57 from all datasets, and its distribution looks approximately normal. However, a between year negative power function relationship between catchability and abundance appears to exist in this prawn species.

Our findings may have important implications in prawn stock assessment and management. To begin with, CPUE could be used as a reasonable index of within-season abundance for the banana prawns in the Gulf of Carpentaria, but not a good index when one compares data across years. Stock assessment models that estimate biomass should either estimate a catchability parameter for each year or estimate a multiple parameter catchability equation that incorporates between year density-dependence on the catchability parameter.

The fact that the results confirm that a large proportion (about 85%) of the stock in any year is caught is also important for the management of this fishery. Although many of the prawns caught during the banana prawn season (April-May) spawn before capture, it has been shown in previous studies that the spawning that contributes most to the next year's population occurs much later in the year (August-September). Therefore, the proportion of banana prawns that escape capture during the fishery is a critical factor for the long-term sustainability of the banana prawn fishery and also an important factor in contributing to annual variation in prawn catches.

In terms of estimating fishing mortality, it is recommended the model be tested with and without within-season density-dependence. In years where the results significantly point to density-dependence, ignoring this fact could result in significant biases in the estimated initial biomass. However, in the case of banana prawns in the NPF, it seems hard to predict in advance whether within-season density dependence would occur. Furthermore, it is also unclear whether density-dependence may exist more commonly but is not easily detected given the data. Further work is therefore required.

1.3 Further research

1.3.1 Spatio-temporal modeling

The inclusion of the rain variables in the analyses is a surrogate for major rain events and changes in salinity. Readings used at any one time are from a single land based weather recording station, which may not necessarily be close to the nursery habitats. This is not optimal. Ideally rain records would be available for each of the nursery habitats and from water based weather stations, helping to better relate rain events to prawn exodus and migration patterns. Unfortunately currently this is not possible because of the expense involved. In the future cheap automatic real time sensor networks may make this a reality.

Apart from the need for surveys that provide more extensive within-year and between-year coverage, it has become clear that trawling only in water deeper than 7–8m has compromised our knowledge about banana prawn densities as these may well peak in shallow waters (2–7m). Recent research on Queensland's East Coast suggests

that increased river flow tends to increase offshore migration and enhance catchability in offshore otter trawls rather than increase the size of the recruiting population per se (Tanimoto et al., 2006). It would be useful to carry out further survey work during the spawning period in close inshore waters using smaller vessels that are able to trawl in waters as shallow as 3m.

1.3.2 Effective spawning populations

One of the fundamental gaps in this research is the lack of detailed larval trajectories for the 7m transition depth at all relevant times – data at this transition depth were only available for one month and the resources of this project did not extend to running the computer-intensive hydrodynamic models for new parameter settings (including larval behaviour), times and locations not covered by Condie et al (1999). It would be desirable to tackle this in future research, preferably running the hydrodynamic model with currents/tides/winds in force at the time of each survey.

A key parameter is larval survival, which is known from field studies to be highly variable both at sea and in coastal areas, and over time due to patchy availability of food and short-term weather patterns that affect the behaviour and movements of prawns. A further aspect that needs more attention is the stochastic component: not all larvae seeded in the same location will follow exactly the same trajectory. This could be tackled by seeding a large number of particles at each seed point.

In using only the larval advection patterns from 1986, we have certainly missed inter-annual changes in the finer scale features of advection. We know, for example, that particles from a larger area north of Duyfken Point were pulled into the Bay in October 1990 than in October 1986.

While it appears that our results are consistent with observations that postlarvae settle in nursery habitat from about 3 weeks of age, we have not examined the extent to which moving them only on night-time flood tides would slow down this process. We have also assumed they become postlarvae within 8 days, then instantly cue into flood tides. These settings are probably optimistic, since larval development and behaviour is likely to vary, depending on their growth in response to available food. For example, less than half of 5-day-old *P. merguiensis* nauplii had reached second protozoeal stage during in situ survival experiments in Albatross Bay (Preston et al, 1992).

It would clearly be beneficial for *P. merguiensis* in particular to collect data on densities of juveniles and adults in waters 2–7m deep in Albatross Bay, probably using beam trawls, in tandem with offshore surveys. Further work on the movement of juveniles in the creeks and estuaries would enhance understanding of both the settlement phase and the recruitment phase. It would be particularly beneficial to have both sources of data covering the same seasons, preferably linked with measurements of river flow. A project that would examine the links between population density and spatio-temporal dynamics of juveniles and river flow during the summer/autumn months in the creeks close to Karumba is planned. Conductivity meters in creeks and estuaries could perhaps be used as a surrogate index of inshore recruits.

1.3.3 Offshore availability of banana prawns

Inspection of annual commercial catches of *Penaeus merguiensis* in the Karumba region suggests that there may be a negative relationship between high

commercial catches and subsequent spawning success. This fishing ground is characterized by large year-to-year fluctuations in banana prawn commercial catches. The years of high catch tend to be associated with high rainfall. However, there is often a year of relatively low catch following a good catch year (Figure 5.1). The reason for these very low catch years may be, at least in part, a result of a lower spawning stock in the previous year, because the high rainfall meant that a larger proportion of the population was available for capture by the fishery. This is contrary to the conclusions stated previously based on the recent survey data at Karumba. This question needs to be revisited in future years when further data has been collected by the NPF Monitoring project.

It is interesting that the largest annual variations in commercial catch of *Penaeus merguiensis* occur in regions where there seems to be a significant relationship between rainfall and commercial catch (Karumba, Mornington, Vanderlins). Commercial catches at Weipa, where there is not a strong rainfall relationship, are much less variable between years.

Clearly, further data and analyzes are needed, particularly for the Karumba region. The Northern Prawn Fishery prawn monitoring series of projects began at about the same time as this project and there has been considerable overlap between the projects. The same sampling sites are used for Albatross Bay, Karumba and Mornington Island. The NPF monitoring surveys will continue into the future, funded largely by the fishing industry so new data on the distribution of prawns in January will continue to become available. The data loggers installed during this project by CSIRO will continue to be serviced and monitored. It is important that catch rates from future January surveys and rainfall and salinity recorded using the loggers should continue to be analyzed to provide further data to help confirm or deny our results.

1.3.4 Density-dependent catchability

To truly separate the correlation between catchability and biomass required fishery independent data. As this information is, at present, being collected annually, it is recommended that when the series is long enough we revisit this question. This still means that the logbook data would be needed. Furthermore, a detailed investigation of the spatial distribution of catch and effort during the season for banana prawns should be included in these analyses.

1.4 About this report

Most of the chapters of this report have been written for publication in journals. The slightly different format of each chapter is due to the requirements of the different journals. Therefore, before the full report is made available for sale or placed on any web site, prior approval from the PI should be requested.

1.5 Acknowledgements

1.6 Background

In recent years, industry, researchers and managers have been concerned about the status of the tiger prawn stocks in the Northern Prawn Fishery and declines in catches of banana prawns. This led to an AFMA Research Fund project to investigate the interaction between the environment and banana prawn catch in the NPF. In some areas, rainfall still best explains the annual variation in catch. Although banana prawn catches improved in some regions in 2001, the extreme catches in the NPF in 2001 have highlighted that we still do not clearly understand all the factors that determine banana prawn catches - particularly at Weipa, where unexplained record-low catches have occurred for three of the last four years.

The first stock assessment model for banana prawns was constructed during this project and used to investigate whether the prawn fishery is governed by an underlying stock-recruitment function, or whether recruitment is largely driven by random environmental influences. The model indicates that there is a stock recruitment relationship in some areas, but the relationship is not consistent between regions. This is a major change in thinking on banana prawns.

The most recent stock assessment for tiger prawns has shown that both species of tiger prawns are overexploited and that brown tiger prawn stocks, in particular, are seriously depleted. This has resulted in a proposal for the introduction of greater restrictions on fishing effort in the NPF.

The results of recently completed research suggest that much of the effective spawning of tiger prawns (and possibly banana prawns) in the Gulf of Carpentaria probably occurs in relatively shallow water (Condie et al. 1999, Vance and Pendrey 2001). All these recent studies have highlighted that we know very little of the inshore distribution (i.e. inshore of where the prawns are fished) of banana and tiger prawns, particularly whether there is significant inshore spawning. The presence of significant inshore spawning is likely to confound the assessment of prawn stocks. The present stock assessment models for both tiger and banana prawns assume catch rates are an index of fishable biomass. However, the spatial and temporal extent of the fishery has been substantially reduced in recent years. This means that if the catch rate assumption is extrapolated to previously fished areas that are now closed or unfished, the results of the models may not represent the true status of the stocks and misleading advice would be provided to managers.

An accurate knowledge of the distribution of adult prawns in inshore waters during the main spawning season is of great importance. If most of the "effective spawning" (the spawning that contributes recruits to the fishery) takes place in these shallow areas, there is an opportunity to protect spawning stocks by closing these waters to fishing, without losing large quantities of potential catch from offshore waters. Knowledge on the distribution of adult prawns is also critical for assessing the status of the prawn stocks because in current stock assessment models, the size of the spawning stock is estimated from the total area where fishing takes place, not the area where effective spawners are located. Thus the current stock assessment models may be using incorrect estimates of the spawning stock. In fact, the large spatial and temporal closures currently in place in the NPF mean that the logbook data from the fishery may no longer be adequately sampling the resource. Industries, managers and researchers are now at a critical junction where previous hypotheses/assumptions about the distribution of the prawn stocks and the interpretation of catch rate data must be thoroughly examined.

The recent advances in understanding of both banana and tiger prawn stock dynamics highlight three important questions for assessment and management:

1. How are banana and tiger prawns distributed between inshore and offshore waters before, during and after the fishing season? For example, in bad rainfall years, does a substantial proportion of the banana prawn population remain in inshore waters where they are protected from fishing? Does the size of the banana prawn stocks change substantially between years or does the location of the main population of prawns simply change in response to rainfall? Another way of phrasing these questions is - in good rainfall years, is the large catch due to an increase in the population size resulting from increased production and abundance of prawns in the estuaries, or is it because the prawns become more available to the fishery because the whole population has moved further offshore onto the fishing grounds? If it is the latter, then the spawning stocks are in greater danger of being over-fished in high rainfall/high catch years.

2. Is there an at-sea indicator that can be used to predict the future catch so that more within-year management can take place? From six years of intensive sampling at Weipa, it was suggested that sampling banana prawns with a grid survey in January when the prawns are dispersed, provides a good prediction of the catch in that year. However, by February, the results showed that prawns had aggregated and a grid survey at this time did not provide a good prediction of catch. The possibility of using an early survey to predict bad years and hence to allow management actions prior to, or during the season, would provide much greater protection for the resource. Management is greatly advanced when stock assessments are able to forward project (i.e. predict) not only based on past estimated recruitment variability (as is used at present) but also on real time data.

3. A further critical problem for the stock assessment model is that the relationship between catchability and total banana prawn biomass is unknown. We know that catchability decreases as fishing reduces the prawn population (Die and Ellis 1999), but we do not know the rate of change of catchability. It is important to know more about this change in catchability for estimating the level of fishing mortality and present stock status, both for tiger and banana prawns.

This project aims to investigate some essential, fundamental questions about the spatial dynamics of the banana and tiger prawn populations that are presently not understood. The answers to these questions are critical for providing more accurate stock assessments and improving advice to management. This work would also greatly enhance our ability to manage the resource proactively, rather than reactively.

1.7 Need

The spatial extent of the NPF has changed over time and now concentrates on relatively small hotspots. This means that the only index of biomass, CPUE (derived from fishery log book returns), is providing little information on the areas no longer fished (including inshore areas that generally have been closed to fishing). However, stock assessment estimates for banana and tiger prawns need to take into account the abundance of prawns in all areas, including those not fished.

Although recent research has suggested that inshore waters are probably the most important spawning areas in the NPF, this conclusion is based on laboratory

research on the behaviour of postlarval prawns, combined with models of the currents in different regions of the NPF. To validate this conclusion we need to confirm that substantial populations of spawners do occur in the inshore waters at the appropriate times of year by targeted field sampling.

The movement patterns of prawn populations over the season and between inshore and offshore areas are highly relevant as they all have a general offshore migration as they increase in size from pre-recruits to recruits and spawners and an inshore migration as larvae. These issues need to be more explicitly investigated with regard to the assumption of the relationship between catch rates and biomass over time.

This project will fill essential gaps in our knowledge and also develop a scientific basis for long-term investments in fieldwork. Although this project will concentrate on the less assessed white banana prawn (*Penaeus merguiensis*) and the tiger prawns (*P. semisulcatus, P. esculentus*), the fieldwork, design and research concepts would probably also apply to endeavour prawns (*Metapenaeus endeavouri, M. ensis*).

1.8 Benefits and adoption

The benefits of this research has already been realised in that much of this work was provided as input to "Variation in banana prawn catches at Weipa: a comprehensive regional study" (FRDC 2004/024).

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CHAPTER 2: DATA COLLECTED

2.1 Offshore survey data

2.1.1 Survey planning using historical CSIRO survey data

Three fishing regions of the Gulf of Carpentaria were sampled during this project: Albatross Bay, Karumba and Mornington Island (Figure 2.1 and Figure 2.2). To facilitate the planning of the surveys, historical CSIRO survey data were analysed. Length-frequency data were available from two CSIRO studies in the Northern Prawn Fishery. These were carried out in Albatross Bay/Weipa from 1986–92 (Crocos & van der Velde; 1995) and in the Eastern Gulf from 1977–79 (Crocos & Kerr; 1983).

In the historical surveys, each study area was visited a number of times, and in particular there were several visits during the months of January and February. Trawls were carried out at night and were of similar duration (15 minutes in Albatross Bay and 30 minutes in the Eastern Gulf). Where repeated trawls had been carried out at the same site during a given cruise, only the first trawl was selected.

We found statistically significant ($p < 10^{-8)}$) differences in mean abundance between the depth strata during January and February surveys, in every study area and for the three species of commercial interest in those areas (Table 2.1). At this time of year, abundance was higher in shallow inshore waters and low in deeper offshore waters. This pattern reflects the migration of young prawns away from nursery habitat in coastal seagrass areas into offshore waters. *P. esculentus* and *P. merguiensis* were present in much higher numbers in 5–20m depth of water than in depths of 21–40m. There was also a decrease in abundance of *P. semisulcatus* with increasing depth, but in some surveys this difference was very small while in others it was substantial. This evidence strongly supports the use of depth stratification to achieve good precision in the surveys.

Initially we considered that the number of trawls carried out in each depth stratum should be in proportion to the area of that stratum. However, after analysis of historical survey data, we agreed that the precision of the surveys could be improved if more trawls were carried out in strata where the mean abundance is typically highest for one or more species. Table 2.2 shows the percentage of each study region represented by each of four depth strata. The Albatross Bay study area spanned depths of 5–40 m, while the other two study areas only sampled out to 20 or 30 m.

The commercial prawns caught in the Gulf of Carpentaria migrate from estuarine and coastal nursery areas to the offshore fishing grounds over a period of some weeks and the timing of this migration is variable from year to year. Therefore, it was important that our surveys sampled a large range of depths from shallow to offshore to make sure that we captured prawns at some point in their migration.
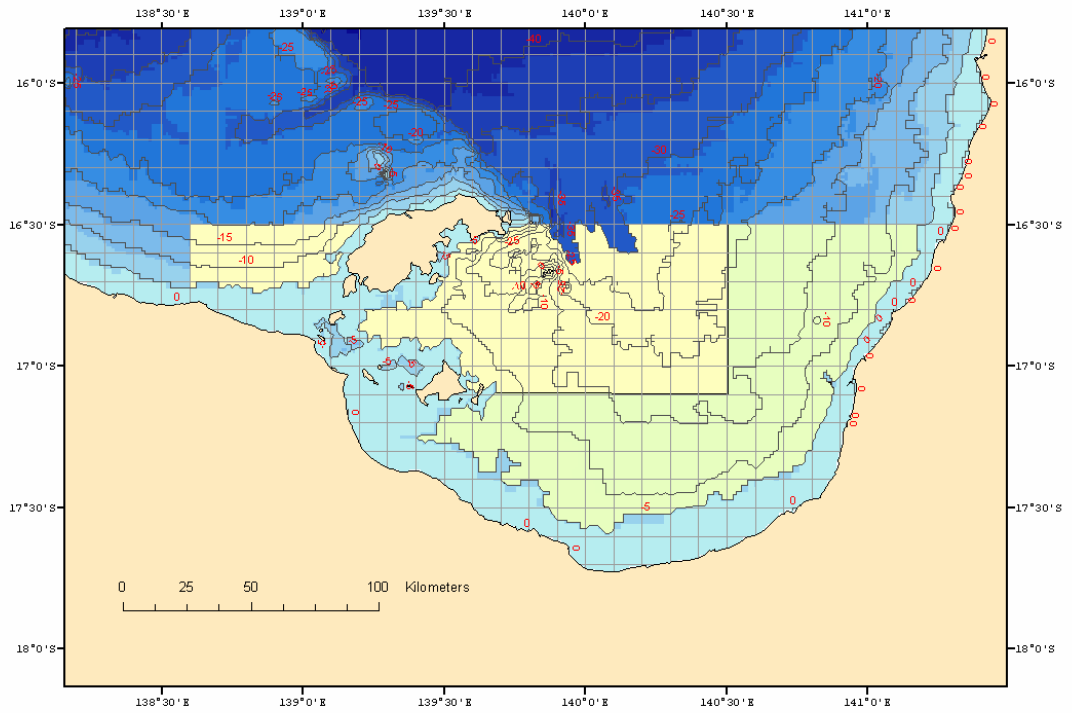
Figure 2.1. Extent of the survey areas proposed for the Mornington (yellow) and Karumba (green) area (depth contours shown in red).
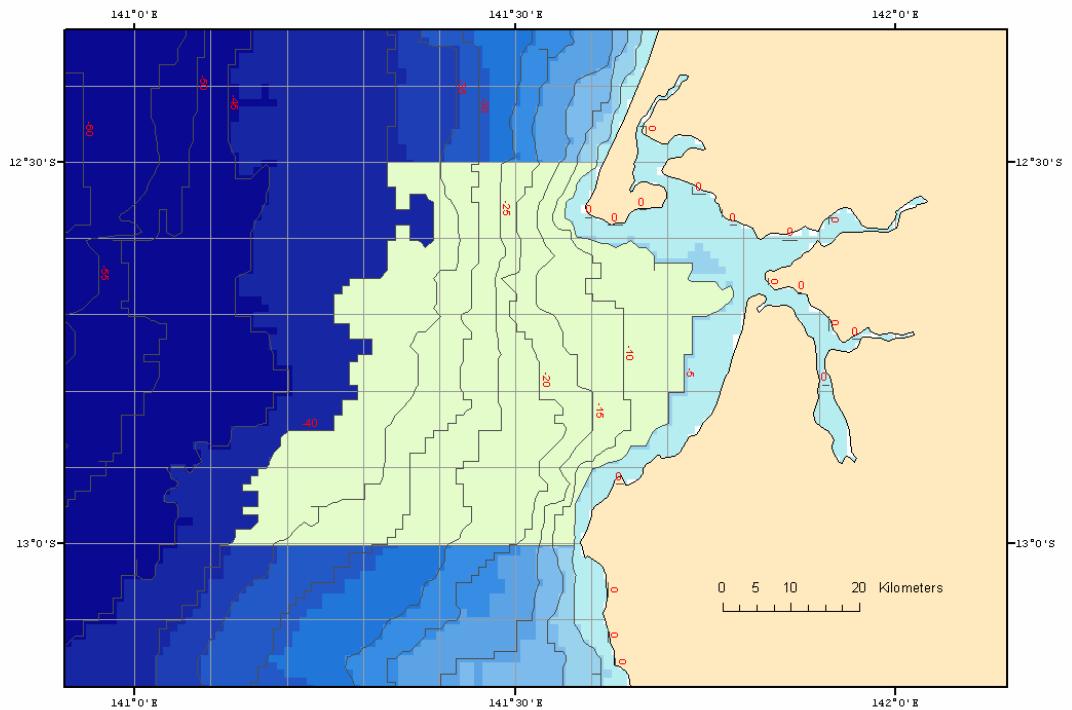
Figure 2.2. Extent of the survey proposed for the Weipa region (depth contours shown in red)

Table 2.1. Analysis of variance of fifth-root transformed counts of sub-adults in each study during January and February surveys

Study	Species	Source	d.f.	F-ratio	p-value
Weipa, 1977-78 & 1987-92	*P. semisulcatus*	Cruise	12	7.0	$< 10^{-8}$
		Depth stratum	4	15.9	$< 10^{-8}$
		Cruise×depth	48	1.4	0.053
		Residual	207	_	_
	P. merguiensis	Cruise	12	10.6	$< 10^{-8}$
		Depth stratum	4	75.6	$< 10^{-8}$
		Cruise×depth	48	1.4	0.044
SE Gulf, 1977-79	*P. esculentus*	Cruise	7	16.8	$< 10^{-8}$
		Depth stratum	2	37.9	$< 10^{-8}$
		Cruise×depth	7	6.9	$< 10^{-7}$
		Residual	358	_	_
	P. merguiensis	Cruise	7	33.6	$< 10^{-8}$
		Depth stratum	2	42.7	$< 10^{-8}$
		Cruise×depth	7	2.4	0.021

Table 2.2. Area of each region, with percentage of region in each depth stratum.

Region	Total area ($n\ m^{-2}$)	Percentage of survey area per depth stratum			
		5–10m	11–20m	21–30m	31–40m
Mornington	3,960	21	49	30	0
South East Gulf	4,680	36	64	0	0
Weipa	720	16	20	27	37

2.1.2 Current surveys - prawn density

For comparison with historical survey data it is more meaningful to calculate the number of prawns per hectare since the configuration of nets has changed between historical and recent surveys. Standardizing by the area trawled also allows us to correct for differences in trawl speed that occurred between and during surveys. It is worthwhile noting that only the effect of trawling speed on coverage area was accounted for, but no others like escape rate, which were believed to be insignificant.

In the calculation of the number of prawns per hectare in the current surveys, the trawl was assumed to sweep a 30 m wide path and the distance covered by the trawl was estimated from difference in location at the start and end of the trawl, except for trawl paths that were appreciably bent to avoid difficult terrain. For these trawls, we estimated the swept area from the product of speed and duration.
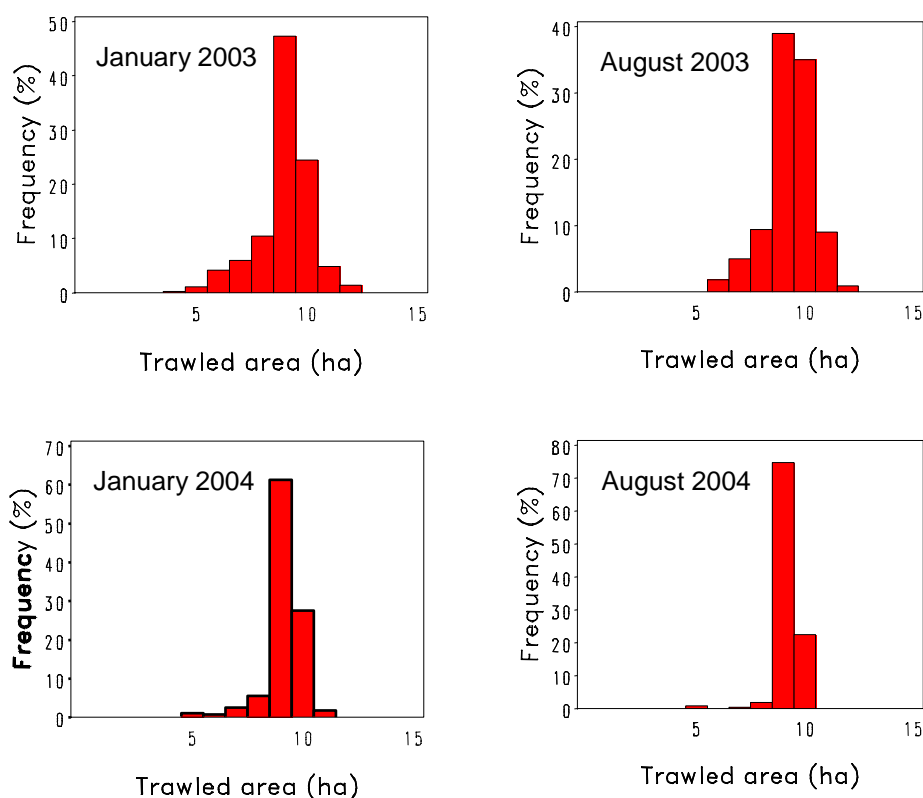
Figure 2.3. Estimated area swept by trawls (in hectares) during January and August 2003 and January and August 2004 surveys.

Most trawls swept an area of 8–10 hectares, with a modal area around 9 hectares (Figure 2.3). The swept area was most variable in August 2003. This was probably because the weather was worse during this survey, resulting in greater variability in the distances trawled. The distributions in 2003 had a wider spread than the corresponding surveys in 2004, indicating that with increasing experience of conducting these surveys, the swept area has become more consistent among trawls.

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CSIRO Marine Research
NPF Monitoring Cruise - January 2004
Trawl Sites
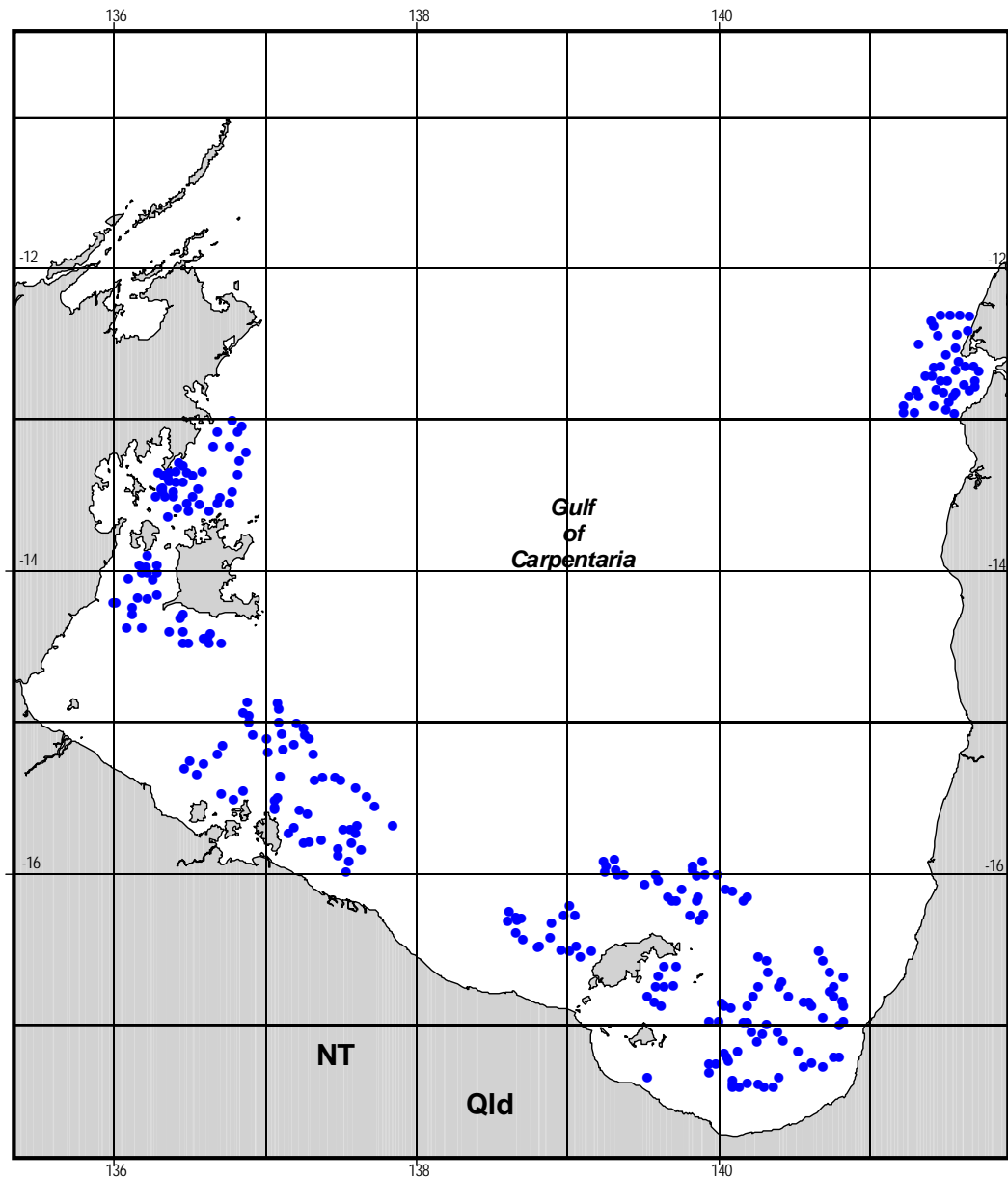
Figure 2.4. Location of trawl sites used in the surveys at Albatross Bay, Karumba and Mornington Island in 2003 and 2004. Sites in the western Gulf were trawled as part of the NPF Monitoring Project which ran concurrently with this project.

2.1.3 Survey vessels

We originally planned to use research vessels for these surveys, however, the research vessels became unavailable for our surveys just before the project was due to commence. We then chartered commercial prawn trawling vessels for all the surveys. Surveys in January, March and August in 2003 and 2004 were carried out outside the commercial fishing seasons and for these surveys we chartered commercial prawn trawlers of about 22 m length from A. Raptis & Sons. In these surveys, we were able to trawl all our planned survey sites in Albatross Bay, Karumba and Mornington Island. For the two surveys in October 2003 and 2004, carried out during the commercial fishing season, we chartered the small prawn trawler Mabel K. Because of the increased charter cost associated with surveying during the fishing season, we were only able to trawl sites in Albatross Bay in October 2003 and 2004.

2.1.4 Trawl gear description

Survey vessels used two 12-fathom tiger prawn nets manufactured for CSIRO by GNM Chandlery. Net and rigging specifications were as follows:

- 400d/30ply 2" stretched mesh net.
- Codend of 400d/4x16ply black braided 1⅞" stretched mesh net, 150 mr (meshes round) x 120 md (meshes deep).
- Fitted with 8mm S/S drop chains and 13mm regular link S/S ground chain.
- Headrope of 8mm S/S wire wrapped in 6mm PE rope.
- Footrope of 10mm S/S wire wrapped in 8mm PE rope.
- Fitted with 150 mr x 75 md skirt.
- An upward-excluding Turtle Excluding Device (TED) was fitted to each net but no Bycatch Reduction Devices (BRD) were fitted.

The nets were attached to Number 9 Bison Boards provided by the survey vessels.

2.1.5 Abiotic data collected

For each trawl, start and finish times and locations were recorded and the GPS plotter track of the vessel during each trawl was recorded. Trawling was commenced each night at about 30 minutes after sunset and the last trawl of the night was completed at least 30 minutes before sunrise. Each trawl was about 30 minutes in length, unless trawling was interrupted due to rough bottom or gear problems. Other details relating to weather, tides, moon and problems with gear were also recorded. We attempted to maintain vessel trawl speed at about 3.2 knots although this was not always possible in strong tidal currents.

Salinity/Temperature: A small Diver datalogger was attached to one trawl net on each vessel during each survey ('Diver' water quality monitoring, Eijkelkamp Agrisearch Equipment, The Netherlands; www.eijkelkamp.com). The logger recorded conductivity (later converted to salinity), temperature and water depth at 1-minute intervals throughout the night and the data was downloaded to a computer at the end of each night's work.

2.1.6 Biological data collected

In most cases, all commercial species of prawns, bugs and scallops were identified to species and total weights and numbers were recorded for each net. For the prawns, the spawning stage, moult stage and presence of any parasites was also recorded. When substantially more than 100 individuals of any prawn species were present in the catch, a randomly selected subsample was measured. The numbers and weights of the subsample and total catch were recorded to relate the subsample details to the total catch.

Summary results for the main prawn species groups caught in all trawls at each site during 2003 and 2004 are presented in Chapter 8.

2.2 Estuarine Environmental data

Data loggers were installed in the Norman River at Karumba in the southeastern Gulf of Carpentaria and in the Embley River at Weipa in the northeastern Gulf. The loggers were attached to wharves at a fixed height above the river bed near the mouth of each river and recorded water conductivity, water temperature and pressure (water depth). Conductivity was later converted to salinity using equations provided by M. Sherlock (CSIRO) and based on PSS78 equations from IEEE Journal of Oceanic Engineering, January 1980.

The loggers were programmed to (a) take 15 measurements over a 1-minute period every 30 minutes, (b) take an average of the 15 measurements and then (c) store the average value for each variable in the logger every 30 minutes. Every one to two weeks, the data was downloaded from the loggers via a modem and telephone to CSIRO at Cleveland Marine Research Laboratories. The loggers were in place for the wet seasons of 2002/03, 2003/04, and 2004/05 (December to April each year).

To make comparisons with salinity data collected in earlier projects, a subset of the salinity data was taken as follows: for three days around each spring tide, three consecutive salinity recordings around each low tide were averaged; i.e. a total of nine recordings contributed to each salinity value. Rainfall was accumulated for each two weeks between spring tides.

Daily rainfall, temperature and three-hourly wind speed and direction data recorded at Weipa airport and Normanton airport (about 40 km inland from Karumba) were obtained from the Bureau of Meteorology.

An example of the raw 30-minute logger data for Karumba is shown in Figure 2.5. The progression of the tidal phase can be clearly seen from the plot of depth by time; from neap tides (low tidal range) to spring tides (high tidal range). In early to mid-January, the conductivity dropped in response to rainfall and then fluctuated dramatically during each daily tidal cycle.
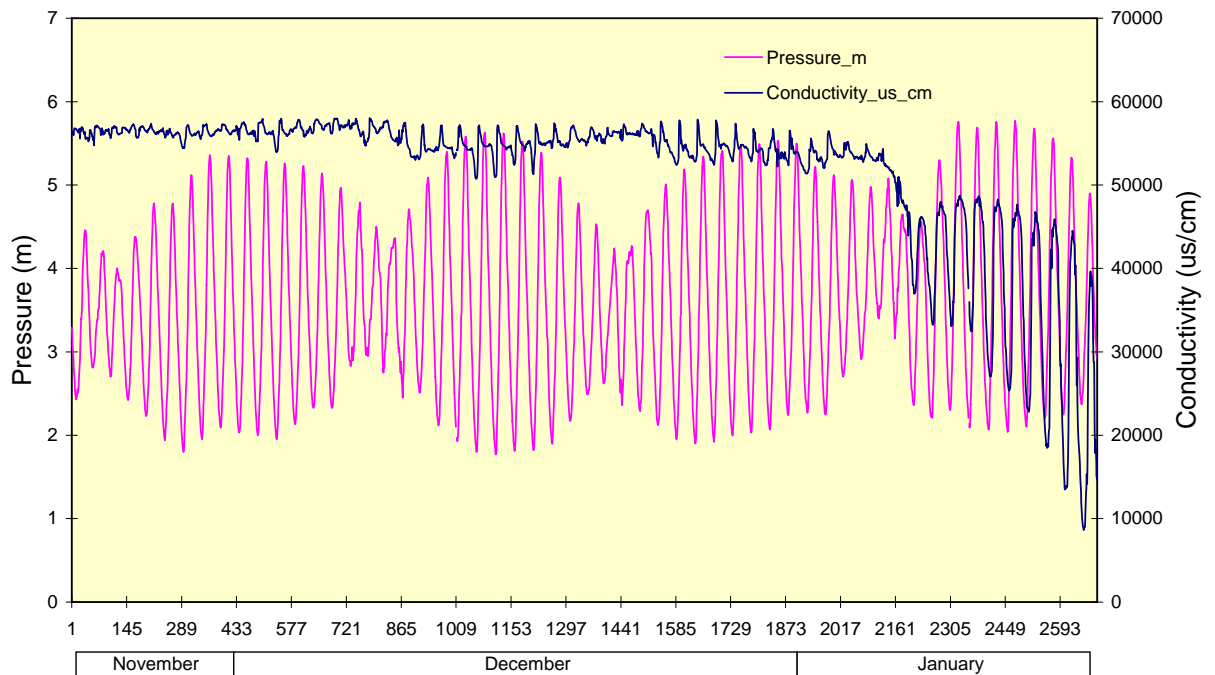
Figure 2.5. Half-hourly records of water pressure (depth) and conductivity recorded at the Raptis wharf in the Norman River, Karumba from 23 November 2004 to 16 January 2005.

The data for January 2005 at Karumba is shown in more detail in Figure 2.6. It can be clearly seen that the conductivity decreases during the ebb tide and reaches a minimum shortly after low tide and then increases again during the flood tide. The decrease is in response to freshwater flowing down from upriver, but this freshwater influence is overcome on the flood tide as high salinity oceanic water re-enters the river.
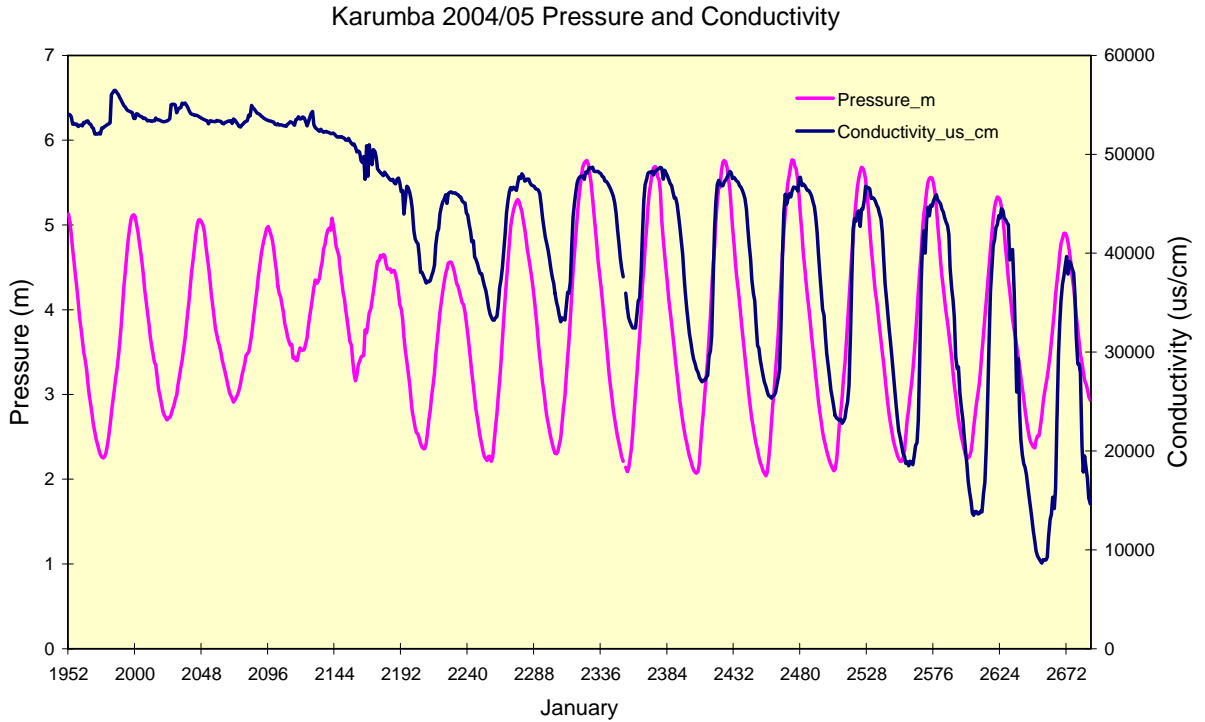
Figure 2.6. Half-hourly records of water pressure (depth) and conductivity recorded at the Raptis wharf in the Norman River, Karumba from 2 to 17 January 2005.

The 30-minute logger data for Karumba was converted to daily values by simply averaging the data for each variable for each day and then compared with daily rainfall data recorded at Normanton (about 40 km inland) (Figure 2.7). It can be seen that a single day's rainfall of around 30 mm in November has almost no impact on the salinity in the river system near the mouth. However, six successive days of rainfall in early January (minimum 16 mm; maximum 41.4 mm) resulted in a substantial drop in average daily salinity; from about 30 to about 13.
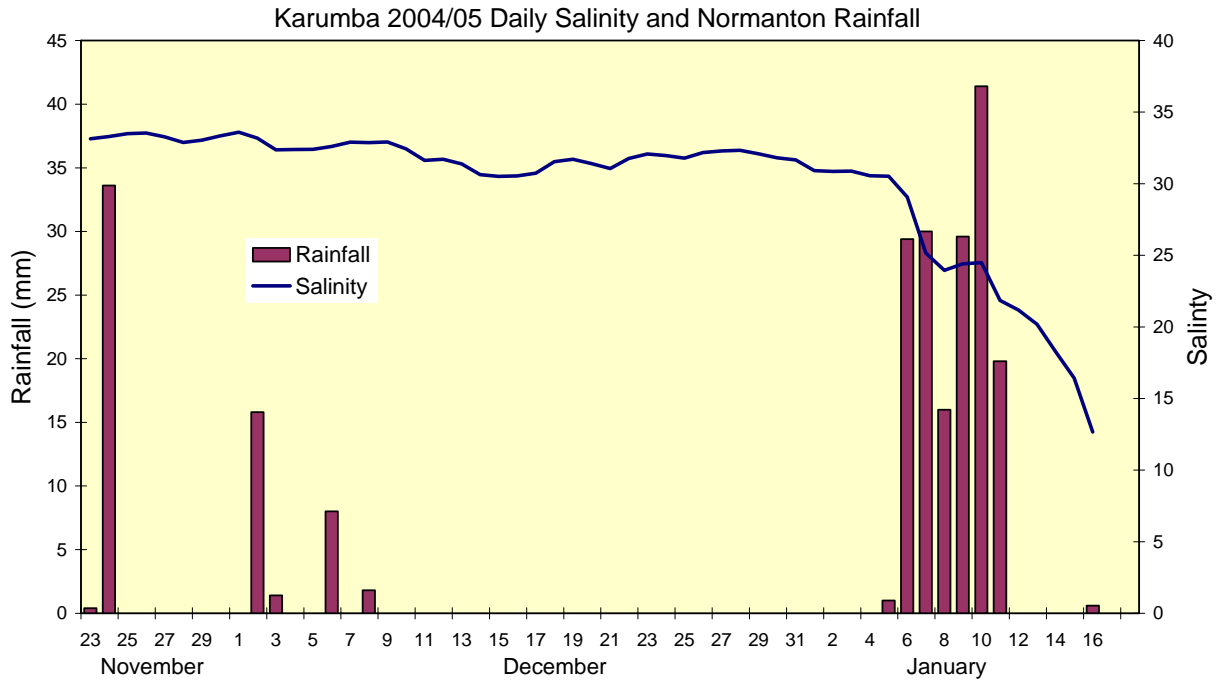
Figure 2.7. Daily summary of salinity recorded at the Raptis wharf in the Norman River, Karumba and daily rainfall recorded at Normanton airport from 23 November 2004 to 16 January 2005.

2.3 Cast net data from Weipa

One of the aims of the project was to collect anecdotal information on recreational cast net catches in the rivers. Sub-adult banana prawns are caught by cast netters along the banks of the rivers near the river mouths as they move out into deeper water. Traditionally this has mostly occurred during the wet season as banana prawns emigrate in response to rainfall and decreasing salinity in the rivers.

We felt that this information might give us an idea of the relative impact of rainfall on the river systems and of the relative abundance of juvenile prawns in the rivers. Furthermore, this information is useful so that we can determine whether a failure to catch banana prawns in the offshore trawl surveys means that there are no prawns or whether prawns have not migrated offshore onto the trawl grounds.

We have had some success in obtaining anecdotal information from cast netters at Weipa. The consensus opinion seems to be that for the last three or four years, streamflow has been below normal (average) levels in the Embley River. Banana prawns have been quite abundant in cast net catches in the estuary but, more importantly, catches have been made much later in the year, well after the end of the wet season.

We have been fortunate in that one recreational cast netter has actually provided us with documented records of his catches. On average he has fished about once per week and provided catch records for us from May 2003 onwards. Samples

were collected from several locations around Weipa (Figure 2.8). His logbooks contain the following headings:

Date, Weather, Location, Type of prawn (banana, leader or other), numbers in a size grade (<20mm, 20-60 mm, 70-90 mm, 90-110 mm, >110 mm), No of casts, and total number of banana prawns. Total catches over time is shown in Figure 2.9. Catch rates (number of banana prawns per cast) is shown in Figure 2.10. Most of the catches and the best catches are generally during the winter months, showing that many banana prawns did not migrate from the estuary during the wet season and were still in the estuary and being caught in good numbers in cast nets from April to July.
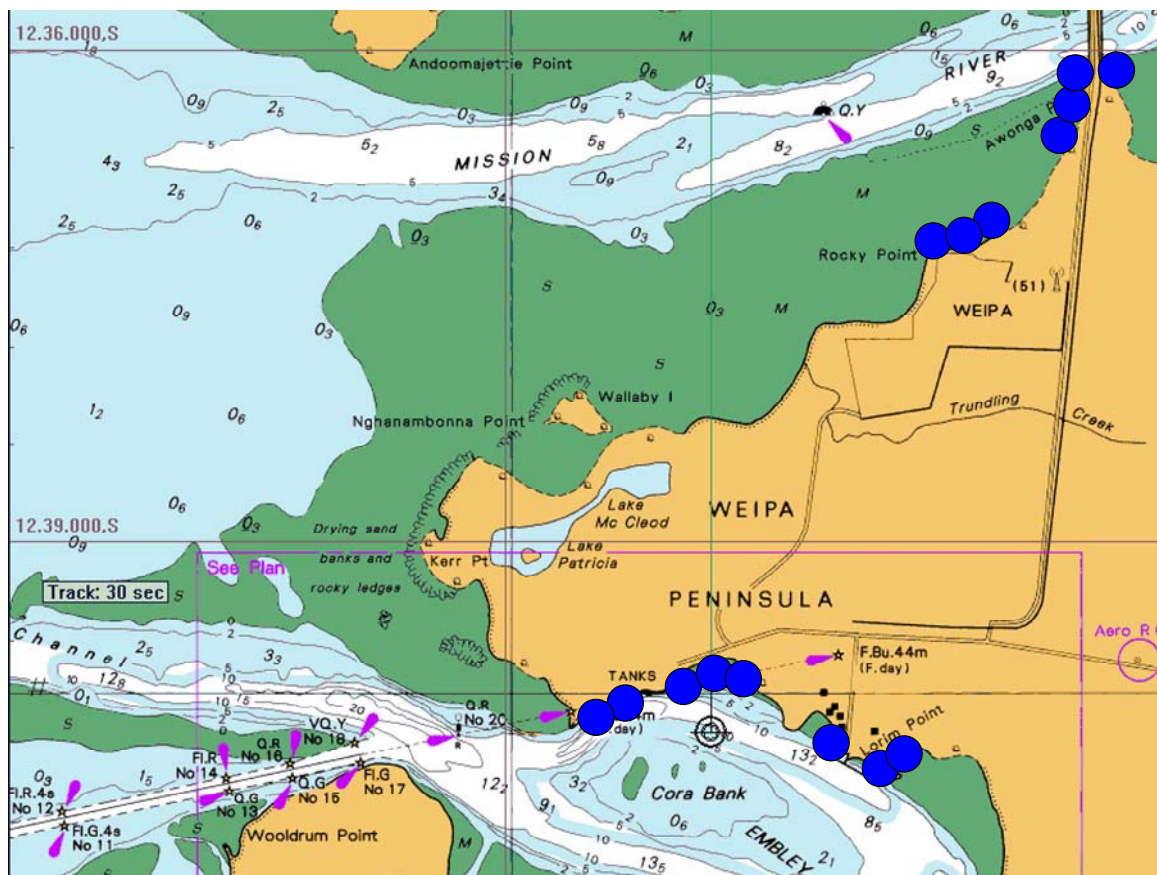
Figure 2.8. Location of cast net sample sites since 2003 in the Weipa region
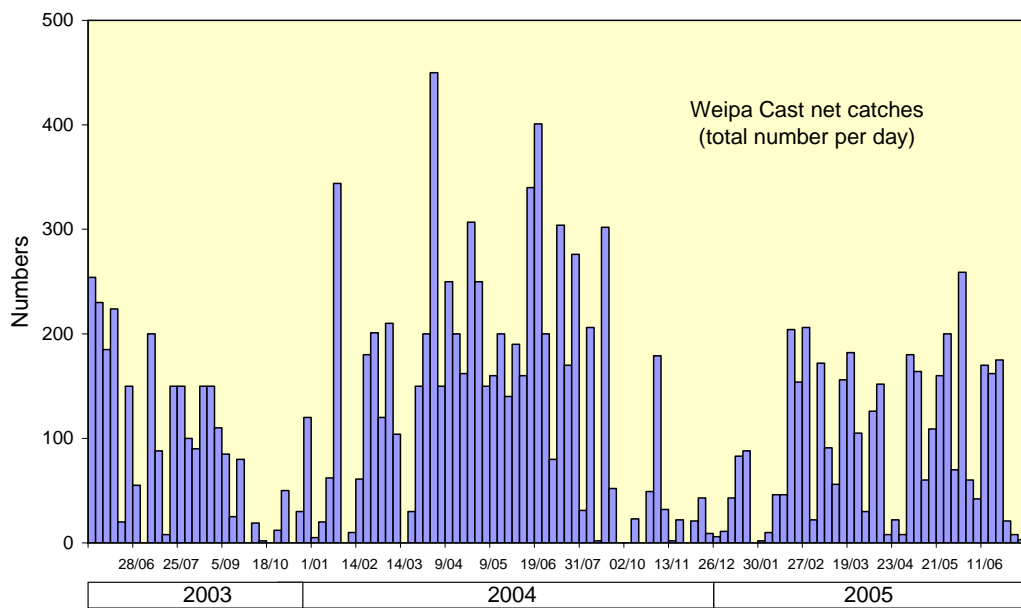
Figure 2.9. Total number per day of banana prawns caught by cast nets in the Weipa estuarine region.
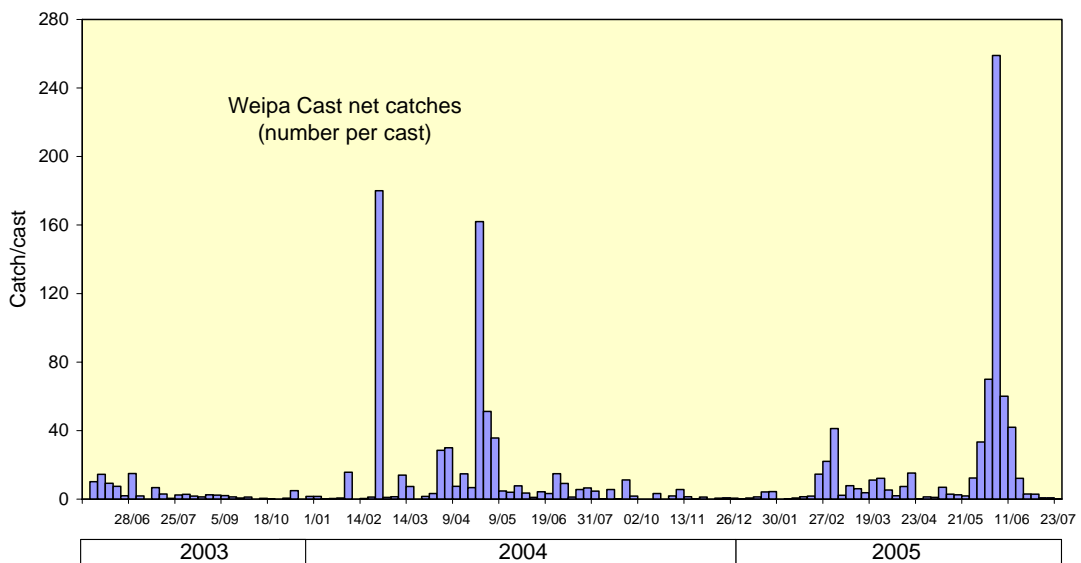
Figure 2.10. Number of banana prawns caught per cast in the Weipa estuarine region.

2.4 References

Crocos, P.J. and Kerr, J.D. (1983). Maturation and spawning of the banana prawn *Penaeus merguiensis* de Man (Crustacea: Penaeidae) in the Gulf of Carpentaria, Australia. *Journal of Experimental Marine Biology and Ecology*, **69**, 37 – 59.

Crocos, P.J. and van der Velde, T.D. (1995). Seasonal, spatial and interannual variability in the reproductive dynamics of the grooved tiger prawn *Penaeus semisulcatus* in Albatross Bay, Gulf of Carpentaria, Australia: the concept of effective spawning. *Marine Biology*, **122**, 557 – 570.

CHAPTER 3: SPATIO-TEMPORAL MODELLING OF PRAWNS IN ALBATROSS BAY, KARUMBA AND MORNINGTON ISLAND

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3.1 Abstract

The seasonal life-history patterns of penaeid prawns are complex and there are distinct differences between species. Better knowledge and understanding of offshore migration to the fishing grounds of penaeid prawns is particularly important for the operation and management of the Northern Prawn Fishery, Australia. Knowledge of the location of prawns during the critical spawning period of the year is important, especially since recent work suggests that inshore areas are critical for effective spawning. This paper explores factors, such as rainfall, water depth and season, impacting prawn migratory patterns, and models the spatial and temporal distribution of three commercially valuable species of prawns (*Penaeus merguiensis, Penaeus semisulcatus* and *Penaeus esculentus*) in Albatross Bay, Karumba and Mornington Island in the Northern Prawn Fishery using modern statistical methodology. The methodology allows for flexible functional relationships between variables, including univariate smooth terms and smooth terms for interactions between covariates: a major advancement on the methodology used in previous analyses of spatial distribution of prawns in the Gulf of Carpentaria. The models interpolate well, but expose the problems associated with extrapolation beyond the data. The results suggest that there are spawners in the important inshore waters during the critical spawning period of the year, although there is no strong evidence for major congregations of prawns in these important inshore regions compared to more offshore regions. Rainfall was significant in many of the models, particularly those describing the distribution of *Penaeus merguiensis*. Increased rainfall mostly had a positive effect on prawn catch rates, possibly by stimulating prawns to move out of shallow coastal areas into the fishing areas. However, in some cases, high levels of rainfall had a negative effect which may be due to storms associated with the heavy rainfall decreasing the effectiveness of the fishing fleet. The analyses showed no signs of major inshore migrations associated with spawning, but there were certainly some spawners close inshore at the critical spawning period.

3.2 Introduction

The seasonal life-history patterns of penaeid prawns are complex and there are marked differences between species (Dall et al. 1990). In the Northern Prawn Fishery (NPF), Australia, all the commercially important species have a life cycle where the adults spawn in offshore waters, larvae and postlarvae move inshore and, after several months in estuarine or coastal nursery areas, the juveniles and subadults move offshore again. Two aspects of the spatio-temporal distribution associated with this life cycle are particularly important for the operation and management of the NPF – the offshore migrations to the fishing grounds and the location and timing of the reproducing adults.

The timing and extent of migration of the young adult prawns from the inshore nursery areas to the offshore fishing grounds largely determines when the prawns are available for capture by the fishing fleet and the size of the catch. For banana prawns, *Penaeus merguiensis*, in some regions of the NPF, it has been shown that migration of the prawns out of the nursery areas is in part related to the amount of rainfall that falls in the coastal areas (Vance et al 1985, Staples & Vance 1986, Vance *et al*. 1998). Increased offshore commercial catches of adults are often associated with high rainfall. However, it is not clear if the increased commercial catch is due to an increase in the population size resulting from increased production, or if it is simply an increase in catchability as the whole population simply moves further offshore into the fishing grounds. If the latter scenario is the case, then the spawning stocks are in much greater danger of being over-fished in high catch years.

Knowledge of the size and location of the spawning stock for each species of prawn is also important for the management of the fishery. Previous work has suggested that tropical penaeids typically have two spawning periods each year (see Pauly *et al*. 1984, Garcia 1985, 1988, Dall *et al*. 1990, Staples and Rothlisberg 1990, and Crocos and van der Velde 1995). However, other work does not always bear this out (see Rothlisberg *et al*. 1987, Crocos 1987a and 1990), suggesting variability exists between years and regions. There is also clearly variability between species. In the western Gulf of Carpentaria, brown tiger prawns were found to spawn for much of the year whereas grooved tiger prawns had a much more limited spawning period (Crocos 1987b). Despite these temporal patterns of spawning it has been suggested that spawning of penaeid prawns in the NPF during only a relatively short period of the year contributes most of the recruits to the next year's commercial catch (Rothlisberg et al. 1985).

In more recent times, a series of studies modelling water currents and the advection of larvae and laboratory studies on the behaviour of postlarvae have suggested that the spawning that contributes most to subsequent generations is quite limited in space, particularly to the inshore areas of the fishery (Condie et al. 1999, Vance and Pendrey 2001). This has given rise to the concept of the "effective spawning" population of the prawn fishery (Crocos and van der Velde 1995). This possibility is supported by the research of Dredge (1985) who found that on the east coast of Australia a small proportion of the adult population of *P. merguiensis* returned from offshore waters and spawned in estuarine areas. This behaviour has also been suggested by Neal (1975) for the white shrimp (*P. setiferus*) fishery in the Gulf of Mexico. In the NPF, *P. semisulcatus* disperse to deep water offshore from the

fishing grounds in the first half of the year and then return onshore to the fishing grounds after July each year. It is not clear what proportion of these prawns move into close inshore waters.

There can be marked variability within and between years in abundance and distribution of penaeid prawns in the NPF. Crocos and van der Velde (1995) show this for adult female *Penaeus semisulcatus* in Albatross Bay, Gulf of Carpentaria, Australia. With long term declining commercial catches of *Penaeus semisulcatus*, *Penaeus esculentus* and *Penaeus merguiensis* in the Gulf of Carpentaria, there is a need to model the spatial and temporal distribution of abundance or the migratory patterns of these species, and to determine the factors driving these patterns.

This paper explores factors impacting migratory patterns and models these patterns for *Penaeus semisulcatus*, *Penaeus esculentus* and *Penaeus merguiensis* in Albatross Bay, Karumba and around Mornington Island in the Gulf of Carpentaria. This is done using a combination of historical survey and recent survey data. Modern statistical methodology such as generalized additive models (GAMs) is used to analyse data and make predictions.

3.3 Data

The data analysed in this paper come from historical and recent surveys. In the Albatross Bay region historical data was collected monthly (at least for the first three years) between March 1986 and March 1992 (see Crocos van der Velde 1995). For Karumba the historical survey data was collected approximately monthly between August 1977 and August 1978 (see Crocos and Kerr 1983). No historical data is available for the Mornington Island region.

For Albatross Bay more recent survey data was collected between January 2003 and January 2005 four times a year, approximately in the months January, March, August and October. For the Karumba region the recent survey data was collected during the same period as that for the recent Albatross Bay survey, except that no sampling took place during October 2003 and 2004. Finally, for the Mornington Island region sampling took place between August 2002 and January 2005, approximately in the months January, March and August. See Chapter 2 for more details on methods used during the surveys.

A clearer picture of when sampling took place can be acquired from the prediction maps in the Results (3.5), since prediction maps were generated only for those months for which samples were collected. The only exception is for the prediction maps for March 1986 in Albatross Bay. Maps were not generated for March 1986 since they are based on only one month's of observation for the fishing year 1985 to 1986 (see section 3.5.1.a for definition of fishing year).

3.4 Statistical Methodology

The variables of interest are the total catch of the three prawn species for each survey trawl. It makes sense to use generalized additive models (GLMs) to model the total catch variables. The Poisson and negative binomial are the natural choices for the distribution of the total catch variables. In this paper only the Poisson distribution

is considered because preliminary work with the negative binomial led to anomalous results.

The Poisson distributed Y_i random variable with mean μ_i has the following probability distribution:

$$P(Y_i = y_i) = \frac{\mu_i^{y_i} e^{-\mu_i}}{y_i!},$$

for $y_i = 0, 1, 2, \ldots$. For the Poisson distribution, covariates can be introduced via the mean μ_i. Letting $\boldsymbol{\beta}^*$ be a $p \times 1$ column vector of coefficient parameters, $\mathbf{x}_i^*$ a $p \times 1$ column vector of covariates, and η_i the linear predictor for observation i, then the canonical link between the linear predictor and the mean of Y_i for the Poisson distribution (McCullagh and Nelder 1989) is:

$$g(\mu_i) = \log(\mu_i) = \eta_i = \mathbf{x}_i'^* \boldsymbol{\beta}^*. \tag{3.1}$$

The Poisson distribution has the property that $\mathrm{E}(Y_i) = \mathrm{Var}(Y_i) = \mu_i$. This property can be too restrictive. Real data regularly exhibit dispersion that is less than (under-dispersed) or greater than (over-dispersed) the mean (McCullagh and Nelder 1989). It is important to account for over-dispersion and under-dispersion when it exists, otherwise misleading inferences can result.

When the mechanism that generated the over-dispersion or under-dispersion is not known it is useful to assume that $\mathrm{Var}(Y_i) = \mathrm{V}(\mu_i) = \phi \mu_i$ holds approximately (McCullagh and Nelder 1989). Under-dispersion and over-dispersion is present when $\phi < 1$ and $\phi > 1$, respectively.

The formulation in (3.1) can be generalized as follows (Wood 2000, 2004 and 2006):

$$g(\mu_i) = \log(\mu_i) = \eta_i = \mathbf{x}_i'^* \boldsymbol{\beta}^* + v_{1i} f_1(w_{1i}) + v_{2i} f_2(w_{2i}) + \ldots, \tag{3.2}$$

where $\mathbf{x}_i^*$ and $\boldsymbol{\beta}^*$ are as above, the v_{ij}s are covariates used in variable coefficient models (Hastie and Tibshirani 1993) and can be dummy variables or take the value 1, and the f_js are smooth functions of covariates w_j. The formulation in (3.2) allows for the smooth function f_j to be a function of multiple covariates. The smooth functions basis can take many different forms such as cubic splines (Lin and Zhang 1999, and Rosenberg *et al.* 2003), P-splines (Eilers and Marx 1996) and thin plate splines (Ruppert, Wand and Carroll 2003 and Wood 2003). For smooth functions of multiple covariates, tensor product based smooths are preferred when the covariates are on different scales (Wood 2006), such as time and space. For tensor product based smooths the marginal basis can take on different forms including cubic splines and thin plate splines.

Penalized maximum likelihood (Wood 2000 and 2004) can be used for model fitting by maximizing:

$$l(\mathbf{\eta}) - \frac{1}{2} \sum_j \left(\theta_j \int \left[f_j''(w) \right]^2 dw \right), \tag{3.3}$$

where l is the log-likelihood of the linear predictor, the second term penalizes models that may have complicated component functions (Wood 2004), and the θ_js are the smoothing parameters that control the trade-off between the two terms in (3.3). Wood (2000) shows that maximising (3.3) is equivalent to minimizing weighted penalized least squares:

$$\left\| \mathbf{W}^{1/2} \left(\mathbf{z} - \mathbf{X}\mathbf{\beta} \right) \right\|^2 + \sum_j \theta_j \mathbf{\beta}' \mathbf{S}_j \mathbf{\beta} \tag{3.4}$$

subject to linear constraints $\mathbf{C}\mathbf{\beta} = \mathbf{0}$. In (3.4) $\|.\|$ is the Euclidean norm, $\mathbf{X}$ is an $n \times q$ design matrix which includes the design basis generated from the $\mathbf{x}_i'^*$s in (3.2) and that generated by the f_j smooth functions, $\mathbf{\beta}$ is the model parameter vector that includes the parameters $\mathbf{\beta}^*$ and those for the f_j smooth functions, $\mathbf{z} = \mathbf{\eta} + g'(\mathbf{\mu})(\mathbf{y} - \mathbf{\mu})$, and $\mathbf{W}$ is a diagonal matrix with the ith diagonal element equal to $1 \Big/ \left\{ \phi \mathrm{V}(\mu_i) \left[g'(\mu_i) \right]^2 \right\}$ with $\mathrm{V}(\mu_i)$ the variance of Y_i. Equation (3.4) can be solved using iterative re-weighted least squares. Wood (2004) improves the stability and efficiency of (3.4) by including a ridge penalty.

Note that the formulation in (3.3) and (3.4) allows for multiple penalties and hence multiple smoothing parameters. The smoothing parameters θ_j can be estimated using Generalized Cross Validation (GCV) (Wood 2000 and 2004). The scale parameter ϕ can be estimated using GCV and the Pearson statistic (McCullagh and Nelder 1989).

The deviance can be used to ascertain the degree to which the model and the data match. The deviance has the following form:

$$D = -2 \left(\log l_c - \log l_s \right),$$

where l_c and l_s are the likelihood for the current and the full or saturated models, respectively. The deviance is approximately chi-square distributed with degrees of freedom equal to the difference between the numbers of parameters for the two models (McCullagh and Nelder 1989).

The analyses in this paper were run in the *R* statistical environment using the *mgcv* library package to perform the GAMs analyses.

3.5 Results

In this section, GAMs analyses are presented that model the temporal and spatial distribution of the different prawn species in Albatross Bay, Karumba and Mornington Island regions of the Gulf of Carpentaria. Temporal and spatial modelling of prawn numbers need to account for the inter-annual and within year

variability and spatial covariates such as longitude, latitude and depth. Other factors such as salinity can impact the temporal and spatial distribution of prawns (Vance et al. 2003). Salinity readings often are not available or are available for only a small subset of the survey sampling sites. As a surrogate for salinity, rainfall at the nearest land-based weather recording station has been used.

3.5.1 Albatross Bay

Figure 3.1 depicts the combined historical and recent sampling sites in Albatross Bay. Given the different migration and distribution ranges of the three prawn species, slightly different sites were used in the analyses for each species. The blue sites in Figure 3.1 were visited irregularly and infrequently during the historical study and hence are omitted from the analyses. The red and green sites are those included in the analyses for *Penaeus semisulcatus* and *Penaeus esculentus*. All the sampling stations west of 141° 25′ in both the historical and recent Albatross Bay studies had few if any *Penaeus merguiensis* catch, and hence are excluded from the analyses for this species. The sites included in the analyses for *Penaeus merguiensis* are coloured green in Figure 3.1.
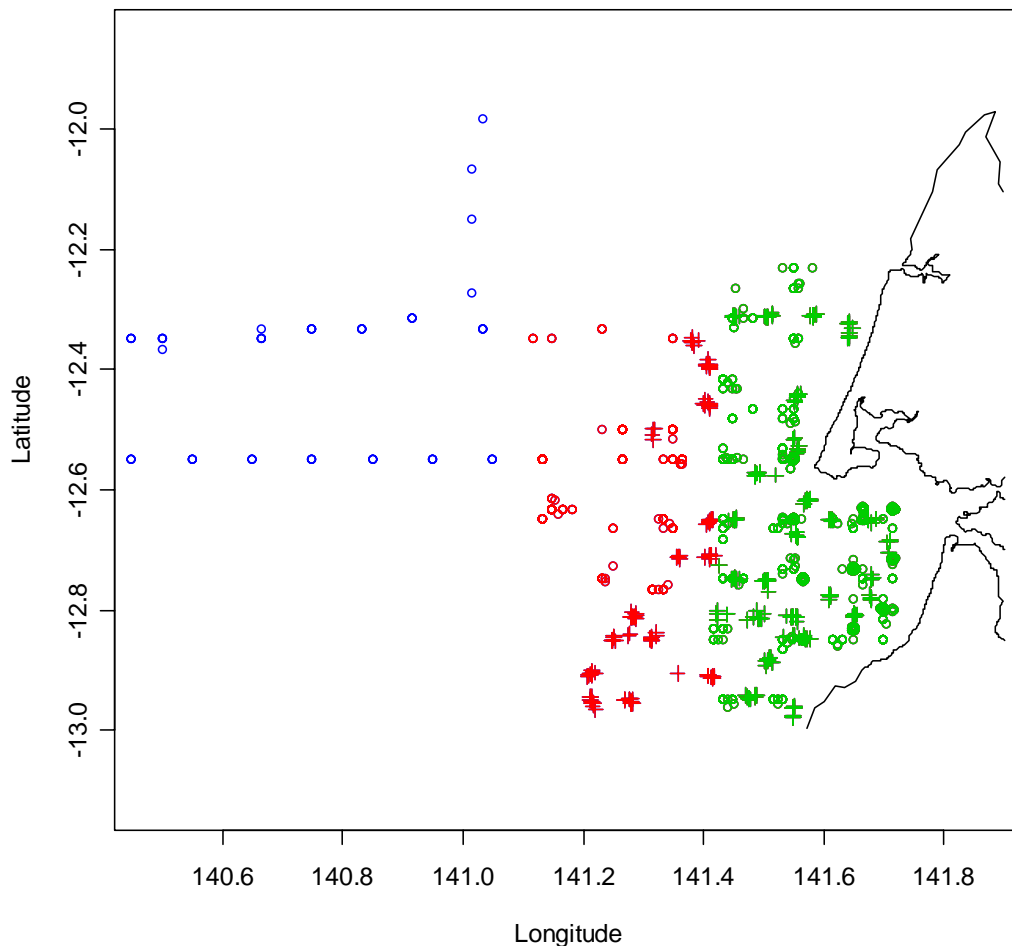

Figure 3.1. Historical (circles) and recent (crosses) Albatross Bay sampling sites. Analyses for *Penaeus merguiensis* include only green sites; analyses for *Penaeus semisulcatus* and *Penaeus esculentus* include both green and red sites. Blue sites were sampled infrequently and were not included in analyses.

3.5.1.a *Penaeus merguiensis*

The over-dispersed Poisson GAM model with linear predictor as given in model (3.5) captures many of the important temporal and spatial features in the historical and recent survey data:

$$g(\mu_i) = \log(\mu_i) = \alpha + \log(\text{area}_i) + s(\text{longitude}_i, \text{latitude}_i)$$
$$+ \sum_{j=2}^{10} v_{ji}\beta_j^* + \sum_{j=1}^{10} v_{ji}s(\text{cosd}_i, \text{sind}_i)$$
$$+ \text{ts}(\text{depth}_i, \text{latitude}_i)$$
$$+ s(\text{rain}1.3_i) + s(\text{rain}4.14_i) + s(\text{rain}15.28_i), \tag{3.5}$$

where $s(.)$ are smooth terms; $\text{ts}(.)$ are tensor smooth terms; the offset (coefficient of 1) log(area) is the log of trawled area measured in hectares; $\text{cosd} = \cos(2\pi d/365.25)$ and $\text{sind} = \sin(2\pi d/365.25)$ are harmonic terms; d is the number of days since April 1 1986; rain1.3, rain4.14 and rain15.28 is the total rain recorded at the local weather station (in millimetres / 100) in the last three days before the survey date; the last four to 14 days before the survey date; and the last 15 to 28 days before the survey date, respectively. The v_j's are dummy or indicator variables for the fishing years which begin on 1 April of each calendar year and end on 31 March the following calendar year. Consequently the term $\sum_{j=2}^{10} v_{ji}\beta_j^*$ in model (3.5) models the fishing year effects, $\sum_{j=1}^{10} v_{ji}s(\text{cosd}_i, \text{sind}_i)$ models the interaction between the harmonic terms cosd and sind and the fishing years, $s(\text{longitude}_i, \text{latitude}_i)$ models the interaction between longitude and latitude, and $\text{ts}(\text{depth}_i, \text{latitude}_i)$ models the interaction between depth and latitude.

All the terms in model (3.5) make significant contributions to the fit. For illustrative purposes, Figure 3.2 gives the contributions to the linear predictor in model (3.5) for the rain variables rain1.3, rain4.14 and rain15.28. The variable rain1.3 models 'short term' rain effects; rain4.14 models 'medium' term rain effects; and rain15.28 models 'longer' term rain effects. Interestingly for rain1.3 and rain4.14 the curves initially increase then they decline or level off before rising steeply for large rain1.3 and rain4.14 values. The steep rise needs to be interpreted with care because both variables have very few large values. For rain15.28 there is a gradual rise and then a levelling off for larger values. Model (3.5) explains 61.6% of the total deviance, and the estimated scale parameter for model (3.5) is 176.6, suggesting that there is considerable over-dispersion relative to the Poisson distribution.
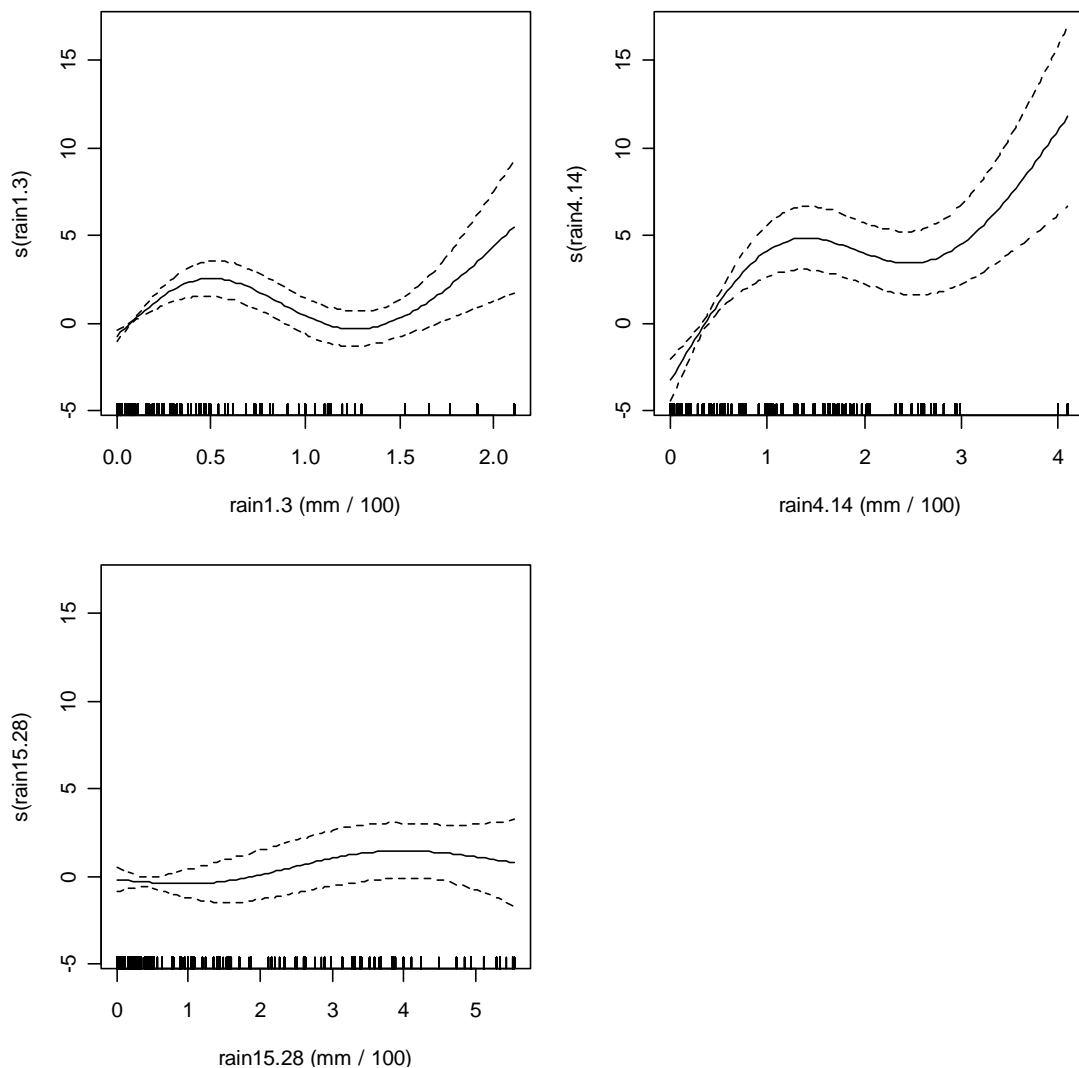
Figure 3.2. The contributions to the linear predictor (3.5) of the smooth terms for rain1.3, rain4.14 and rain4.28 for *Penaeus merguiensis* in Albatross Bay. The dashed lines are the approximate 95% confidence intervals. Tick marks show the locations of the observations.

Figure 3.3 plots the log predicted *Penaeus merguiensis* counts per hectare based on model (3.5) for the second day of sampling for each sampling period in the historical and recent surveys. The spatial prediction is restricted to be within the sampling sites, so that there is no spatial extrapolation. An examination of Figure 3.3 reveals that, although more prawns are in the area of study during the first four months of the year, there is a great deal of variability between years, both in predicted numbers and when the peak occurs. Of particular interest for this project is the distribution of prawns in the important spawning period of the year (August-October). Inspection of Figure 3.3 suggests that, although the densities of prawns are lower than early in the year, the highest densities of prawns during August to October are often in the inshore areas.

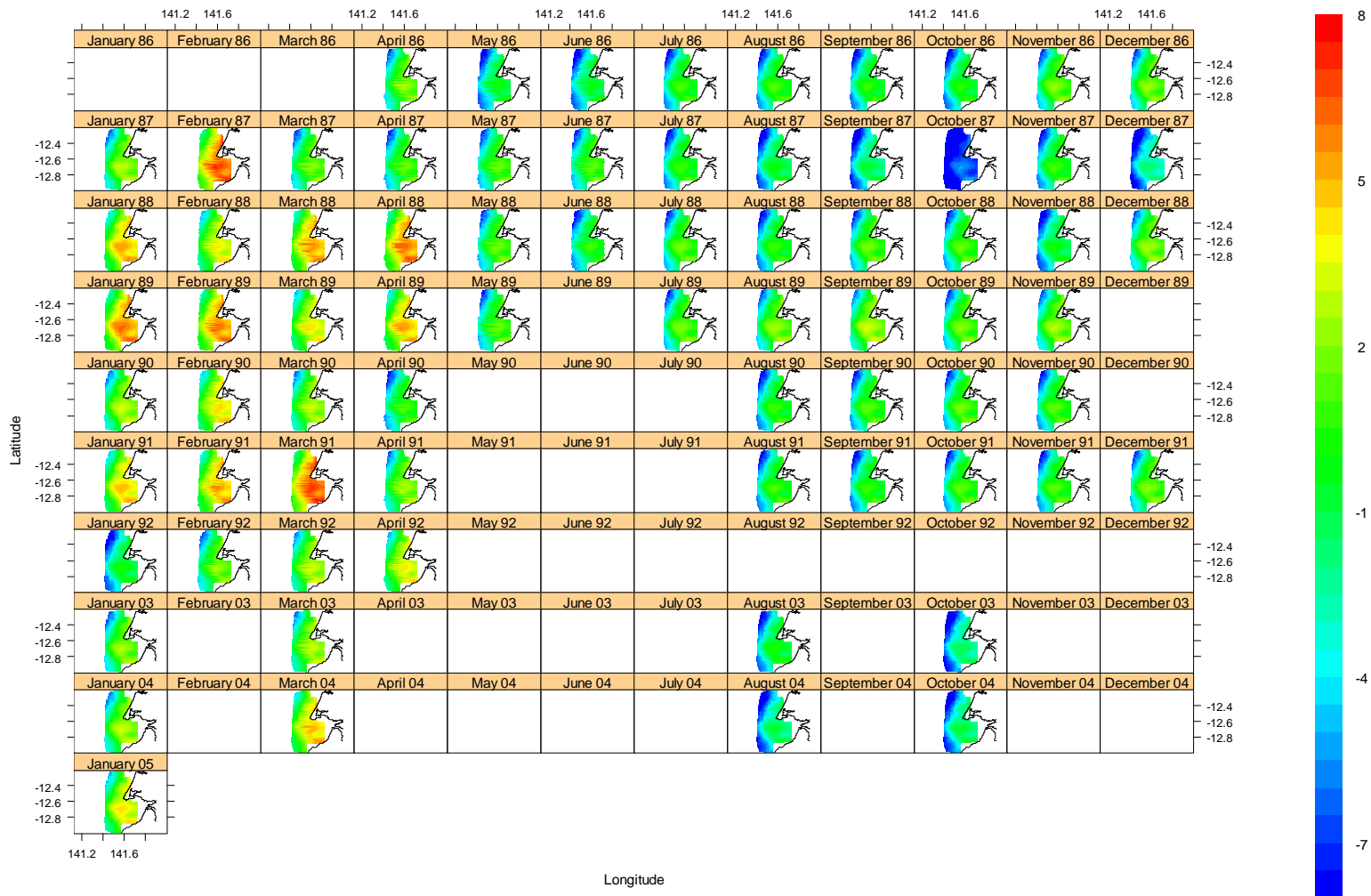**Figure 3.3. Spatially interpolated log predicted *Penaeus merguiensis* counts per hectare for model (3.5) in Albatross Bay.**

Figure 3.4. Spatially interpolated log predicted *Penaeus semisulcatus* counts per hectare for model (3.6) in Albatross Bay.

3.5.1.b *Penaeus semisulcatus*

For *Penaeus semisulcatus* the important spatial and temporal features of the historical and recent survey data are modelled by the over-dispersed Poisson GAM model with linear predictor as in (3.6):

$$
\begin{aligned}
g(\mu_i) = \log(\mu_i) = {} & \alpha + \log(\text{area}_i) + s(\text{longitude}_i, \text{latitude}_i) \\
& + \sum_{j=2}^{10} v_{ji}\beta_j^* + \sum_{j=1}^{10} v_{ji} s(\text{cosd}_i, \text{sind}_i) \\
& + \text{ts}(\text{cosd}_i, \text{sind}_i, \text{depth}_i) + \text{ts}(\text{depth}_i, \text{latitude}_i) \\
& + \text{rain}1.3_i \beta_{1.3}^* + \text{rain}4.14_i \beta_{4.14}^* + \text{rain}15.28_i \beta_{15.28}^*.
\end{aligned}
\tag{3.6}
$$

Interestingly, the coefficients for the rain terms rain1.3, rain4.14 and rain15.28 paint a contradictory story. The coefficients for these variables are significantly different from zero, but that for rain4.14 is negative ($\hat{\beta}_{4.14}^*$=-0.234 with standard error 0.084) and that for rain1.3 and rain15.28 is positive ($\hat{\beta}_{1.3}^*$=0.306 with standard error 0.120 and $\hat{\beta}_{15.28}^*$=0.171 with standard error 0.036). All the terms in model (3.6) make significant contributions to the fit. The scale parameter for model (3.6) is 33.2 suggesting that the data is over-dispersed relative to the Poisson distribution, but by not as much as *Penaeus merguiensis*. Model (3.6) explains 66.1% of the total deviance.

The interpolated log predicted *Penaeus semisulcatus* counts per hectare based on model (3.6) for the second day of sampling for each sampling period can be found in Figure 3.4. From Figure 3.4 it can be seen that *Penaeus semisulcatus* numbers are generally greatest in January, although this is not consistent for all years, and the numbers available in January can vary considerably between years. In addition, there are few *Penaeus semisulcatus* in the study area during May to July. From August to October, prawns are usually found through much of the area of Albatross Bay with occasional increased densities in some of the inshore areas.
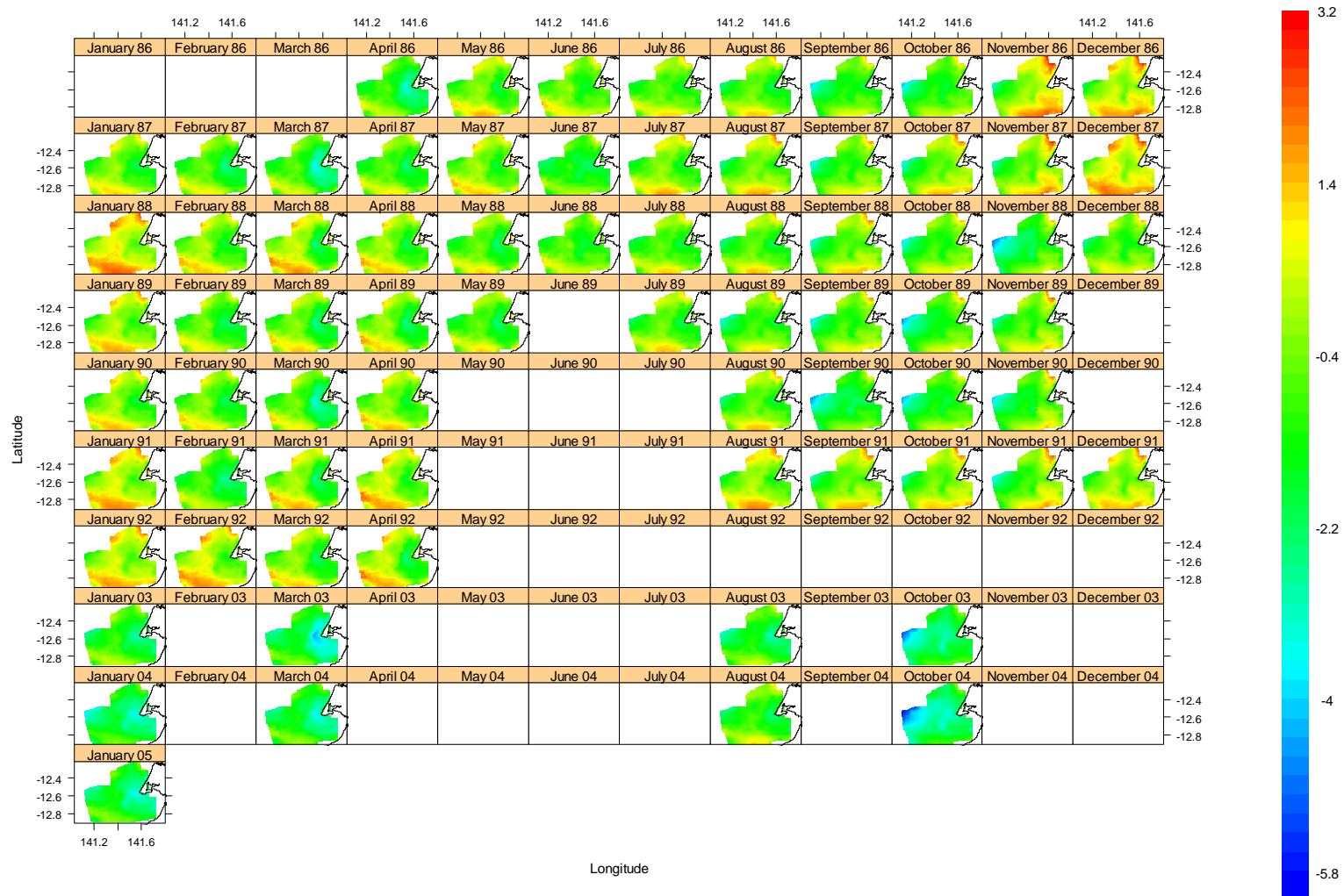
Figure 3.5. Spatially interpolated log predicted *Penaeus esculentus* counts per hectare for model (3.7) in Albatross Bay.

3.5.1.c *Penaeus esculentus*

The number of *Penaeus esculentus* caught in the Albatross Bay region for both the historical and recent studies was much smaller than that for *Penaeus semisulcatus* and *Penaeus merguiensis*. This is reflected in the smaller estimated scale parameter value of 2.67 for the over-dispersed Poisson GAM model with linear predictor as in (3.7):

$$g(\mu_i) = \log(\mu_i) = \alpha + \log(\text{area}_i) + s(\text{longitude}_i, \text{latitude}_i)$$

$$+ \sum_{j=2}^{10} v_{ji}\beta_j^* + \sum_{j=1}^{10} v_{ji}s(\text{cosd}_i, \text{sind}_i)$$

$$+ \text{ts}(\text{cosd}, \text{sind}, \text{depth}) + \text{ts}(\text{depth}_i, \text{latitude}_i) + s(\text{mud})$$

$$+ \text{rain}1.3_i\beta_{1.3}^* + \text{rain}4.14_i\beta_{4.14}^* + \text{rain}15.28_i\beta_{15.28}^*,$$

$$(3.7)$$

where mud is a sediment variable representing percent mud. Model (3.7) explains 50.4% of the total deviance.

The coefficient for rain15.28 is not significant, suggesting that the "longer" term rain does not appear to have a strong impact on the number of *Penaeus esculentus* in the study area. The variable rain1.3 is significant with a positive coefficient ($\hat{\beta}_{1.3}^*$, =0.42 with standard error 0.17), suggesting that rain in the last few days before sampling may increase the number of *Penaeus esculentus* in the study area. On the other hand, rain4.14 appears to have the opposite effect since the coefficient for this variable is negative and significantly different from zero ($\hat{\beta}_{4.14}^*$=-0.14 with standard error 0.07).

The log predicted *Penaeus esculentus* counts per hectare based on model (3.7) for the second day of sampling for each sampling period are plotted in Figure 3.5. An examination of this figure reveals that the largest predicted counts per hectare often occur in areas where there are relatively small predicted counts per hectare of *Penaeus semisulcatus* and *Penaeus merguiensis*. In addition, relatively large predicted counts per hectare can be found during different periods of a calendar year; for example in November and December 1986, December 1987, January 1988, April 1991 and February 1992. In the main spawning period, the densities of *Penaeus esculentus* were relatively low in the inshore areas of Albatross Bay.

For *Penaeus esculentus* the inclusion of a smooth term for percent mud is statistically significant as evidenced by its inclusion in model (3.7). The contribution of this term to the linear predictor (3.7) can be found in Figure 3.6. From this figure it appears that in Albatross Bay *Penaeus esculentus* are less likely to be found in areas with very low percent of mud. The peak is approximately at the 40% mud mark suggesting that *Penaeus esculentus* are more likely to be found in such areas. Interestingly there is a small trough approximately at the 70% mud mark and then the curve rises again, although the confidence interval increases for the large percent mud values, suggesting there is more uncertainty for these values. The percent mud contours and the log predicted *Penaeus esculentus* counts per hectare for January 1988 are plotted in Figure 3.7. The highest predicted values are generally found in the 20 to 40 percent mud range. *Penaeus esculentus* in Albatross Bay are more likely

to be found in areas with at least 20% mud, with a suggestion that the largest numbers may be found in areas with approximately 40% mud.
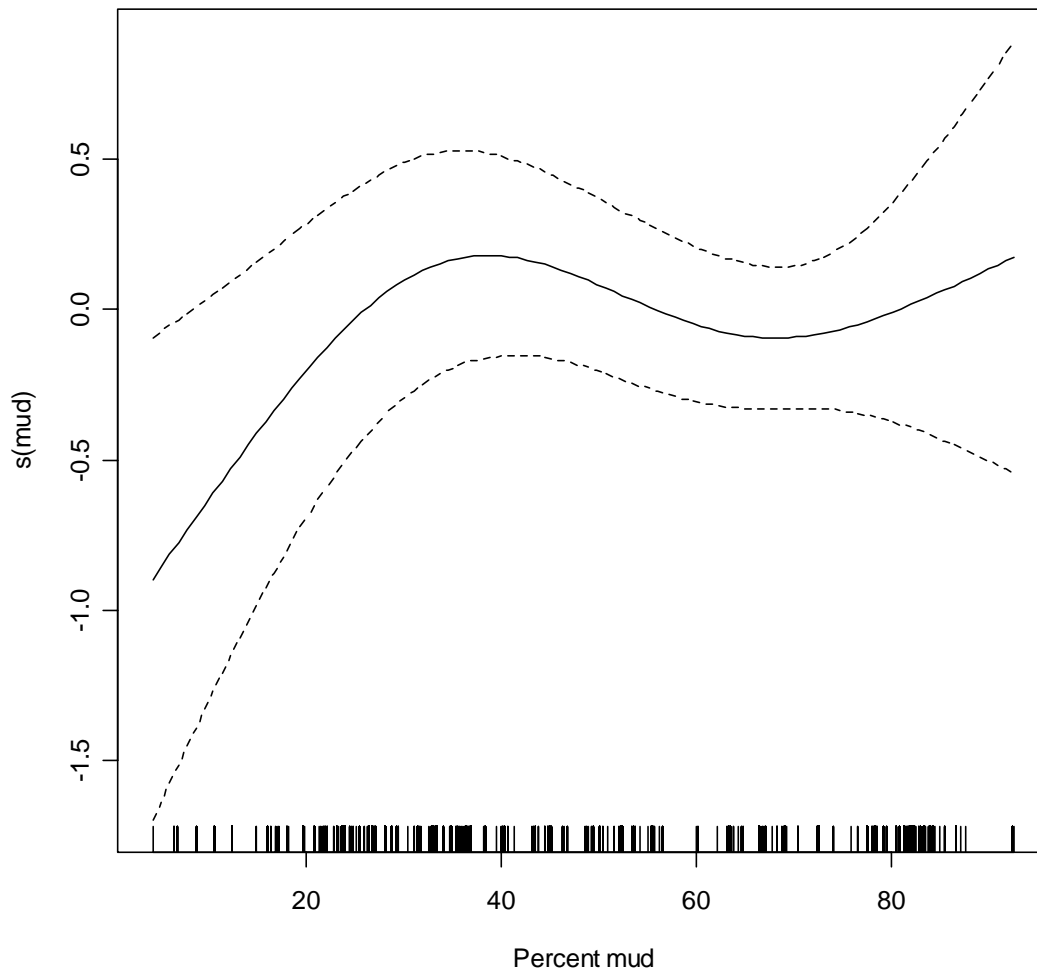
Figure 3.6. The contribution to the linear predictor (3.7) of the smooth term for percent mud. The dashed lines are the approximate 95% confidence intervals. The tick marks show the location of the predictor values.

In Somers (1994) the distribution analysis of the prawn species is based on a polynomial regression model for depth and percent mud, allowing for interaction between the two predictor variables. Including tensor product smooth terms for depth and percent mud interaction in models (3.5), (3.6) and in place of the smooth term for percent mud in model (3.7), the results suggest that these terms are statistically significant. Predictions for these models, however, can be anomalous. For example, the largest observed *Penaeus esculentus* catch per hectare in Albatross Bay from both the historical and recent surveys was 21.45. Including tensor product smooth terms for the interaction of depth and percent mud in place of the smooth term for percent mud in model (3.7), however, results in a spatially interpolated prediction that is over 17 times larger than this maximum catch per hectare! The reason for this can be seen in Figure 3.8, which plots percent mud against depth for both survey data and the

spatially interpolated prediction sites. This figure reveals that all prediction catches per hectare greater than 50 are outside of the convex hull of the observed samples or just inside the border of the convex hull. In other words, the problem arises because of extrapolation in the depth and percent mud predictor space.
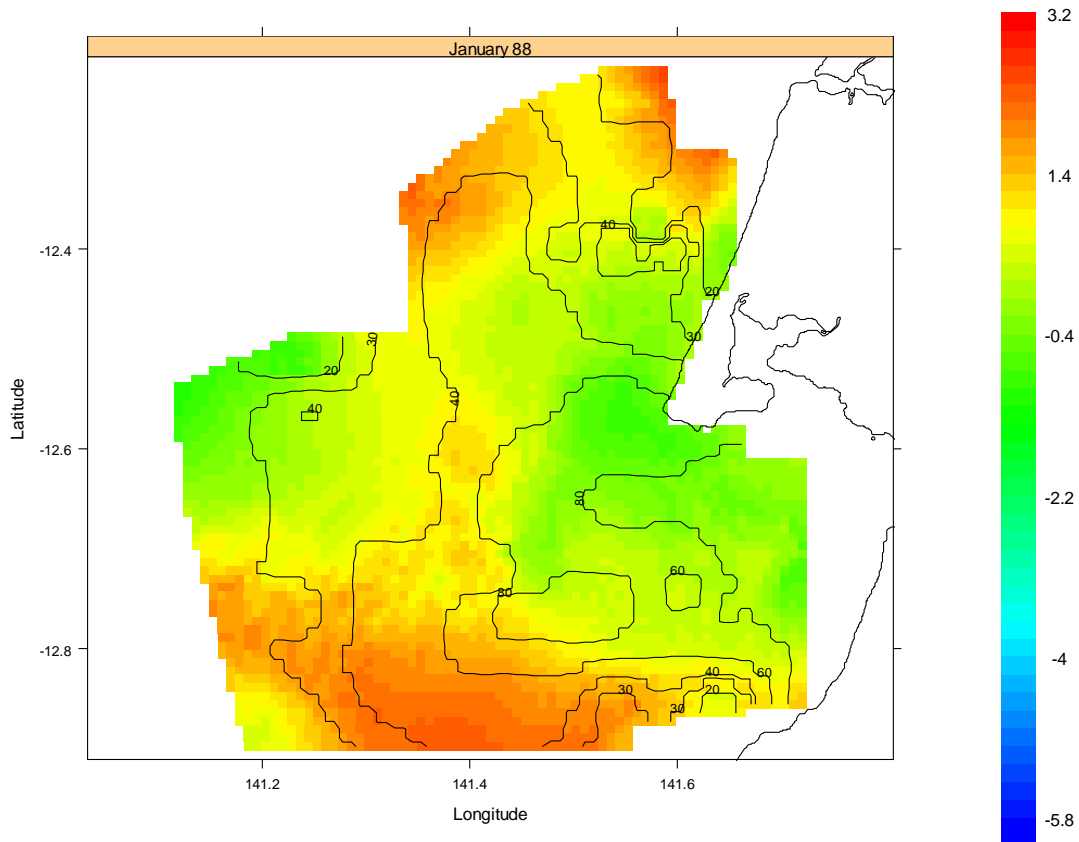
Figure 3.7. Mud contours (% mud) and spatially interpolated log predicted *Penaeus esculentus* counts per hectare in Albatross Bay for January 1988.

Similarly spatial extrapolation can be problematic. A check of Figure 3.9 reveals that it is the same as Figure 3.3, except the spatial prediction area has been extended closer to land. In Figure 3.9 the largest predicted count per hectare is an improbable 8.5 times larger than the largest spatially interpolated predicted count per hectare in Figure 3.3. It is not advisable to extrapolate for any model, but in particular models that include smooth terms or tensor product smooth terms.
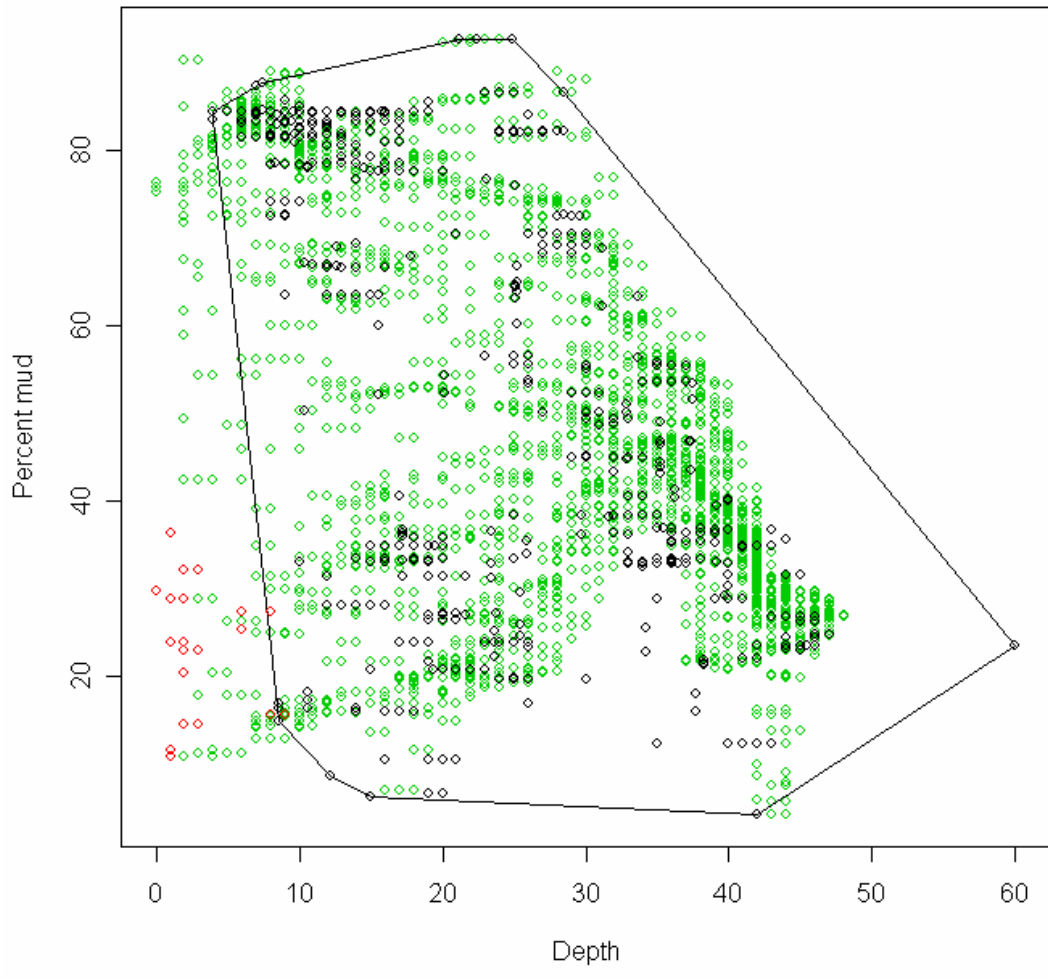
Figure 3.8. The depth and percent mud values for the observations (black) and the depth and percent mud values for the spatially interpolated prediction sites (green and red). The polygon represents the convex hull of the observations and the red points are those prediction sites with predicted catch per hectare values greater than 50.
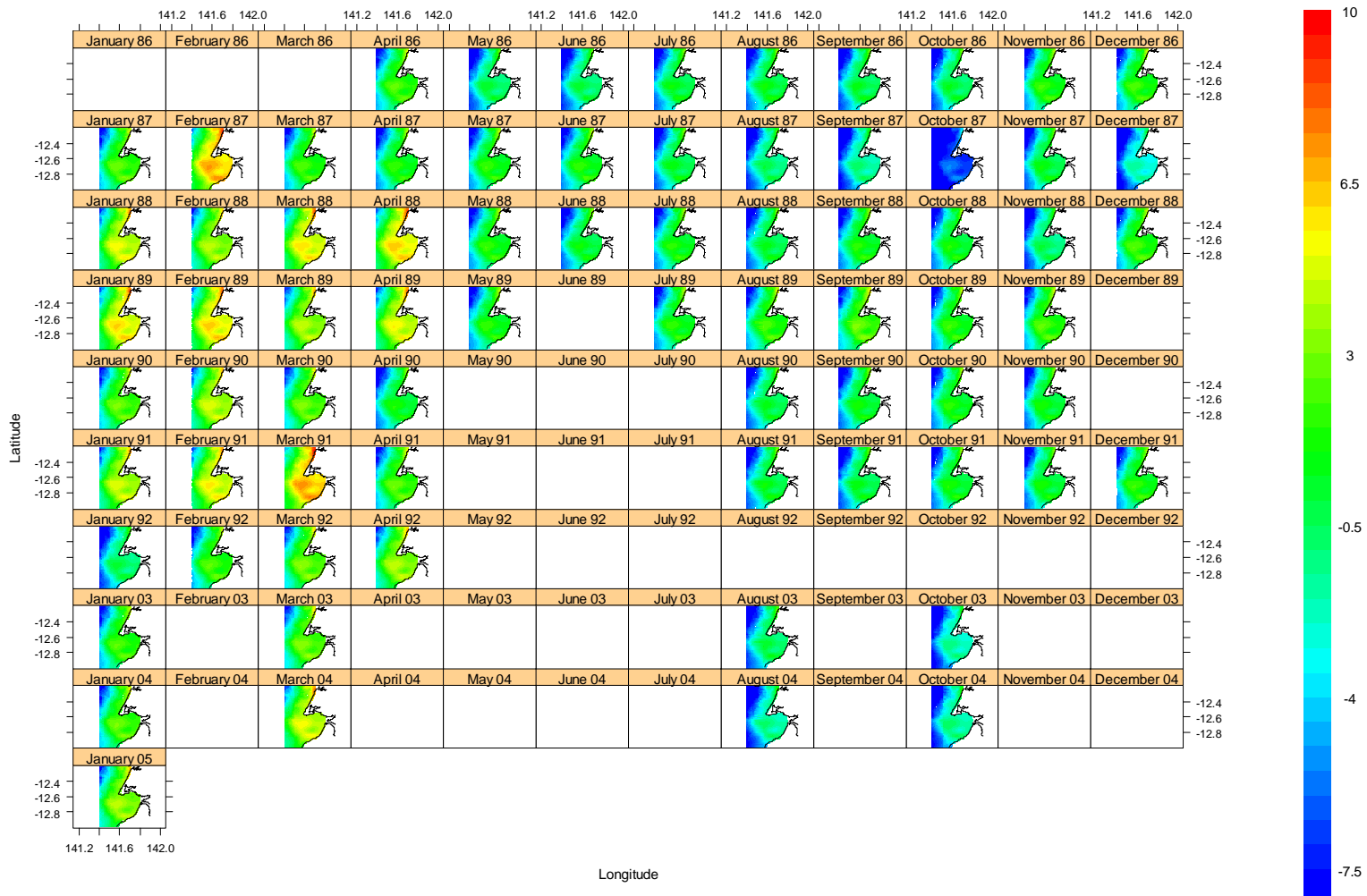
Figure 3.9. Log predicted *Penaeus merguiensis* counts per hectare in Albatross Bay for model (3.5) with spatial extrapolation.

3.5.2 Mornington Island

The analyses for Mornington Island are based exclusively on recent survey data collected between August 2002 and January 2005. This area predominantly consists of tiger prawns, therefore no analyses were undertaken in this region for *Penaeus merguiensis*. Sampling took place west, north and east of Mornington Island (Figure 3.10). For *Penaeus semisulcatus* the analyses are based on the samples west and north of Mornington Island (green and blue coloured sites in Figure 3.10) as virtually no *Penaeus semisulcatus* were caught to the east of Mornington Island. The analyses for *Penaeus esculentus* were based on all three sampling areas.

For the Mornington Island analyses longitude and latitude are not used as location predictors; the use of these predictors often resulted in convergence problems. Rather, RDist and RLand are used. RDist is the distance to the coastline and RLand is the distance of a curve that runs almost parallel to the northern prawn fishery coastline. (For more information on these variables see Venables and Dichmont 2004)

Further, the cosd and sind predictors used for Albatross Bay are not used in the analyses for Mornington Island. This is because the survey data used in the analyses for Mornington Island are collected only three times in a calendar year, around January, March and August and there are only two years of data. Consequently only a very narrow band of the cosd and sind predictor space is covered by the survey data, resulting in unstable predictions that can be markedly different from one day to the next. This problem can be overcome by defining a new variable representing the sampling period within the calendar year as shown in models 3.4 and 3.5.
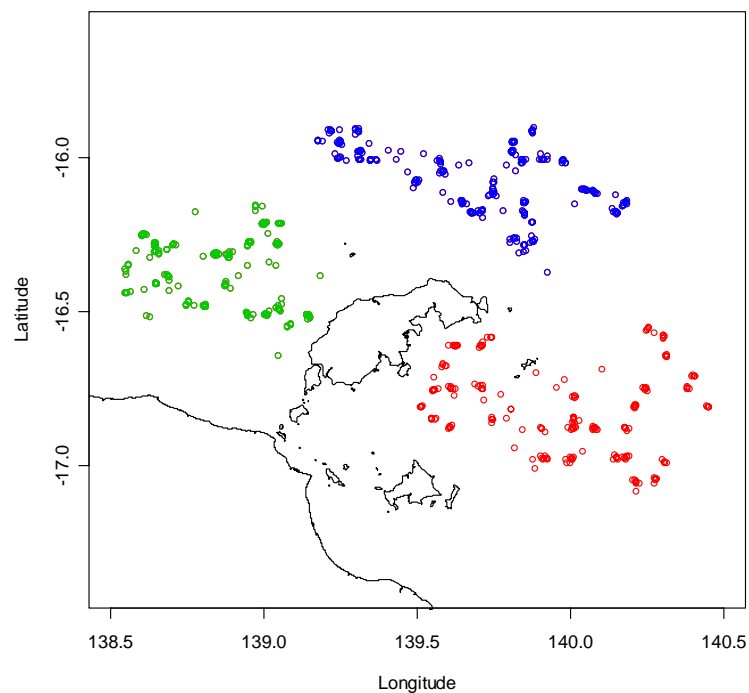

Figure 3.10. Mornington Island sampling sites. Analyses for *Penaeus semisulcatus* include only green and blue sites; analyses for *Penaeus esculentus* include all sites.

3.5.2 a *Penaeus semisulcatus*

The *Penaeus semisulcatus* counts per hectare for the west and north Mornington areas are well described by the over-dispersed Poisson model with linear predictor given in (3.8):

$$g\left(\mu_i\right) = \log\left(\mu_i\right) = \alpha + \log\left(\text{area}_i\right) + s\left(\text{RDist}_i, \text{RLand}_i\right)$$

$$+ \sum_{j=2}^{3} u_{ji}\beta_{1j}^* + \sum_{j=2}^{3} v_{ji}\beta_{2j}^* + \sum_{\substack{j=1 \\ j=k\neq3}}^{3}\sum_{k=1}^{3} u_{ji}v_{ki}s\left(\text{depth}_i\right), \tag{3.8}$$

where the v_i's are as in (3.1) and the u_i's are dummy variables for the time of year, January, March and August. The estimated scale parameter for this model is 4.27, suggesting the data are over-dispersed relative to the Poisson distribution. Model (3.8) explains 79.2% of the total deviance.

The spatially interpolated log predicted *Penaeus semisulcatus* counts per hectare can be found in Figure 3.11. This figure reveals that there is interaction between years and months. For example, in the southern part of the west Mornington prediction area there are very low log prediction counts per hectare in August 2002 and 2004 (the main spawning period) but also some quite high densities in August 2002 close in to the shore of west Mornington Island. These high inshore densities were not seen in the other two years. In August 2003 the log prediction counts per hectare are not as low in this area. On the other hand, there are some large log prediction counts per hectare in the west Mornington prediction area in January 2004 and 2005, while for January 2003 the largest log prediction count per hectare in this area is not nearly as large. In addition, there are large log predicted counts per hectare in both the west and north Mornington areas, however, not always at the same time.

3.5.2.b *Penaeus esculentus*

The over-dispersed Poisson model with the linear predictor, (3.9), is used to model the *Penaeus esculentus* count data in the west, north and east Mornington areas:

$$g\left(\mu_i\right) = \log\left(\mu_i\right) = \alpha + \log\left(\text{area}_i\right)$$

$$+ s\left(\text{RDist}_i, \text{RLand}_i\right) + ts\left(\text{RLand}_i, \text{depth}_i\right) \tag{3.9}$$

$$+ \sum_{j=2}^{3} u_{ji}\beta_{1j}^* + \sum_{j=2}^{3} v_{ji}\beta_{2j}^* + \sum_{\substack{j=1 \\ j=k\neq3}}^{3}\sum_{k=1}^{3} u_{ji}v_{ki}s\left(\text{depth}_i\right),$$

This model accounts for 60.7% of the total deviance, and the estimated scale parameter is 23.23, suggesting that the data are over-dispersed relative to the Poisson distribution.

An examination of Figure 3.12, which plots the spatially interpolated log predicted *Penaeus esculentus* counts per hectare, reveals that at any given time the largest log predicted counts per hectare are in the east Mornington area. There can also be large log predicted counts per hectare in the west Mornington area. However,

there are not too many hotspots of *Penaeus esculentus* catch in the north Mornington area. In August, there are some *Penaeus esculentus* caught in the inshore areas although the densities are lower than in the more offshore areas.
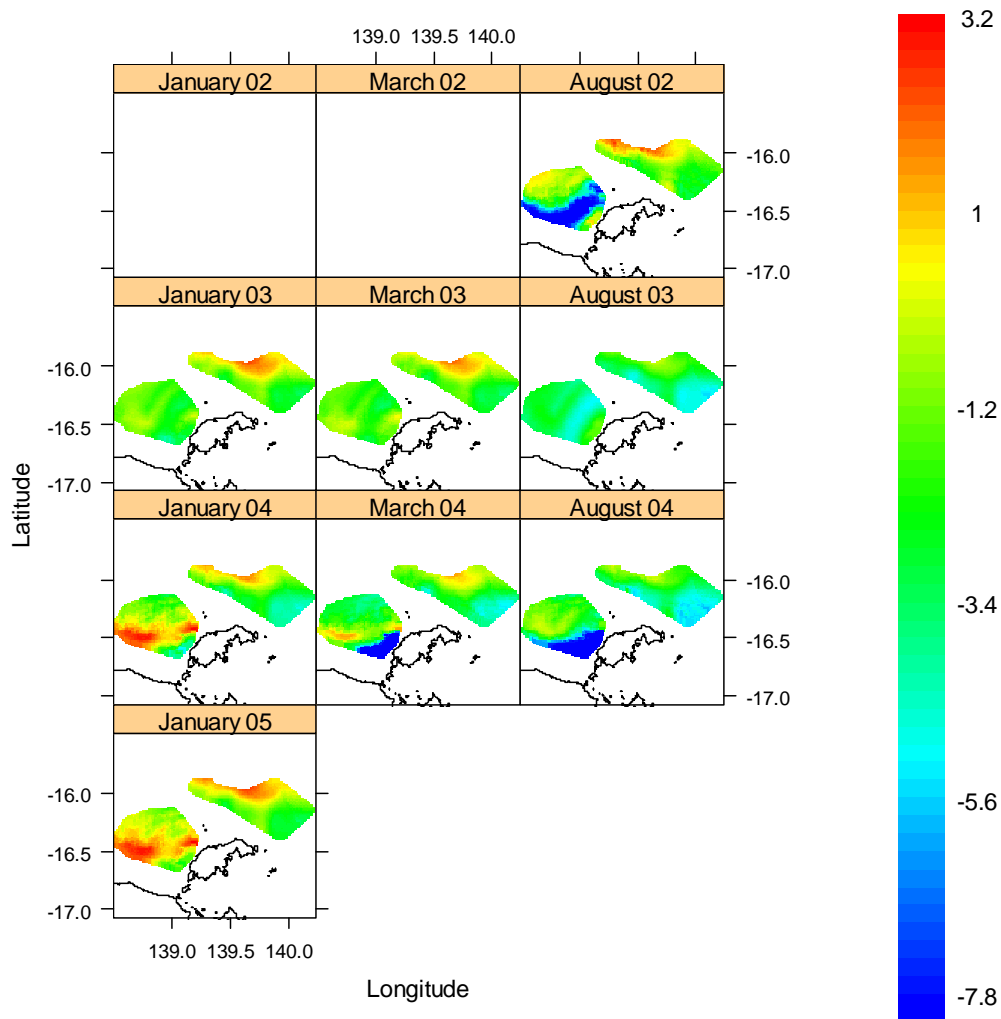
Figure 3.11. Spatially interpolated log predicted *Penaeus semisulcatus* counts per hectare for model (3.8) around Mornington Island.
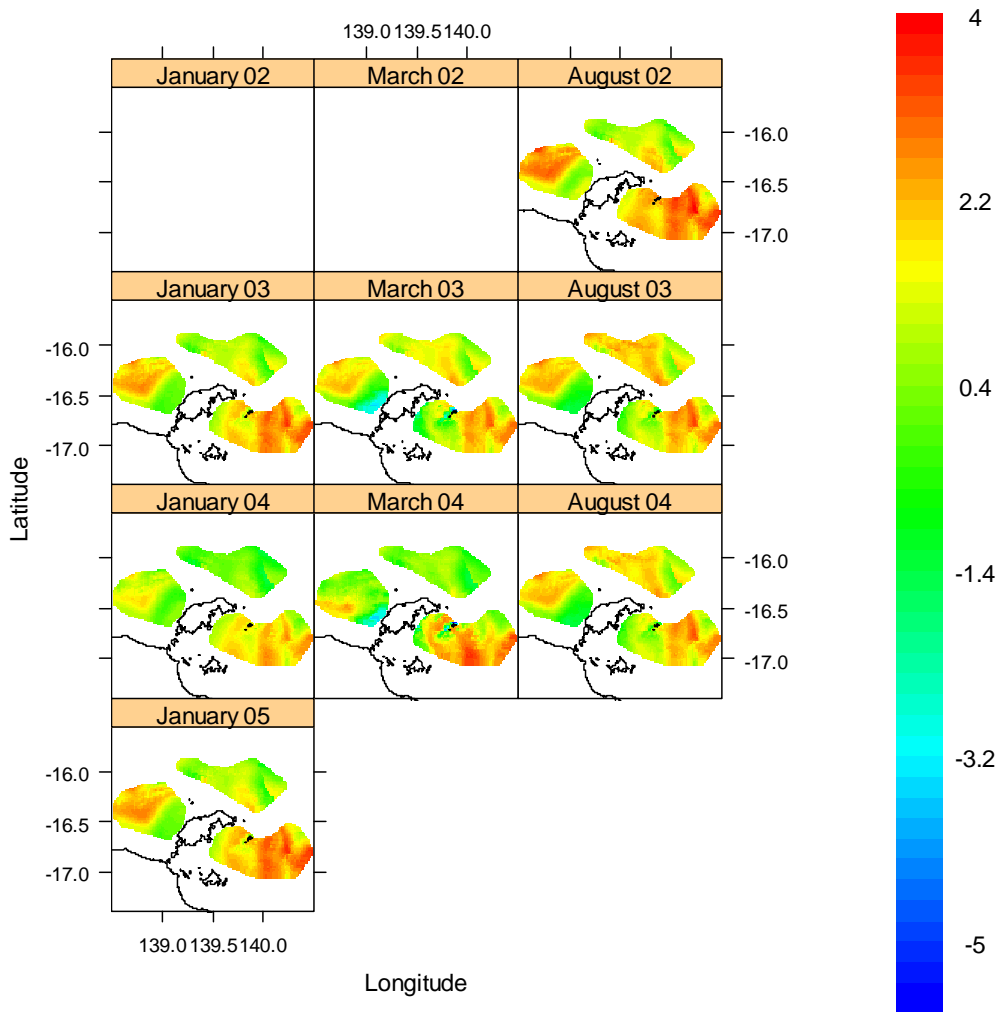
Figure 3.12. Spatially interpolated log predicted *Penaeus esculentus* counts per hectare for model (3.9) around Mornington Island

3.5.3 Karumba

In the Karumba region *Penaeus merguiensis* is the main commercial prawn species fished, consequently analyses are presented only for this species. The analyses incorporate both historical survey data collected between August 1977 and August 1978 (see Crocos and Kerr, 1983) and recent survey data collected between August 2002 and January 2005. The sampling sites are plotted in Figure 3.13, with the green and red sites representing the recent and historical survey sites, respectively.
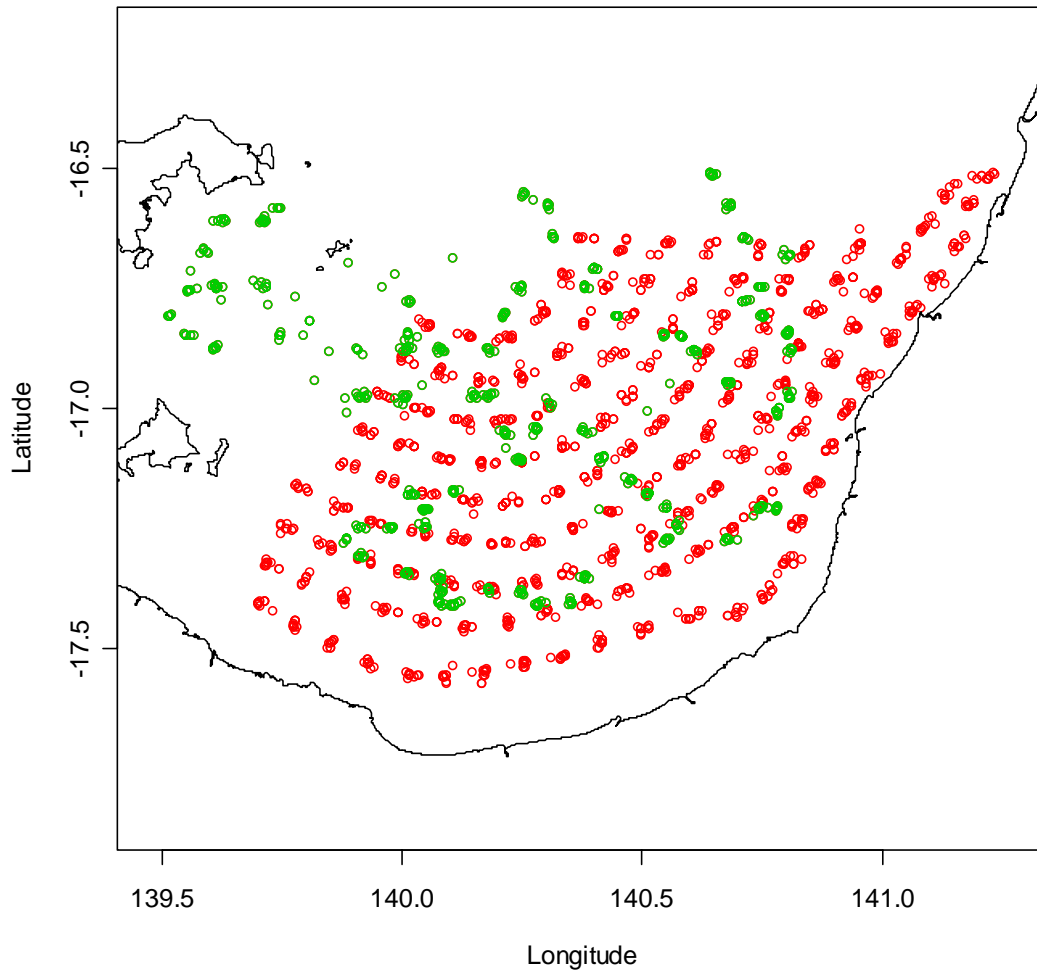
Figure 3.13. Karumba sampling sites for *Penaeus merguiensis* analysis. The red sites are the historical sampling sites and the green are the recent sampling sites.

The log predicted *Penaeus merguiensis* counts per hectare can be found in Figure 3.14. These are generated from the following over-dispersed Poisson GAM model with linear predictor (3.10):

$$g(\mu_i) = \log(\mu_i) = \alpha + \log(\text{area}_i) + s(\text{RDist}_i, \text{RLand}_i)$$

$$+ \sum_{j=2}^{10} v_{ji}\beta_j^* + s(\text{cosd}_i, \text{sind}_i) + ts(\text{cosd}_i, \text{sind}_i, \text{depth}_i)$$

$$+ ts(\text{depth}_i, \text{RDist}_i)$$

$$+ s(\text{rain1.3}_i) + s(\text{rain4.14}_i) + s(\text{rain15.28}_i).$$

$$(3.10)$$

The estimated scale parameter for this model is 22.83, suggesting the data are over-dispersed relative to the Poisson distribution. Model (3.10) accounts for 53.4% of the total deviance.
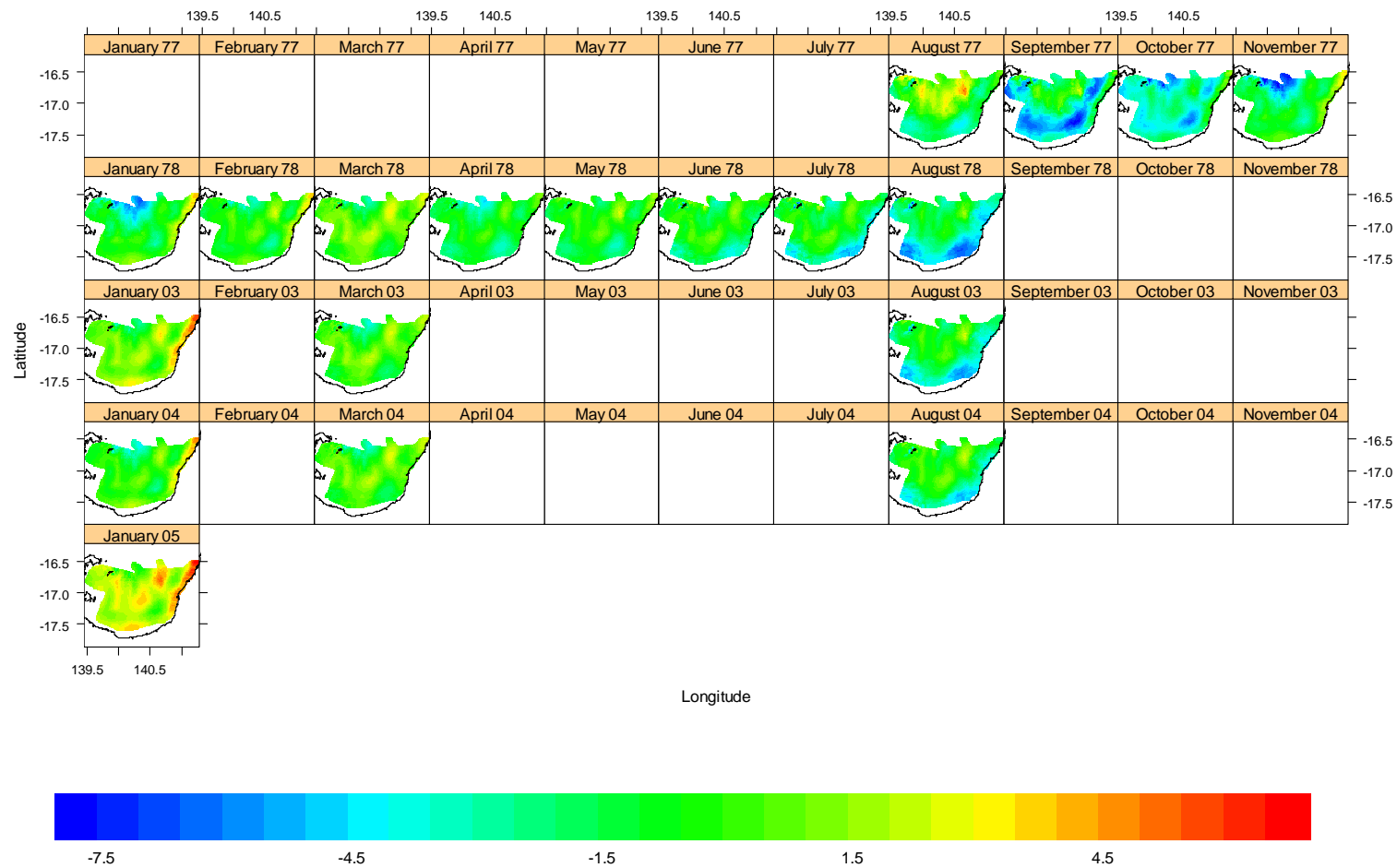
Figure 3.14. Log predicted *Penaeus merguiensis* counts per hectare for model (3.10) in the Karumba region.

The log prediction counts per hectare for model (3.10) can be found in Figure 3.14. The largest log predicted counts per hectare are generally in January, especially during the recent survey period. For January, it appears that there are pockets of areas with relatively high predicted counts per hectare. In August, densities of prawns were lowest in the inshore waters.

The contributions to the linear predictor (3.10) for the rain variables rain1.3, rain4.14 and rain15.28 are plotted in Figure 3.15. For rain1.3 the curve initially increases then drops and increases again. The last increase is based on a small number of observations so should be interpreted with care. Rain4.14 increases nearly linearly, while the curve for rain15.28 marginally increases until approximately 40 mm then declines.
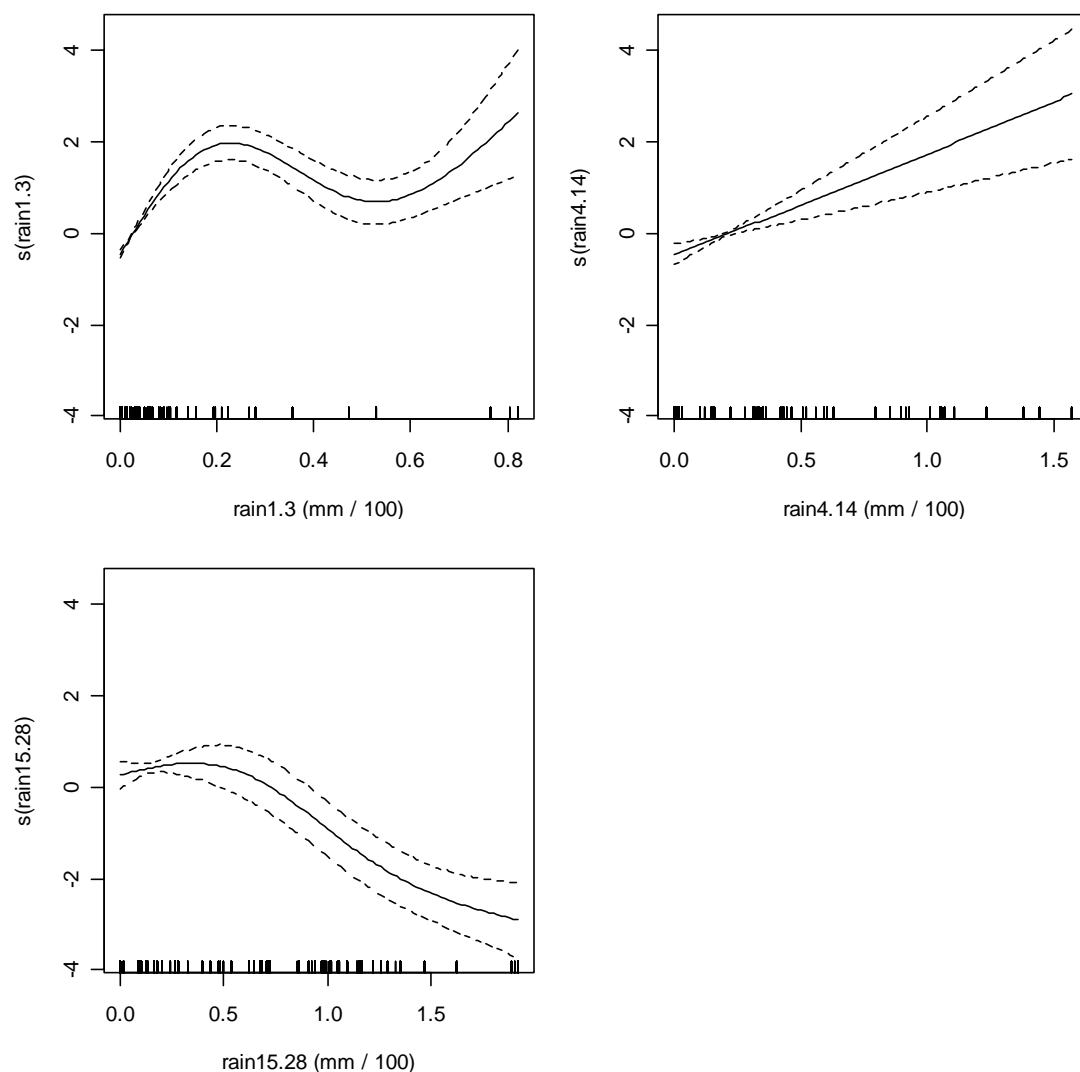
Figure 3.15. The contributions to the linear predictor (3.10) of the smooth terms for rain1.3, rain4.14 and rain4.28 for *Penaeus merguiensis* in Karumba. The dashed lines are the approximate 95% confidence intervals. Tick marks show the locations of the observations.

3.6 Discussion

3.6.1 Rainfall effects

Rainfall variables were significant in many of the models describing the distribution of prawn catch rates for several species and areas. However, in some cases it is difficult to understand the biological mechanism underlying the relationships described by the models.

Short, medium and long term rainfall variables were all significant in models describing *Penaeus merguiensis* distribution in the Albatross Bay and Karumba regions. In the Albatross Bay region, the pattern of short and medium term rainfall contributions to the model were similar, with a positive effect at low rainfall levels, a negative or neutral effect at mid-level rainfalls and a strongly positive effect at higher rainfall levels. Long term rainfall was neutral over most of the range of rainfall values but was slightly positive at higher rainfall levels (Figure 3.2). It is unlikely that the low levels of rainfall recorded in the 1-3 days before a survey would really have any effect on prawn abundances or catchability. High levels of rainfall in the mid and long term rain variables are more likely to have affected the prawn catches, possibly by stimulating prawns to move out of shallow coastal areas into the fishing areas.

At Karumba, mid term rainfall had a positive effect on catch rates throughout the whole range of rain values while the long term rainfall had a negative impact on catch rates at high levels of rainfall. Positive relationships between rainfall and migration of juvenile *Penaeus merguiensis* and between rainfall and commercial prawn catches have been well-described (Staples & Vance 1986, Vance et al. 1998, Vance et al. 1985) so the positive effect of mid term rainfall is not surprising. However, a negative relationship between catch rates and rainfall has not been described before. Previous analyses have not used individual survey catches. It is possible that high levels of rainfall may be associated with storm activity and it is the impact of the storm activity that decreases the catchability of the prawns, either by affecting their behaviour or by affecting the efficiency of the trawl gear.

In Albatross Bay, for both *Penaeus semisulcatus* and *Penaeus esculentus*, the patterns of short and medium term rainfall contributions to the model were similar to those for *Penaeus merguiensis*; a positive effect at low rainfall levels, and a negative effect at mid-level rainfalls. The mechanism for the negative effects at mid-level rainfalls may be similar to that described for *Penaeus merguiensis* at Karumba; high rainfall associated with storm activity and therefore decreased catchability of prawns. For *Penaeus semisulcatus* and *Penaeus esculentus*, rainfall variables were not significant in the models at Mornington Island. This may be because the fishing grounds in this region are much larger distances away from large river systems and therefore there is less impact of rainfall on nursery areas.

The inclusion of the rain variables in the analyses is a surrogate for major rain events and changes in salinity. Readings used at any one time are from a single land based weather recording station, which may not necessarily be close to the nursery habitats. This is not optimal. Ideally rain records would be available for each of the nursery habitats and from water based weather stations, helping to better relate rain events to prawn exodus and migration patterns. Unfortunately currently this is not

possible because of the expense involved. In the future cheap automatic real time sensor networks may make this a reality.

3.6.2 Distribution of prawns during the spawning season

The overall abundance of most species in most areas was lower during the main spawning period (August – October), but the distribution of the prawns is still of importance. In Albatross Bay, there were some signs of slightly higher densities of *Penaeus merguiensis* in the close inshore areas during this period. In particular, during late 1989, densities were much higher in inshore waters than in other years. This coincided with high levels of prawn emigration from the nearby Embley River during the wet season earlier in 1989. However, the increased densities of inshore spawners in late 1989 did not lead to high levels of postlarval and juvenile prawns in the estuarine nursery areas of the Embley River in late 1989 and early 1990 (Vance et al. 1998). It would seem that a high density of inshore spawners, by itself, is not enough to guarantee good recruitment of young to the inshore nursery areas.

Densities of *Penaeus semisulcatus* also seemed to be slightly higher in inshore waters in the last part of the year in Albatross Bay. In particular, densities were highest in late 1989 and this led to high catch rates of *Penaeus semisulcatus* postlarvae on the seagrass nursery areas in the Embley River at the end of 1989 (Vance et al. 1996). There were quite high densities of *Penaeus esculentus* in inshore waters to the south and north of Albatross Bay during August – October in most years, however there is no estuarine postlarval or juvenile prawn data for this species to compare with the adult catches.

In the Mornington Island region, there were large annual variations in the densities of *Penaeus semisulcatus* and *Penaeus esculentus* in close inshore waters, particularly west of Mornington. In Karumba, densities of *Penaeus merguiensis* were relatively low inshore although prawns were caught there.

Larval and postlarval penaeid prawns are advected from their offshore or inshore spawning location to coastal or estuarine nursery grounds by a combination of prevailing water currents and vertical migration behaviour of the larvae and postlarvae (Condie et al. 1999). Initially, larvae respond only to the day/night cycle; they move into the water column at night and descend during the day. By the time they have reached estuaries as postlarvae, they can also cue to tidal cycles and rise into the water column on flood tides but descend to the seabed on ebb tides. Once they have adopted this behaviour they can move inshore to their nursery areas quite rapidly. The maximum distance that larvae can be spawned from the nursery areas and still successfully reach the nursery areas depends on accurate modelling of the water currents, but also involves making some assumptions about when (at what water depth) postlarvae can begin to detect and cue to tidal currents. Condie et al. (1999) published estimates for the effective spawning area for penaeid prawns for several regions of the Gulf of Carpentaria based on a range of assumptions for postlarval behaviour.

Vance & Pendrey (2001) carried out laboratory studies on the response of postlarvae to simulated tidal cycles at simulated water depths and concluded that penaeid postlarvae probably only began to detect tidal cycles after they reached a water depth of between 4 and 8 m. If this is correct then the effective spawning area is

much less than the total area where prawn are caught in the fishery; e.g. less than 30% of the total area for Mornington Island.

The results of the analyses carried out in this project show that there are certainly spawners in the inshore waters at the time of year when the critical spawning happens, although there is little evidence of major congregations of prawns in these inshore regions compared to more offshore waters.

3.6.3 Depth and sediment

Somers (1994) used depth and sediment type, in particular percent mud, to model the species distribution of a number of commercial prawn species for a large part of the Gulf of Carpentaria. In our study, depth was found to be an important predictor for all species and location combinations, however, the use of sediment type predictors such as percent mud is problematic.

Sediment type sample locations for the Gulf of Carpentaria can be found in Hill *et al*. (2002, chapter 3.3). This work reveals that there are no sediment type sample locations in the Mornington Island area where the recent sample surveys have taken place, implying that any sediment type predictions for the three Mornington Island sampling areas cannot be validated. For Karumba there are a small number of sediment type sample locations and not all the region is covered. Consequently percent mud is not considered as a predictor variable for Mornington Island and Karumba.

Hill *et al*. (2002, chapter 3.3) reveals that for Albatross Bay there are a number of sediment type sampling locations, with locations spread across most of the region of interest, thus increasing the appeal of using percent mud as a predictor for this region. For *Penaeus semisulcatus* the incorporation of a smooth term for percent mud into the linear predictor is not statistically significant, while for *Penaeus merguiensis* the inclusion of such a term is marginally not statistically significant (p-value ≈ 0.07).

The inclusion of a smooth term for percent mud was significant in the model for *Penaeus esculentus*. The results suggested that *Penaeus esculentus* was more likely to be found in areas with at least 20% mud and with maximum densities possibly associated with about 40% mud. This agrees with Somers (1994) who found that the highest abundances of *Penaeus esculentus* in the southern and western Gulf of Carpentaria were usually associated with sediments with less than 50% mud. In contrast, catch rates of *Penaeus semisulcatus* were usually associated with sediments containing more than 50% mud.

3.6.4 Periodic variation

The cosd and sind variables in the results section are harmonic terms used to model the yearly periodic nature of prawn behaviour. Ideally these variables would be included in all the analyses. As noted in the results section this is not the case for the Mornington Island analyses because of the lack of year wide coverage. For Albatross Bay in the first three years of the historical survey, sampling took place nearly every month of the year, while for the last three years of the study no sampling took place during the period May to July. This frequent sampling across the years gave good coverage of the parameter space of cosd and sind, improving the stability

of the models that included these terms and even allowed the inclusion of interaction terms with fishing year. For the Karumba region the historical survey data sampling took place twelve times between August 1977 and August 1978, giving reasonable coverage of the parameter space for cosd and sind. The lack of good parameter space coverage over multiple years for cosd and sind, however, means that models that include terms for the interaction of cosd, sind and fishing year are not very stable resulting in convergence problems.

This study has adopted the use of modern statistical methodology to evaluate covariates for the spatial and temporal distribution of prawns and to spatially and temporally predict survey sample prawn catches in Albatross Bay, Karumba and Mornington Island regions of the Gulf of Carpentaria. The methodology allows for flexible functional relationships between the response variable, number of prawns caught, and the covariates. Univariate smooth terms and even smooth terms for interactions between covariates are allowed, thus representing a major advancement on the polynomial methodology employed by Somers (1994) to analyse the spatial distribution of prawns in the Gulf of Carpentaria. It has shown that the models interpolate well between points, but expose any extrapolation beyond the data for that predictor. It shows particularly, that care should be taken with spline and tensor spline terms, where very spurious results can be observed.

Apart from the need for surveys that provide more extensive within-year and between-year coverage, it has become clear that trawling only in water deeper than 7–8m has compromised our knowledge about banana prawn densities in shallow waters (2–7m). Recent research on Queensland's East Coast suggests that increased river flow tends to increase offshore migration and enhance catchability in offshore otter trawls rather than increase the size of the recruiting population per se (Tanimoto et al., 2006).

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CHAPTER 4: PREDICTING POSTLARVAL SETTLEMENT IN ESTUARINE HABITAT FROM OFFSHORE SPAWNERS VIA A LARVAL ADVECTION MODEL

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4.1 Abstract

A fundamental feature of stock assessment models is the stock-recruitment relationship, which has proven highly variable in many commercial fisheries. In Australia's Northern Prawn Fishery, the short lifecycle of the prawns and the spring pulse in spawning should result in a well-defined stock-recruitment relationship. However, this has proven particularly elusive for the common banana prawn, *P. merguiensis*, and it appears that the tiger prawn species are over-fished despite a long history of management supported by a significant body of research on these prawn species. One explanation may be that only a subset of the spawning stock contributes effectively to next year's recruits. It is known that postlarvae are transported from offshore spawning areas to coastal nursery habitat by rising in the water column on flood tides and remaining on the bottom otherwise, but only when they find themselves in water shallower than a transition depth. In deeper water they exhibit a diurnal vertical migration unrelated to tides that generally leaves them offshore outside the 'advection envelope'. We have used offshore trawl surveys of three commercial species (*P. merguiensis*, *P. semisulcatus* and *P. esculentus*) to model density of nauplii and then linked this with a larval advection model coupled with location-based survival and travel time to (a) determine the locations where spawning is most effective and (b) estimate the total number of month-old postlarvae arriving in estuaries of Albatross Bay. We have compared the effect of two transition depths (7m and 15m) on the number of postlarvae that successfully settle and found that the effects vary considerably among the three species due to the differences in spatial distribution of adult spawners. The peak density of *P. merguiensis* in shallow waters (<10m) ensures successful advection of larvae in Albatross Bay at both transition depths, producing 300-400 small juveniles per spawner. In contrast, the offshore peaks in spawner density of both *P. semisulcatus* and *P. esculentus* imply that far fewer larvae reach the estuaries (ratios of ~70 and ~30 respectively for 15m transition depth). The numbers drop to a tenth of this for the 7m transition depth, which may partly explain the relative abundance of these species in the Albatross Bay region. For the period 1986-1992, we compared the new effective spawner index with density of small juvenile *P. semisulcatus* and *P. merguiensis* juveniles in nursery habitat. The new index appears to set an upper limit on recruitment to nursery habitat, but other environmental factors not incorporated in the model appear to reduce the actual number arriving and settling. These findings are not mature enough to lead to an improved stock-recruitment model at this stage for all three species. Further modeling is needed to reach firmer conclusions. However, since *P. merguiensis* densities peaked in waters mainly shallower than the given transition depths, this is probably not the main determinant of the stock-recruitment relationship for this species.

4.2 Introduction

Knowledge of the relationship between spawning stock size and the subsequent recruitment of the next generation of adults to a fishery is of great importance to managers. For example, many of the fishery reference points (e.g. Caddy and Mahon 1995) and therefore long-term objectives are based on the stock-recruitment relationship. In the Northern Prawn Fishery (NPF) in Australia it has traditionally been accepted that all the adults present in the fishery at the appropriate time of year are part of the spawning population. However, this paradigm has increasingly been challenged in recent years; Crocos & van der Velde (1995) discussed the concept of "effective spawning" area in the context of the NPF. Genetic studies have also shown that only a very small part of the population successfully contributes to the next generation (Ovenden, 2005). "Effective spawning" means that only the larvae released from the inshore component of the spawning are able to reach nursery grounds. This successful region is called the "effective spawning area".

The main commercial penaeid prawn species in the NPF have a life cycle that involves the adults spawning in offshore waters, after which, the larvae and postlarvae move inshore. After several months in estuarine or coastal nursery areas, the juveniles and subadults move offshore again and become the next year's fishing stock. Although the young larvae and postlarvae have very limited swimming power, Rothlisberg et al. (1983) initially demonstrated that vertical migration behaviour of the larvae combined with prevailing currents could allow the larvae to be advected towards the coastline. Penaeid larvae in the Gulf of Carpentaria were observed to move up into the water column at night and moved down towards the seabed during the day when in 20 m of water.

Field studies by Staples & Vance (1985) found that the vertical migration behaviour of postlarval *Penaeus merguiensis* when they reached the estuaries was actually cued to the tidal cycle rather than just the day-night cycle. Postlarvae moved upwards in the water column during the flood tides and descended to the seabed on ebb tides, and therefore were moved quickly inshore and upstream by tidal currents.

Further studies that included hydrodynamic modeling by Rothlisberg et al. (1996) and Condie et al. (1999) made some allowance for the fact that the vertical migration behaviour of larvae/postlarvae changes from being cued to the day-night cycle when in offshore waters to being cued to the tidal cycle when they reached estuaries. However, they were unable to reach a firm conclusion on effective spawning areas because they had no information on what depth the larvae or postlarvae began to respond to the tidal cycles. They presented several options for effective spawning areas in the main fishing regions of the Gulf of Carpentaria using different assumptions for the transition depth; i.e. the depth at which postlarvae can begin to detect tidal cycles.

Recent laboratory studies by Vance & Pendrey (2001) have shown that this transition depth is likely to be less than 8 m of water depth. This means that the effective spawning area would be at the lower end of the range of effective spawning areas defined by Condie et al. (1999). In fact, most of the effective spawning would comprise of prawns that occur quite close inshore.

In this paper, we have combined data from several sources in an attempt to refine the results of Condie et al. (1999) and more accurately define the areas of effective spawning in the NPF. We have used results from the hydrodynamic modeling of Condie et al. (1999). We have reanalyzed data collected from six years (1986-1992) of offshore trawl surveys in Albatross Bay, Weipa (Crocos & van der Velde 1995) and we have used the results of postlarval prawn surveys carried out in estuaries at Weipa over the same six-year period (Vance et al. 1996 1998).

4.3 Methods

4.3.1 Outline

Our concept of effective spawning is that the currents and tides that prevail during the first month of life of a prawn larva will determine whether or not it can reach and settle in nursery habitat by the time it is about 30 days old. This is a critical step in the life-cycle of a prawn, and it could be expected to have a strong influence on the number of recruits to the fishery the following year.

We have combined two main components in constructing an effective spawning index:

- a model of the spatial distribution (density) of day-old nauplii, derived from size and density of females observed in trawl surveys of the Albatross Bay region, as fecundity is related to size (Crocos and van der Velde, 1995); and

- a model of the probability of a larva being able to reach nursery habitat, given the location where it is spawned; the currents and tides that prevail during the first month of its life; and its own response to the diurnal cycle and the depth and movement of water.

We have also constructed an index of spawners based on spatial modelling of the density of ripe prawns, which ignores the role played in larval advection by the currents and tides.

We have compared both indices with densities of small juvenile prawns found in nursery habitat in the Mission and Embley rivers 30 days after the trawl survey. This was feasible for the period 1986 to 1992 as both offshore trawl surveys (Crocos & van der Velde, 1995) and estuarine surveys (Vance et al; 1996 & 1998) were carried out over this six-year period.

4.3.2 Fieldwork methods, and standardisation

Offshore trawl data came from two major studies in the Albatross Bay region near Weipa that carried out night-time trawl surveys around new moon, but with differences in trawl gear, spatial coverage, temporal coverage and methods of selecting sample sites. Spawning in the second half of the year contributes most to recruitment the following year (Crocos & van der Velde, 1995), so we restricted our analysis to the months of July through to December.

During the first study (March 1986 to March 1992—Crocos & van der Velde, 1995), sites were based on the 6 n.mile grid used for reporting commercial catch and effort data. From 1989, the intensity of trawling in each grid was increased to two or three trawls in the second phase of that six-year study. In the last year or so, the area covered by trawls was extended westwards to the deepest part of the Gulf to monitor

winter migration of *P. semisulcatus*. Sampling was monthly, in phase with the lunar cycle so that the survey was centred on new moon to ensure greatest and consistent catchability. Some winter months were dropped in later years. Most surveys used four 9m (headrope length) nets, generally towed for 15 minutes at 3.2 knots.

For surveys in 2003 and 2004, we defined a sampling frame based on 2 n.mile grid units (Dichmont et al, 2003), partitioning the Albatross Bay region into four strata (north/south; deep/shallow). From this sampling frame, locations were chosen from two random sets such that roughly 10 trawls could be carried out per night and longer distances reserved for daytime travel. The same suite of sites was visited during all surveys, with some additional sites in 2004 as surveys became more efficient. Surveys were carried out in January, March, August and October. In January, March and August, trawls covered the South East Gulf as well as Albatross Bay, using two 12 fathom (headrope length) nets. In October, during the fishing season, we chartered a smaller vessel with two 6 fathom nets. The target towing speed was 3.2 knots, with an intended duration of 30 minutes. Speed, duration and location of trawling were recorded using GPS and SeaPlot.

In order to ensure consistency of prediction over time, we defined a common prediction region that was adequately sampled by both studies (Figure 4.1), and retained only those sites inside this region. Sample size for each survey ranged from 16–37 in the 1986–1992 surveys and 25–35 in recent surveys (Table 4.1). The common prediction region excluded the western transects of the six-year study and six sites in the south-western part of the recent study. We augmented the inner area to a depth of 3m (lowest astronomical tide) using a Geosciences Australia bathymetry dataset. Estimated area swept by each trawl for historical surveys was calculated from trawl duration, speed, total headrope length and an assumed net opening of 70%. For recent surveys, the separation between start/end positions was generally used, unless the trawl path was curved. This was used in conjunction with sampling fraction for each species to standardize catch.
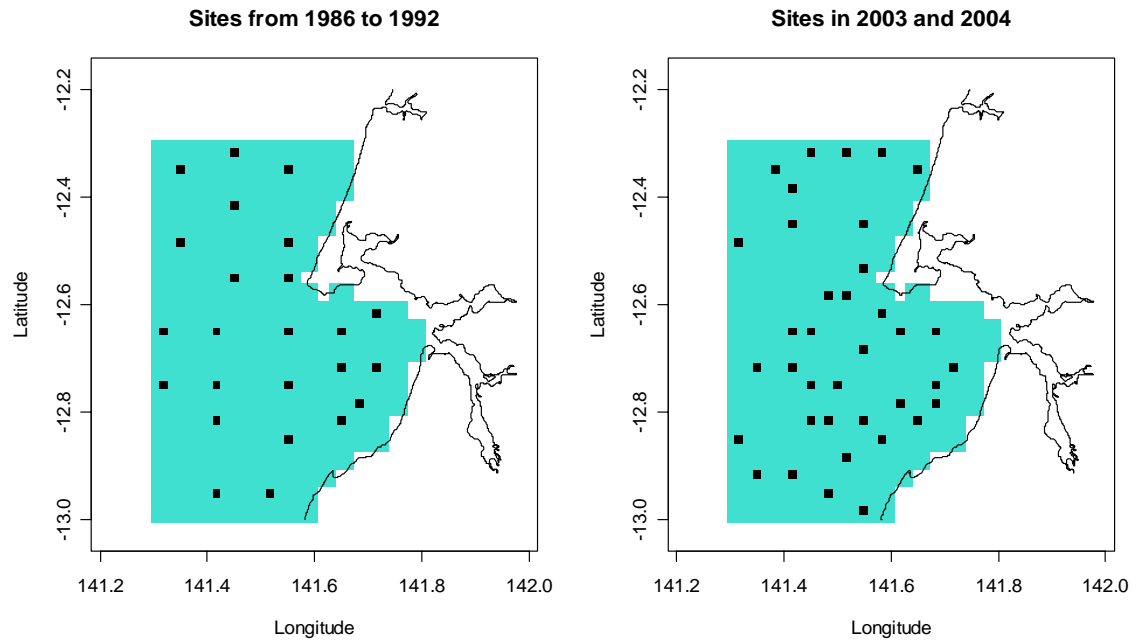
Figure 4.1: Locations of sites (black squares) trawled during the Albatross Bay study (1986-1992) and more recently (2003 and 2004), with the composite prediction region (turquoise shading).

Table 4.1: Number of trawls within the combined prediction frame.

Year	July	August	September	October	November	December
1986	22	18	22	22	22	21
1987	23	22	22	23	24	23
1988	27	37	37	35	36	22
1989	33	34	37	34	34	0
1990	0	36	35	36	16	0
1991	0	36	15	35	34	25
2003	0	26	0	25	0	0
2004	35	0	0	34	0	0

4.3.3 Time for larvae to reach the coast, and location of arrival

Larval advection files from the research reported in Condie et al. (1999) for all months in 1986 and for October 1990 were kindly supplied by Scott Condie. Those for 1986 applied a transition depth of 15m, while those for October 1990 also applied a transition depth of 7m, which we consider to be more realistic in the light of laboratory experiments carried out by Vance and Pendrey (2001).

For each month, particles were initially seeded on a 5 km grid over the whole of the Gulf of Carpentaria. We focused on the area around Albatross Bay. The movement of each particle was modeled according to a hydrodynamic model incorporating currents and tides, and a model of larval behaviour. This model assumes the larva migrates vertically on a diurnal pattern until it is eight days old, when it cues into the flood tide if it is in water shallower than the transition depth. This model is probably rather optimistic, in that larvae are assumed to become postlarvae (with some swimming ability) within eight days and to cue into all flood tides, day and night, whereas Vance and Pendrey (2001) observed peaks in the marine environment only on the flood tide.

The position of each particle was tracked over a period of 38 days, positional data having been output at the start, then daily from the ninth day. We retrieved the positional data every 3rd day from the start of the 12th, and geo-referenced this with the Geoscience Australia bathymetry dataset to obtain water depth (lowest astronomical tide) at that position. By day 34 those particles that could reach the coast (locations with lowest astronomical tide of 1m or less) had already done so.

Motivated by the need to convert all 1986 results to a 7m transition depth, we modelled the proportion of particles that had arrived with each of four time periods (1–15 days, 16–24 days, 25–33 days, and >33 days) as a function of depth at the initial location, using proportional odds logistic regression.

Treating arrival interval as a four-level ordinal response variable, proportional odds logistic regression (POLR) was fitted to water depth (lowest astronomical tide) at the initial position for each 'larva' particle (Venables and Ripley, 2004; R Development Core Team, 2005). For numerical stability, depth was centred on 40m and the difference expressed in 10m units. The proportional odds model was:

$$\log(\pi_{k,i} / (1 - \pi_{k,i})) = \varsigma_k - \beta d_i \qquad (1)$$

where d_i is the standardised initial water depth for the i'th particle;

$k=1$ for arrival within 15 days, $k=2$ for arrival in 16–24 days, $k=3$ for arrival in 25–33 days, and $k=4$ for arrival after 33 days;

ς_k is the water depth at which 50 percent of particles have arrived by the end of the k'th time interval ($\varsigma_4 = \infty$); and

β is the rate of increase in the log-odds ratio in relation to depth.

This then enabled us to predict arrival times from arbitrary locations in the Albatross Bay region, which would be needed in order to use the spawning survey data.

We also wished to determine whether a larva spawned in an arbitrary location could not only reach the coast, but also arrive close to the rivers that flow into

Albatross Bay (Pine River, Mission River and Embley River) as this is where mangrove nursery habitat is available for banana prawns and seagrass habitat is available for tiger prawns. Coastline with suitable habitat was defined by locations with a lowest astronomical tide of less than 3m, no further than 0.36° from a central point with longitude 141.96°E and latitude 12.64°S.

There is a highly non-linear relationship between the location of particles after 33 days and their initial location, due to the combination of the hydrodynamics and the shape of the coastline in Albatross Bay. Rather than model this relationship directly, we identified close neighbours at the larva's start location and carried out a weighted average of the location of these neighbours after 33 days. The neighbours consisted of particles within 0.07° of the larva's start location and the weight was the reciprocal of the 6th root of the distance between the particle and the larva. This choice of neighbourhood size and weights produced the most sensible final location for particles 'seeded' in the 2 n.mile cells of the prediction region shown in Figure 4.1.

4.3.4 Conversion of larval advection models with 15m transition depth to 7m transition depth

Condie et al. (1999) applied a 15m transition depth to all months and only applied a 7m transition depth to October 1990. Subsequent experimental results of Vance & Pendrey (2001) support the 7m model rather than the 15m model for common banana prawns. Resources were unavailable to re-run the hydrodynamic models for 7m transition depth, so we used a statistical modeling approach to convert the 15m results to 7m, based on the two sets of results from October 1990. The larval advection patterns were seen to vary substantially over the course of a year, but not much between years, so we postulate that a conversion based on one month will capture the main features of the full hydrodynamic model.

4.3.5 Probability larvae have settled in nursery habitat by 34 days of age

Weekly mortality rates of larvae offshore are high (70% per week according to Dall et al, 1990). The highest survival of *P. merguiensis* nauplii over a 4-day period was 70% during feeding and survival experiments conducted in 10m water depth in Albatross Bay (Preston, 1992).

Weekly mortality appeared to decrease with prawn size for *P. merguiensis* in estuaries of Albatross Bay: from 89% for 2 mm carapace length postlarvae to 2% for 15mm CL juveniles (Wang and Haywood, 1999). Assuming constant mortality, O'Brien (1994) had observed 20% mortality of *P. esculentus* in coastal seagrass habitat in Moreton Bay, south-east Queensland.

In laboratory experiments, Liu & Loneragan (1997) documented the growth of *P. semisulcatus* from hatching to juveniles of 3–4 mm and monitored their movements in tanks that were partitioned into seagrass and bare sand. Postlarvae with a carapace length of up to 1.6 mm (22 days old) showed no preference for seagrass and tended to swim rather than settle on the substratum or perch on the seagrass. In contrast, the larger postlarvae and small juveniles were mostly found either on the substratum or perched on seagrass, with densities 50%–200% higher in seagrass than on bare sand during the day.

We modelled the probability that a larva would arrive in nursery habitat, settle and survive to 34 days of age, starting with a daily mortality of 20% offshore,

decreasing to 10% in the estuary and 3% once settled in nursery habitat. We required the postlarvae to be at least 22 days old and to have spent at least one day in the vicinity of nursery habitat before settling.

4.3.6 Spatial distribution of nauplii and spawners, and comparison with juvenile densities in estuaries

The spawning rate and number of nauplii that successfully hatch were found in laboratory experiments to be related to the size of the spawning female for wild *P. semisulcatus* broodstock that spawned in an aquaculture facility (Crocos & Coman; 1997). The peak nauplius production rate was ~37000 per female per month for prawns 43 mm in carapace length, up from ~11000 for 36 mm prawns and down to ~26000 for 45 mm prawns. Previously Crocos (1987a) found the smallest mature *P. semisulcatus* in trawls from the western Gulf had a carapace length of 29 mm.

To characterise the relationship between carapace length and nauplius production rate, we used an asymmetric curve, which rises steeply and falls slowly, as follows:

$$N_{nauplius} = 37000 \times \exp\left\{ -\left(\frac{l - l_{peak}}{\sigma_l} \right)^2 \right\} \qquad (2)$$

where $N_{nauplius}$ is the expected number of nauplii produced by a female

of carapace length l, given that the peak production rate occurs at l_{peak};

$\sigma_l = \sigma_{low}$ when $l < l_{peak}$ and $\sigma_l = \sigma_{high}$ when $l \geq l_{peak}$;

$\sigma_{low} = (l_{peak} - l_{min})/2.5$ and $\sigma_{high} = l_{peak} - l_{min}$;

where l_{min} is the carapace length of the smallest mature female.

The same model was used for *P. esculentus* (minimum carapace length of 25 mm at maturity; Crocos, 1987b), with a peak length set to 38 mm. Likewise for *P. merguiensis* (minimum carapace length of 23 mm at maturity; Crocos and Kerr, 1983), for which the peak length was set to 35 mm. Using this equation, each female of a given species in a trawl was converted to the number of nauplii she could be expected to produce that month, and the resulting nauplius production rates were summed over all measured females for that trawl. At the same time, a more traditional measure of spawning activity was obtained by counting the females with ovaries in stage III or IV.

We fitted a variety of generalized additive models involving splines in depth and latitude combined with linear terms for timing of survey, using the mgcv package in R (Wood, 2000; R Development Core Team, 2005) to both nauplius count and spawner count. We chose to model the counts as negative binomial, to handle zero inflation and high dispersion. The variance, σ^2, is proportional to the mean, μ, via the equation $\sigma^2 = \mu + \mu^2/\theta$. Nauplius count was expressed in units of 10,000, reflecting the actual number of independent observations (females) that produced this count. We used a log link and an offset consisting of the area swept by that trawl multiplied by the fraction of that species measured relative to the total caught.

For banana prawns (*P. merguiensis*), we restricted model-fitting to sites shallower than 30m since they were never found beyond this depth in the Albatross Bay area (leaving 816 trawls out of 1018). For the two tiger prawn species, we restricted model-fitting to sites shallower than 40m (dropping 10 trawls).

4.3.7 Effective spawner index, and comparison with juvenile densities in estuaries

The next step in evaluating an index of effective spawning was to multiply the density of nauplii spawned at a given location by the probability they would arrive and settle in estuarine nursery habitat by 34 days of age. This yields the density of successful 34-day-old postlarvae (PL34) that will emanate from each 2 n.mile grid. Taking account of the area in each grid, this can be converted to a total number per grid and then summed over all grids to produce a 'PL34' index.

A spawner index was also evaluated, by converting the density in each grid to a total number and summing over all grids. The 'PL34' index was regressed on the spawner index for all 36 surveys, yielding a ratio of the number of small benthic juveniles successfully produced by each spawner.

Juvenile prawns with carapace length 3–4mm were extracted from data collected in two estuarine studies (Vance et al, 1996 & 1998) and their density 30 days after the mid-date of each offshore trawl survey was evaluated. The 'PL34' index and the spawner index were compared with the juvenile index.
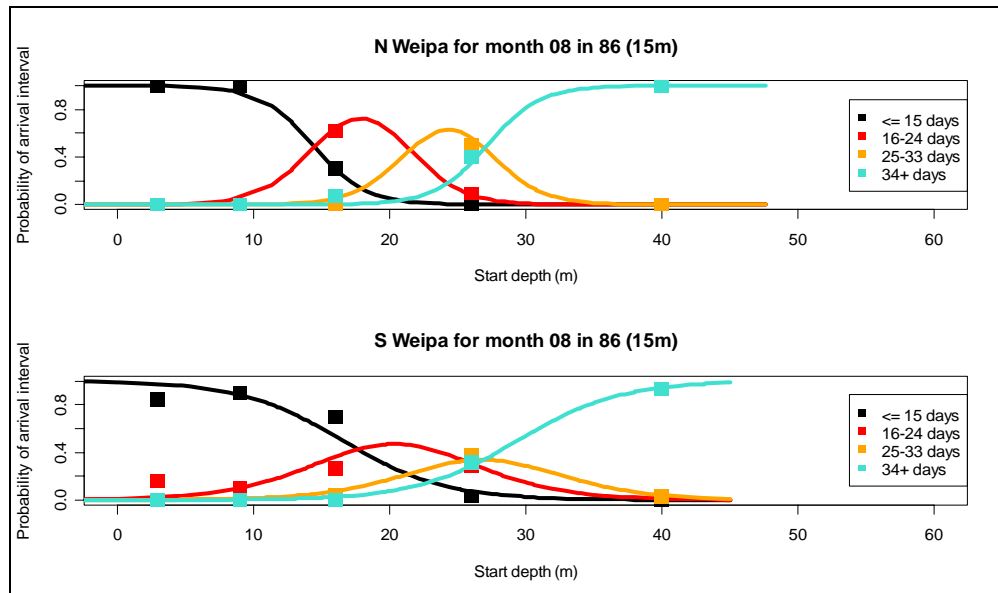
4.4 Results

4.4.1 Time for larvae to reach the coast, and location of arrival

Figure 4.2 shows the results of fitting POLR to individual arrival times (smooth curves) for larvae that start in the Albatross Bay region during the months of August and October 1986, with a transition depth of 15m. Also plotted are the observed proportions of larvae arriving within each time interval. Larvae were grouped according to starting depth, the average depth for each group being shown on the x-axis. Given the shape of the coastline around Albatross Bay, we obtained better results when we split the region at latitude 12.6°S and fitted a separate model to the northern and southern sectors. The slope for the southern sector was markedly shallower than that for the northern sector: 4.16 for the southern sector in both months compared with 5.18 and 5.40 for August and October in the northern sector.

For both sectors (in August and October), the probability of arriving at the coast within the first 15 days (black curve) was 90% or more when the larva is spawned in less than 10m of water. This probability dropped close to zero for larvae spawning in 20m of water in the northern sector, compared with 30% for the southern sector. The difference is also apparent for larvae that had not reached the coast by the 33rd day — more than 80% of those in water deeper than 30m in the northern sector compared with 60% or more for those in the southern sector. In the southern sector in August, in water 2m deeper than in October, larvae have the same probability of arrival. This is particularly noticeable for those that arrive in 16–24 days (red curve). In the northern sector, the main difference between August and October is the increase in probability of arrival in 16–24 days compared with 25–33 days (yellow curve).

Figure 4.3 shows the initial location of those particles that reached estuaries in Albatross Bay (red squares), and their final location. Larval advection carried

unsuccessful larvae much further south in October, and the advection envelope for successful larvae extended further west in August than October. In both months, some larvae in shallow waters north of Duyfken Point were advected into the Bay. Prawns outside the advection envelope are considered unable to reach suitable nursery habitat, and given a zero probability of survival.
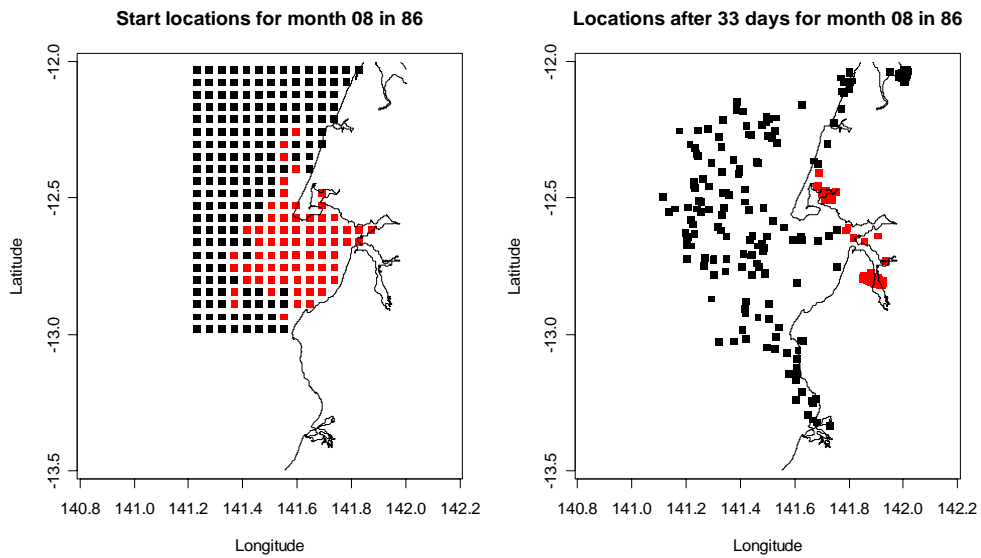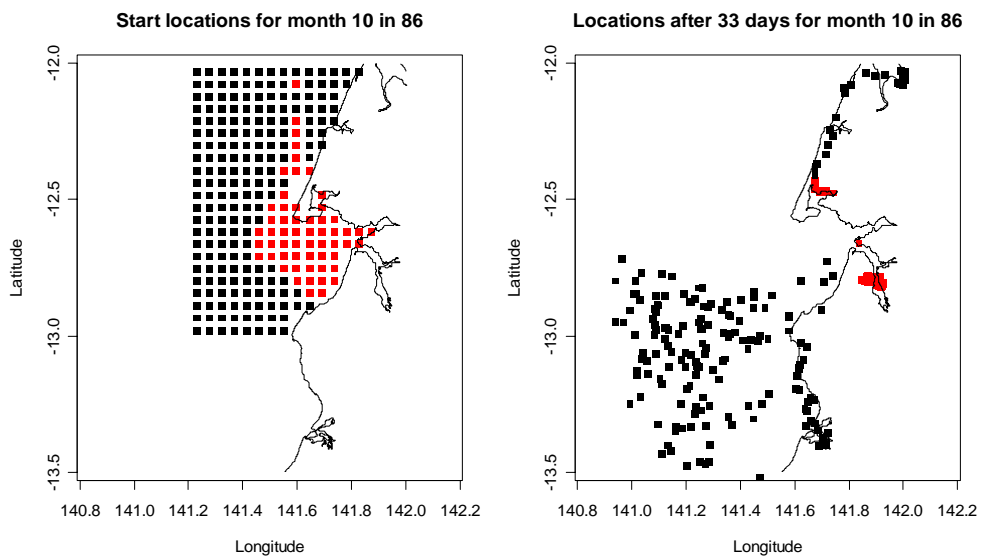

(a)
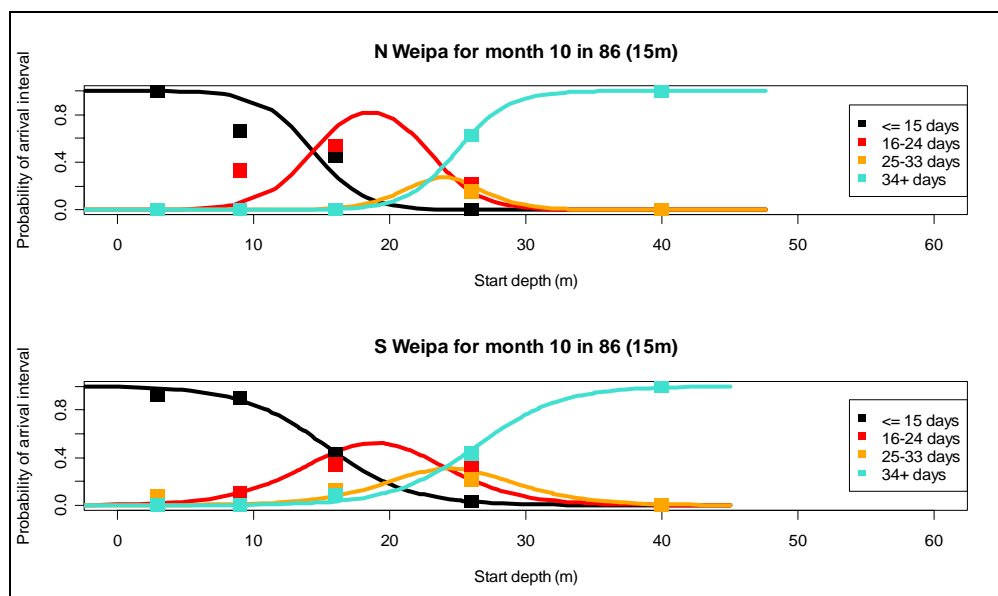
(b)

Figure 4.2: Results of fitting proportional odds logistic regression (POLR) to the final location of particles in the hydrodynamic advection model, separately for a) northern and b) southern sectors of the Albatross Bay region in the months of August and October 1986. The transition depth was 15m.

Start locations for month 08 in 86

Locations after 33 days for month 08 in 86

(a)

Start locations for month 10 in 86

Locations after 33 days for month 10 in 86

(b)

Figure 4.3: Start (left) and final (right) locations of particles in (a) August and (b) October 1986, red squares indicating those that arrive at estuaries which contain the key nursery habitats in Albatross Bay.

4.4.2 Conversion of larval advection models with 15m transition depth to 7m transition depth

Figure 4.4 shows POLR for individual arrival times in October 1990, with transition depths of both 15m and 7m. The probability of arriving within 15 days, 24 days, 33 days and unlimited days is also shown, indicating the depth at which 50% of larvae will have arrived within the given interval. For example, when the transition depth was set to 15m, 50% of larvae spawned in water shallower than 23m in the

southern sector took less than 25 days to reach the coast (red curve). In that month, 50% of larvae spawned in water up to 26m deep in the northern sector reached the coast in less than 25 days. Once the transition depth was reduced to 7m, the relevant depths decreased to 17m and 23m respectively.
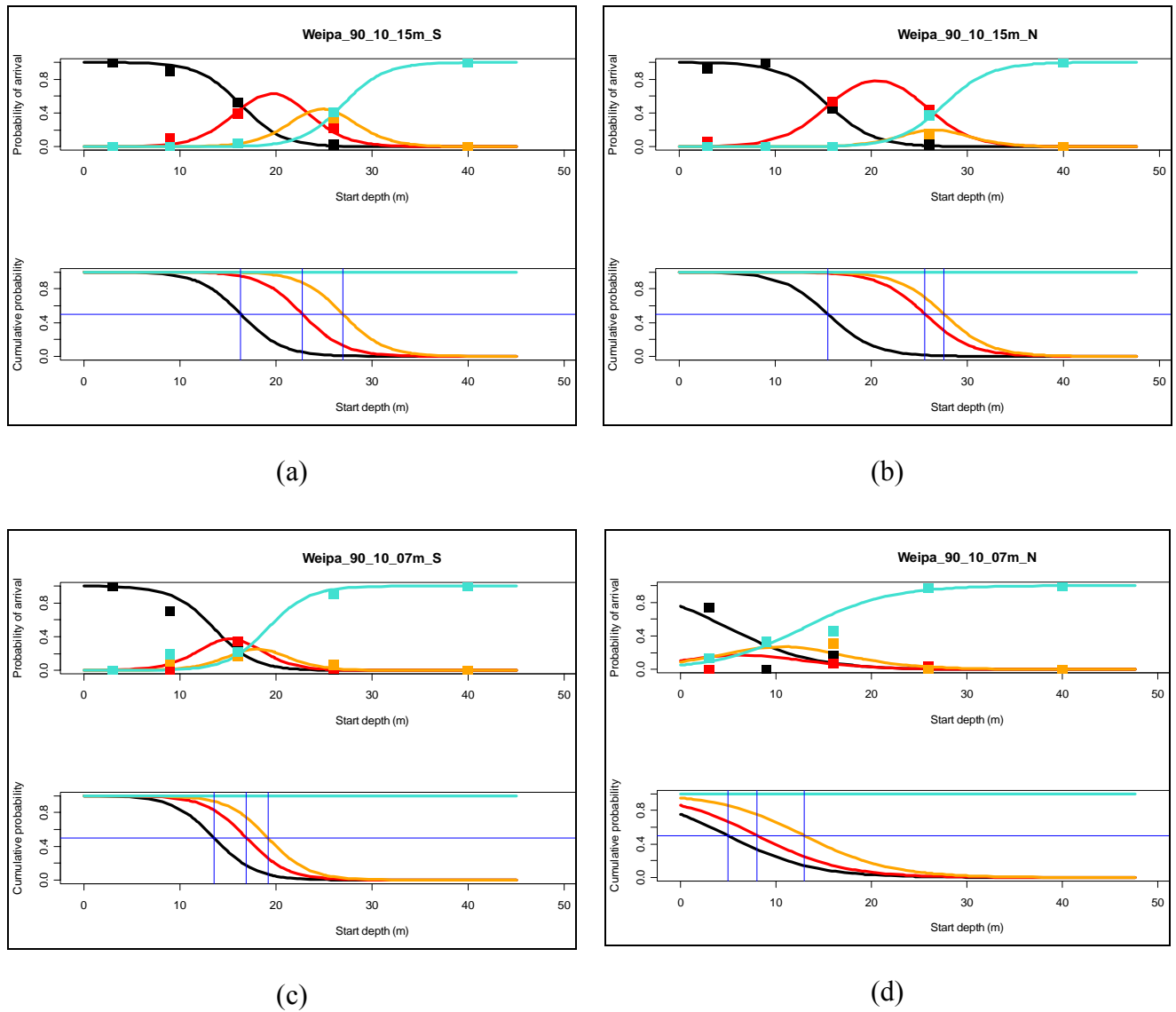

(a)　　　　　　　　　　　　　　　　　(b)

(c)　　　　　　　　　　　　　　　　　(d)

Figure 4.4: Proportional odds logistic regression curves (POLR) for larval advection movements in October 1990, with transition depths of 15m (a and b) and 7m (c and d). Separate POLR has been fitted to the southern (a and c) and northern sectors (b and d) of the region, split at 12.6°S. The second figure in each pair illustrates the cumulative probability, in relation to starting depth, of arriving in 1–15 days (black curve), 16–24 days (red curve), 25–33 days (yellow curve) or later/never (turquoise curve). The vertical blue lines represent the depth at which the probability is 50% for a given time interval.

Conversion of larval advection for 1986 was carried out as follows. The slope (β) from the 15m model was multiplied by the ratio of the 7m slope to the 15m slope for the relevant sector in October 1990. A straight line was fitted to the pairs of intercept values from the 15m and 7m advection models, and the parameters of this used to convert the intercepts (ς_1, ς_2 and ς_3) from the 15m advection models. This was

reasonably successful for the southern sector, where the spacing of the intercepts is roughly constant (16, 23 and 27 compared with 13, 17 and 19) and not as good for the northern sector (15, 26 and 28 compared with 5, 8 and 13).

The 7m transition depth results in a much smaller advection envelope from which spawned larvae can reach the estuaries of Albatross Bay (Figure 4.5). In effect, the area containing effective spawners is halved, extending only to roughly the 15m depth contour as opposed to the 25m contour (Figure 4.6).
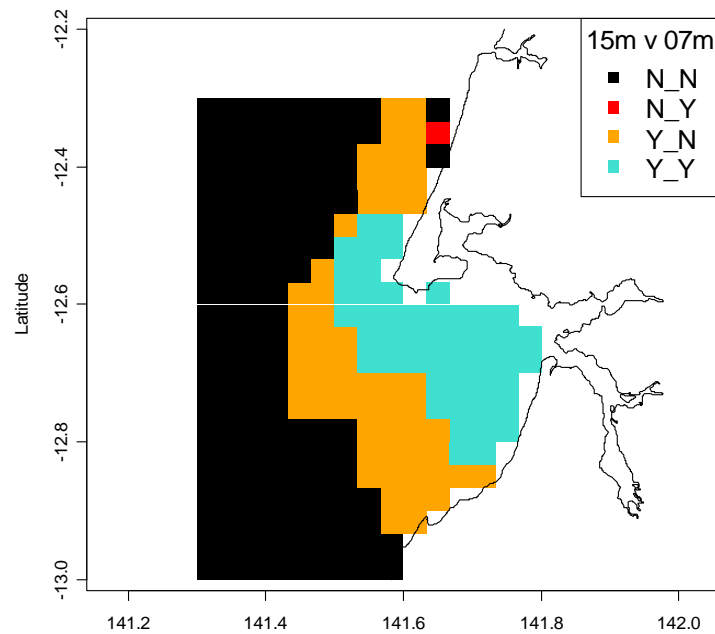
Figure 4.5: Comparison of starting locations from which particles will arrive at the estuaries of Albatross Bay, in relation to transition depth. Particles seeded in the turquoise area succeed under both 7m and 15m transition depths (Y_Y), those starting in the yellow area succeed only under the 15m transition depth (Y_N), those starting in the black area fail under both schemes (N_N). A particle starting in the red grid was successful only under the 7m transition depth (N_Y).
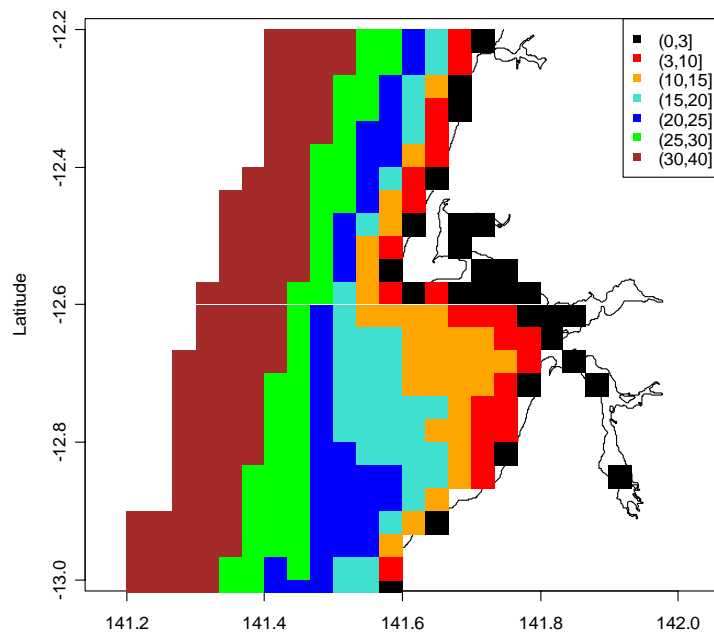
Figure 4.6: Bathymetry of the Albatross Bay region, expressed as water depth (in metres) at lowest astronomical tide.

4.4.3 Probability larvae have settled in nursery habitat by 34 days of age

With the assumed daily mortality rates of 20% offshore, 10% in estuaries and 3% in nursery habitat, the arrival times from the advection model were converted to the probability of a prawn arriving at the coast by the age of 34 days. This survival model is species-independent. With these mortality rates, even those grids with the best success rate deliver only 1–2% of the larvae spawned there (Figure 4.7). If the transition depth is 15m, larvae spawned throughout Albatross Bay (up to 15–20m depth) will have a relatively high probability of survival. In contrast, the probability is about one tenth of this for larvae spawned deeper than than 7–10m deep, when the transition depth is 7m. This confirms the importance of the transition depth to the effectiveness of larval advection on flood tides.
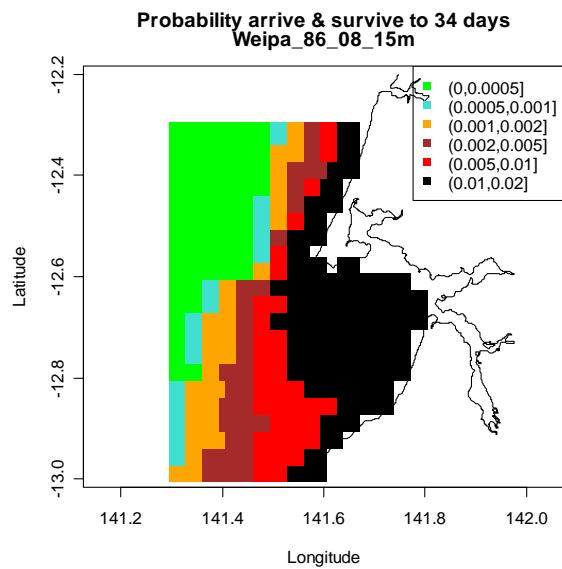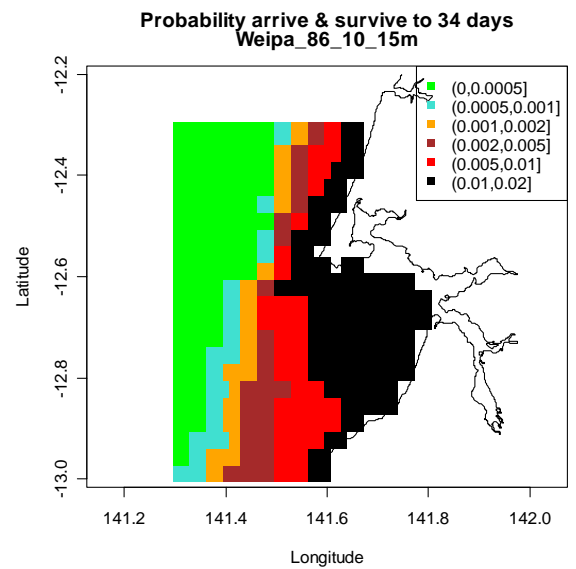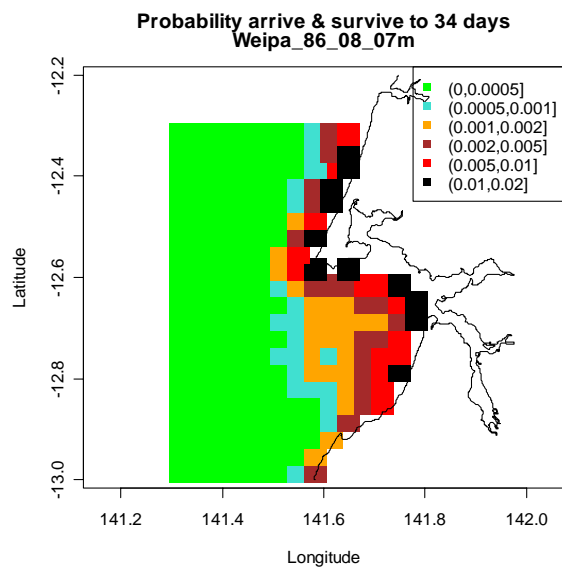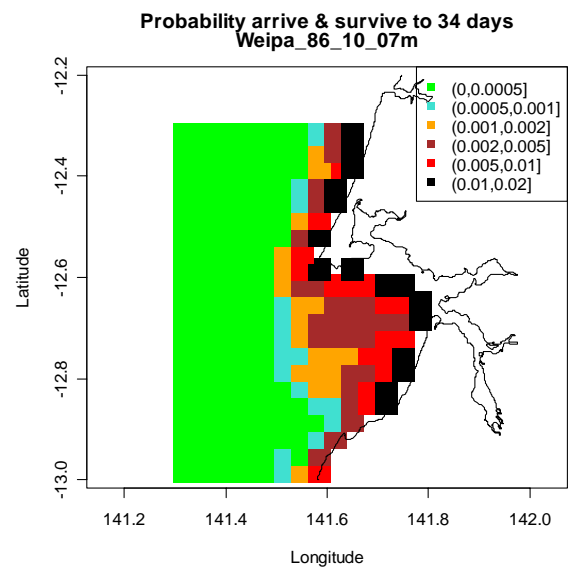
Figure 4.7: Probability of larvae from a given start location reaching the coast in the Weipa region for August (a and c) and October (b and d) 1986 for the 15m (a and b) and 7m (c and d) transition depths, settling and surviving to 34 days. Probable travel times have been converted to overall survival by assuming stepped, decreasing mortality rates at sea, in the estuary and in nursery habitat.

4.4.4 Spatial distribution of nauplii and spawners

A similar suite of models was fitted to the nauplius and spawner count data for all three species, essentially exploring whether separate splines in depth and latitude were needed in different seasons and whether temporal changes could be captured with a more structured model than simply fitting a separate mean for each survey. Since there were only two surveys in the last two years, we chose a common spatial distribution model over all years.

The best-fitting model for nauplius abundance of any particular species (Table 4.2) was generally the same as for spawners (Table 4.3), but slightly different models were needed for the three species.

The trend over the months July to December was very similar from year to year for *P. semisulcatus*: additive terms for year and month fitted better than a separate mean for every survey and both terms were highly statistically significant.

The spatial distribution of *P. semisulcatus* nauplii (Table 4.2) in relation to depth and latitude remained essentially constant during winter and spring. The highest abundance was found in water 20–25m deep, slightly lower when further offshore than 25m, and roughly ten times as abundant as in water 5–10m deep (Figure 4.8a; scale of y-axis is logarithmic due to the choice of link function). Abundance was higher south of 12.8°S and north of 12.6°S (Figure 4.8b). Spawner and nauplius density were both generally higher in October 1986 than in August (Figure 4.9). The distribution of the two response variables at each time was very similar in August, suggesting a homogenous distribution of adult prawn size by this time of year. In October, the north-west sector of the spawner distribution had a lower density than the south-west sector but there was no difference for the nauplius distribution, suggesting adult prawn sizes in the north-western sector were closer to the most productive size of 43mm than elsewhere.

Table 4.2: Statistical significance of factors for the nauplius models of *P. semisulcatus*, *P. merguiensis* and *P. esculentus*.

Model term	d.f.	*F*-ratio	*p*-value	Other information
		P. semisulcatus		
Year (factor)	7	6.30	$< 10^{-6}$	$\hat{\theta} = 0.541$
Month (factor)	5	18.61	$< 10^{-15}$	Resid. Deviance=836
s(depth, k=4)	2.9	94.65	$< 10^{-15}$	Residual d.f.=990
s(latitude, k=4)	2.5	8.18	$< 10^{-4}$	
		P. merguiensis		
Year (factor)	7	8.16	$< 10^{-8}$	$\hat{\theta} = 0.173$
Month (linear trend)	1	0.86	0.354	Resid. Deviance=546
s(depth, k=4):winter	2.1	27.78	$< 10^{-15}$	Residual d.f.=803
s(depth, k=4):spring	1.0	115.37	$< 10^{-15}$	
s(latitude, k=4):winter	1.0	14.58	0.0001	
		P. esculentus		
Year (factor)	7	4.62	$< 10^{-4}$	$\hat{\theta} = 0.333$
Season (factor)	1	6.46	0.0112	Resid. Deviance=871
s(depth, k=4):winter	1.3	11.56	$< 10^{-6}$	Residual d.f.=992
s(latitude, k=4):winter	2.9	56.80	$< 10^{-15}$	
s(latitude, k=4):spring	2.9	26.13	$< 10^{-15}$	

Table 4.3: Statistical significance of factors for the spawner models of *P. semisulcatus*, *P. merguiensis* and *P. esculentus*.

| Model term	d.f.	*F*-ratio	*p*-value	Other information
P. semisulcatus				
Year (factor)	7	5.55	$< 10^{-5}$	$\hat{\theta} = 0.515$
Month (factor)	5	16.53	$< 10^{-14}$	Resid. Deviance=751
s(depth, k=4)	2.9	51.20	$< 10^{-15}$	Residual d.f.=990
s(latitude, k=4)	2.1	7.01	0.0001	
P. merguiensis				
Year (factor)	7	6.36	$< 10^{-6}$	$\hat{\theta} = 0.214$
Month (linear trend)	1	0.12	0.731	Resid. Deviance=472
s(depth, k=4):winter	1.6	24.71	$< 10^{-14}$	Residual d.f.=804
s(depth, k=4):spring	1.0	98.34	$< 10^{-15}$	
P. esculentus				
Year (factor)	7	7.56	$< 10^{-8}$	$\hat{\theta} = 0.610$
Season (factor)	1	5.67	0.0175	Resid. Deviance=688
s(depth, k=4):winter	1.9	10.18	$< 10^{-5}$	Residual d.f.=991
s(latitude, k=4):winter	2.9	43.67	$< 10^{-15}$	
s(latitude, k=4):spring	2.9	30.51	$< 10^{-15}$	
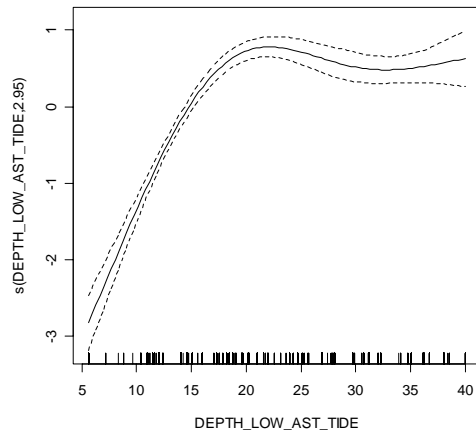
(a)
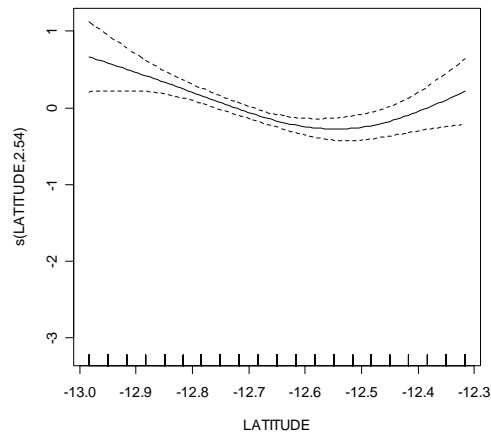
(b)

Figure 4.8: Fitted spline curves relating abundance, on a logarithmic scale, of *P. semisulcatus* nauplii to (a) depth and (b) latitude over all years, with confidence interval. Ticks on x-axis show values of predictor present in the dataset.
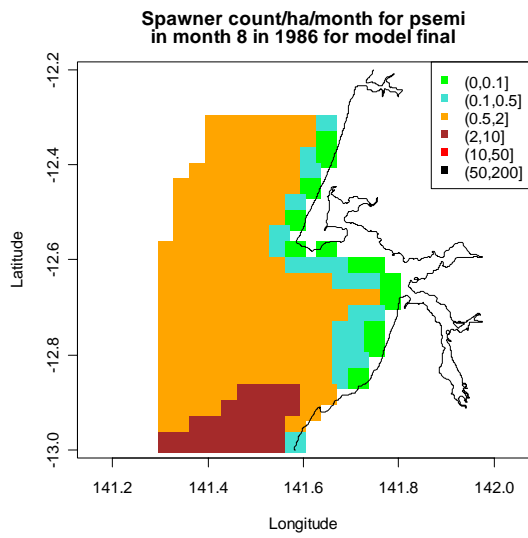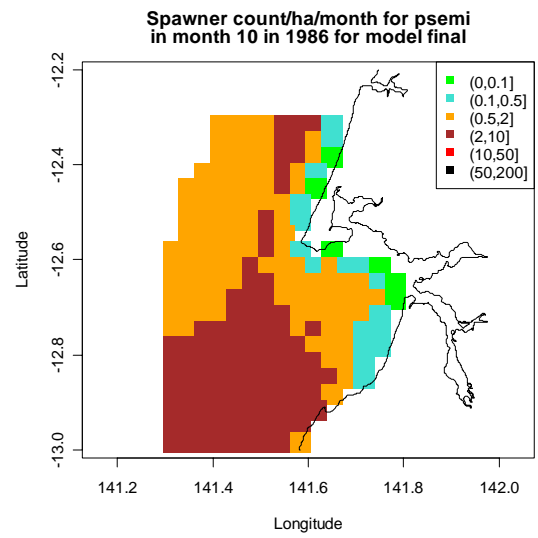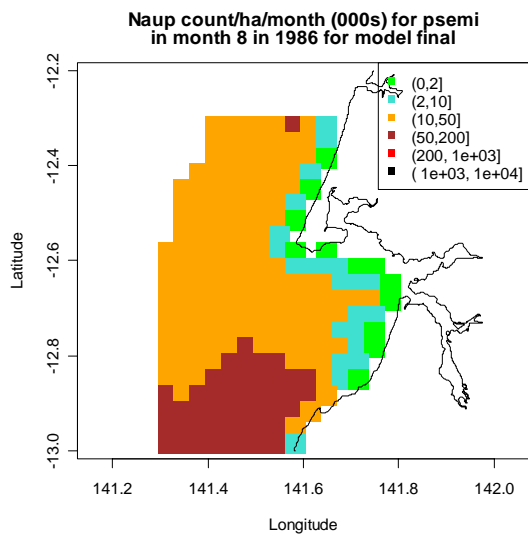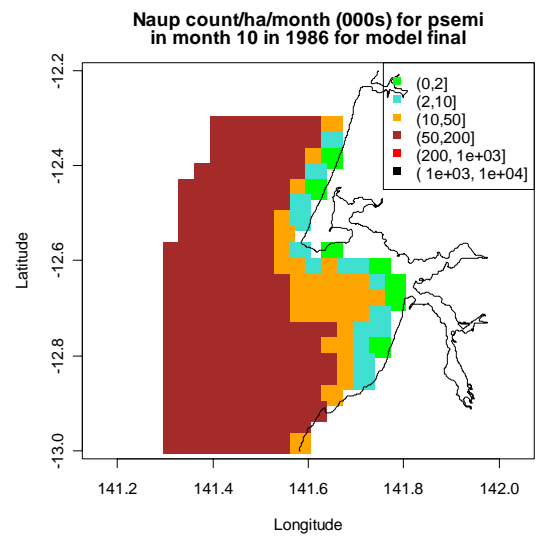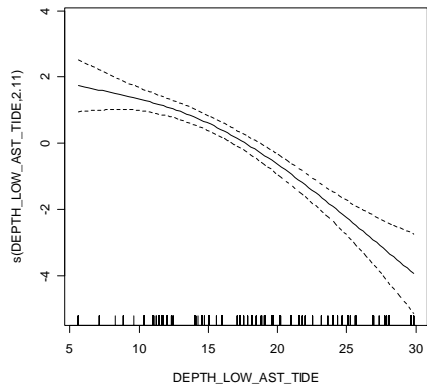
Figure 4.9: Maps of predicted spawner (top) and nauplius (bottom) density for *P. semisulcatus* in August (a and c) and October (b and d) 1986.

The banana prawn, *P. merguiensis*, tended to have the patchiest distribution in terms of zeros and skewness. Estimates of the dispersion parameter (θ) were 0.173 for nauplii and 0.214 for spawners (Tables 4.2 & 4.3) compared with 0.515 and 0.541 for *P. semisulcatus* and 0.333 and 0.610 for *P. esculentus*.

Abundance of *P. merguiensis* nauplii remained essentially constant within each year: a linear trend over months gave the best fit but was still not statistically significant (Table 4.2). However, differences among years were highly statistically significant. The spatial distribution of *P. merguiensis* (Table 4.2) in relation to depth and latitude was different for winter and spring, though in both cases abundance was highest inshore in 5–10m of water (Figures 4.10a and 4.10b) and the main difference was a faster decline in abundance with depth during spring than winter. Abundance increased in a northerly direction during winter, more or less linearly with latitude (Figure 4.10c), but in spring there was no clear latitudinal trend. For spawners (Table 4.3), there was no latitudinal trend in either season, whereas the depth trend was very pronounced during spring. Maps of *P. merguiensis* spawner and nauplius density in August and October 1986 (Figure 4.11) are almost a mirror image of the *P. semisulcatus* distribution (Figure 4.9), with almost no spawners outside Albatross Bay. Nauplius and spawner distributions were very similar.

P. esculentus nauplius abundance varied substantially from year to year (Table 4.2). Within-year variation was less marked, differences being detected only when months were grouped into seasons. Abundance increased with water depth in winter (Figure 4.12a) but no relationship with depth was detected in spring (Table 4.2). However, the distribution of this prawn has a marked trough at latitudes corresponding to Albatross Bay itself, being much more abundant to the north and the south. The relationship with latitude was more marked in winter than in spring (Figures 4.12b and 4.12c). Generally, results were very similar for spawners, except that the difference in abundance between seasons was more marked and statistically significant (Table 4.3). Spawner and nauplius distributions were similar (Figure 4.13). This species displays a different pattern from the other two species: it was more abundant in deeper waters to the north and south of Albatross Bay and much less abundant in an area extending roughly 15 n.mile around Duyfken Point.

(a)
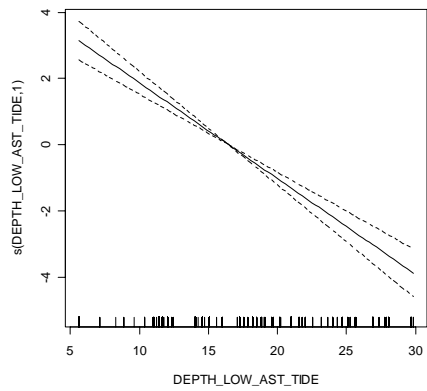
(b)
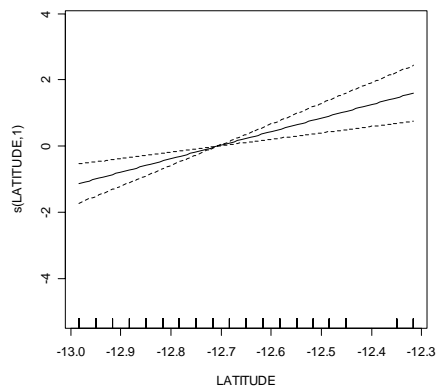
(c)

Figure 4.10: Fitted spline curves relating abundance, on a logarithmic scale, of *P. merguiensis* nauplii, to (a) depth in winter, (b) depth in spring and (c) latitude in winter, with confidence interval. Ticks on x-axis show values of predictor present in the dataset.
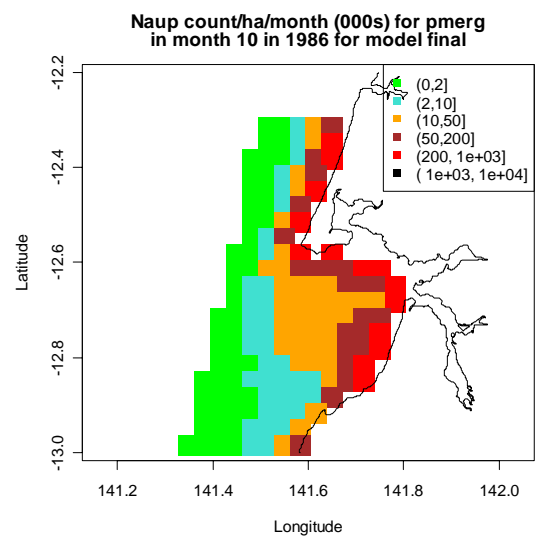
Figure 4.11: Maps of predicted spawner (top) and nauplius (bottom) density for
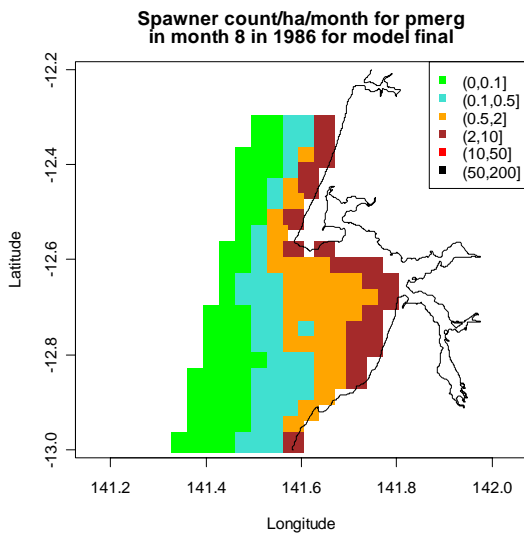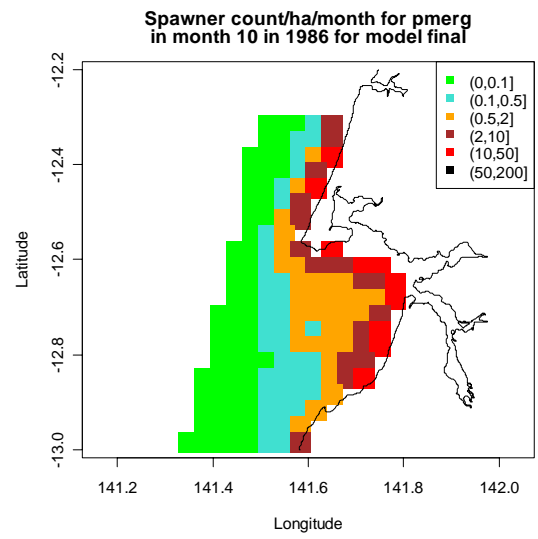*P. merguiensis* **in August (a and c) and October (b and d) 1986.**
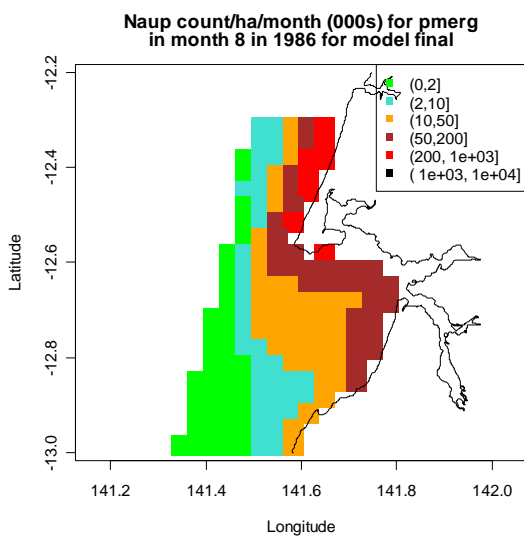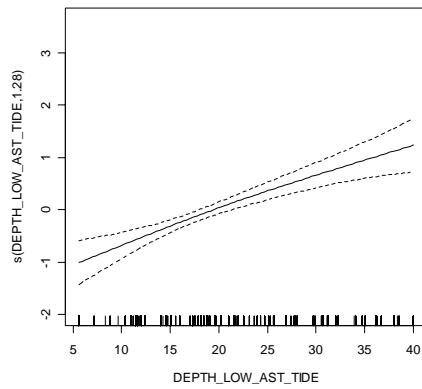
(a)
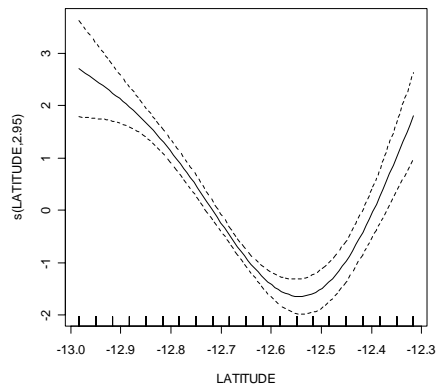
(b)
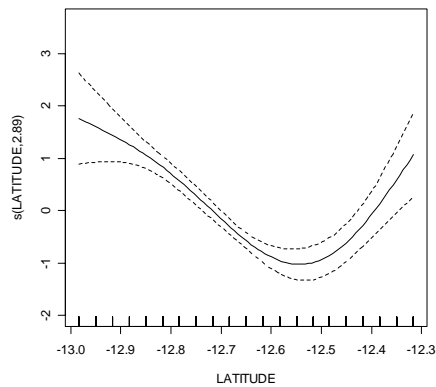
(c)

Figure 4.12: Fitted spline curves relating abundance, on a logarithmic scale, of *P. esculentus* nauplii, to (a) depth in winter, (b) latitude in winter and (c) latitude in spring, with confidence interval. Ticks on x-axis show values of predictor present in the dataset.
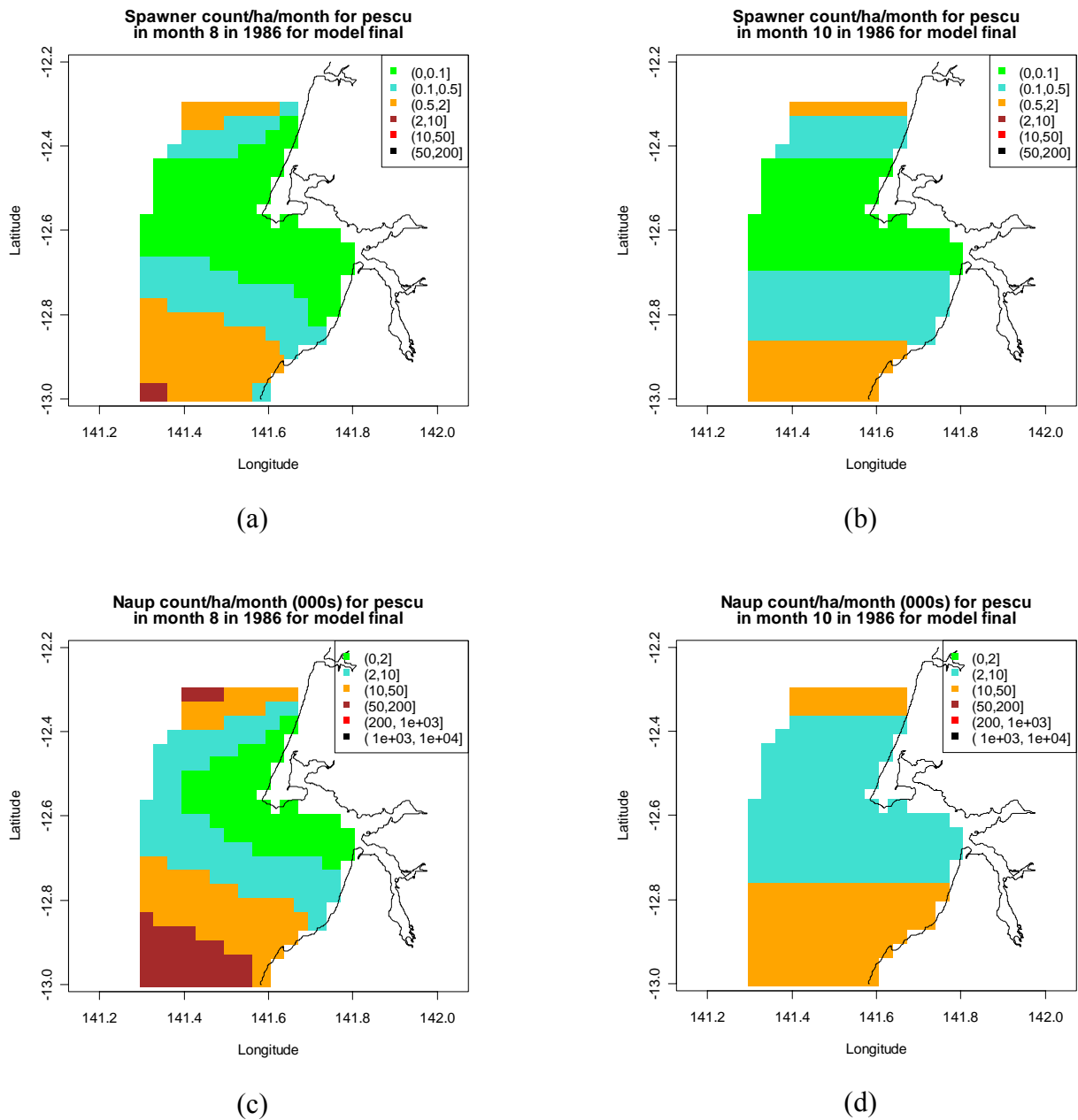
Figure 4.13: Maps of predicted spawner (top) and nauplius (bottom) density for
***P. esculentus* in August (a and c) and October (b and d) 1986.**

4.4.5 Spatial contribution to population of benthic postlarvae in nursery habitat

We evaluated the number of 34-day-old postlarvae from each 2 n.mile
spawning grid that would have reached the nursery habitat and moved into the benthic
stage of the life-cycle by combining (a) the spatial distribution of nauplii in the
spawning grounds (b) the likely length of time to reach nursery habitat in the estuaries
of Albatross Bay, given transition depths of 7m and 15m; and (c) the probability of
surviving that journey.

As expected, a much smaller region contributed benthic postlarvae of all three
species when the transition depth was set to 7m (Figures 4.14–4.16) compared to

15m. For this transition depth, grids with water 6–15m deep contributed most benthic *P. semisulcatus* postlarvae (Figure 4.14), while grids in shallower water were more productive for *P. merguiensis* (Figure 4.15). Grids in the southern part of the Bay were the most productive sources of *P. esculentus* benthic postlarvae (Figure 4.16), and a couple of coastal grids 20 n.mile north of Duyfken Point were as productive as the best in the Bay. This northern enclave expanded when the transition depth was set to 15m, contributing quite large numbers of *P. semiculatus* and *P. merguiensis* to nursery habitat in the estuaries.


(a)

(b)

(c)

(d)
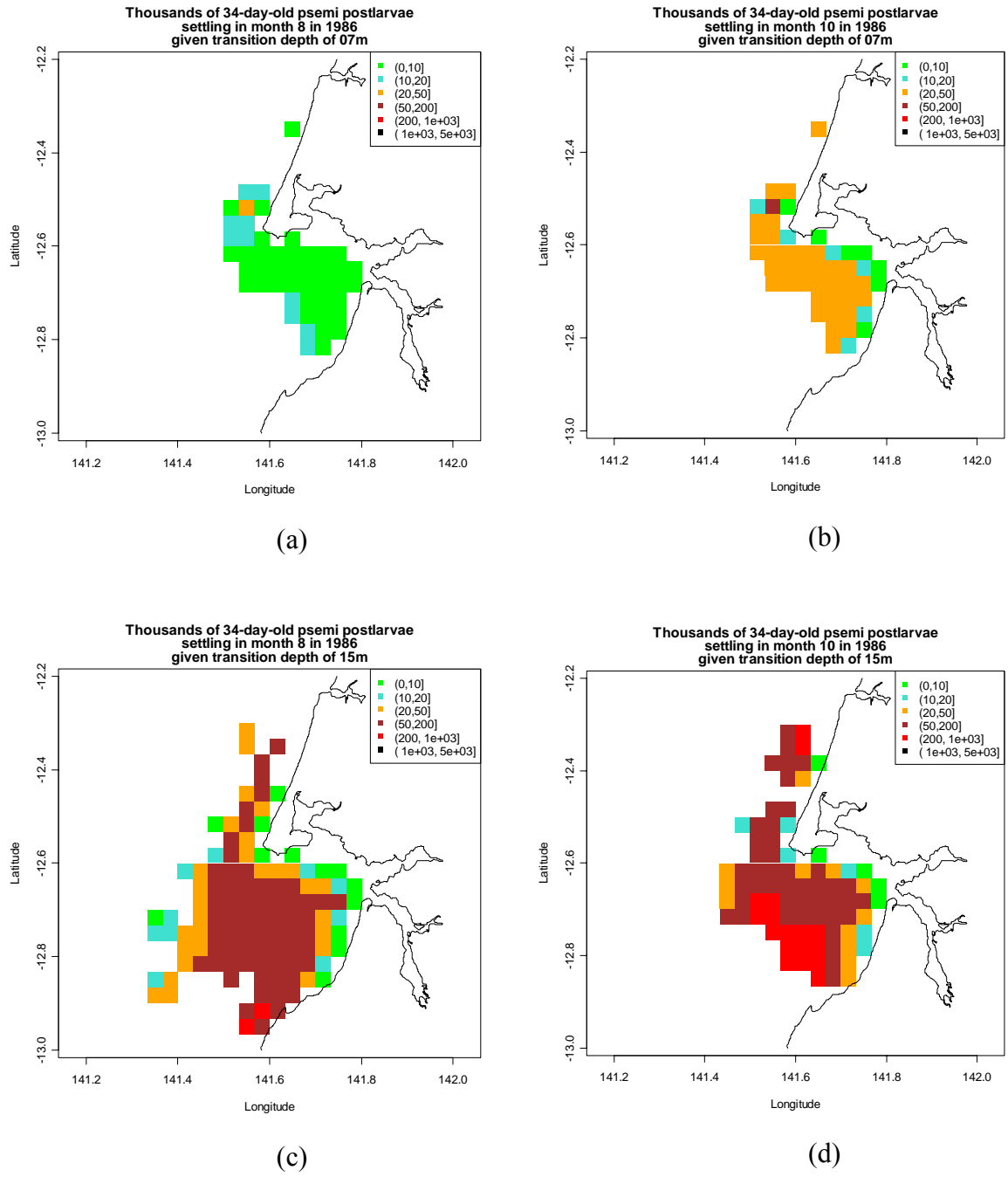
Figure 4.14: Maps of predicted number of *P. semisulcatus* nauplii spawned in August (a and c) and October (b and d) 1986 that will settle in estuarine nursery habitat, for transition depths of 7m (top) and 15m (bottom).
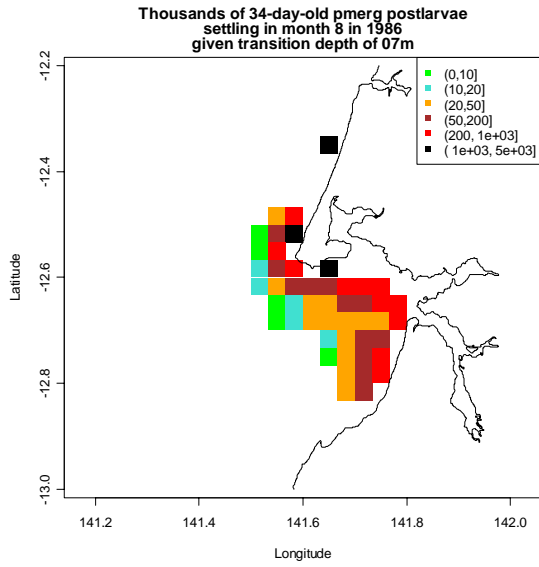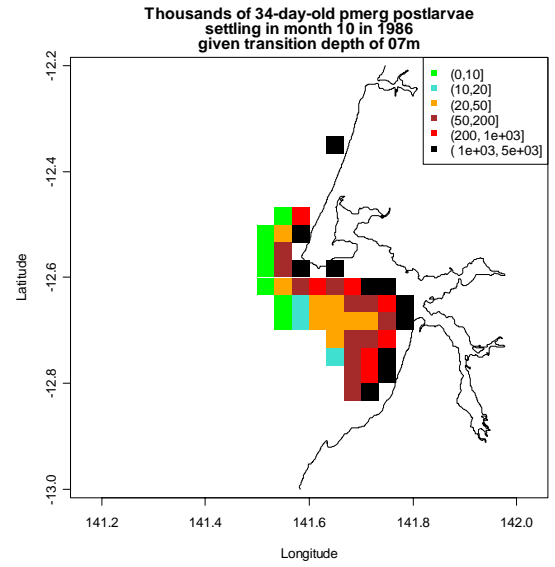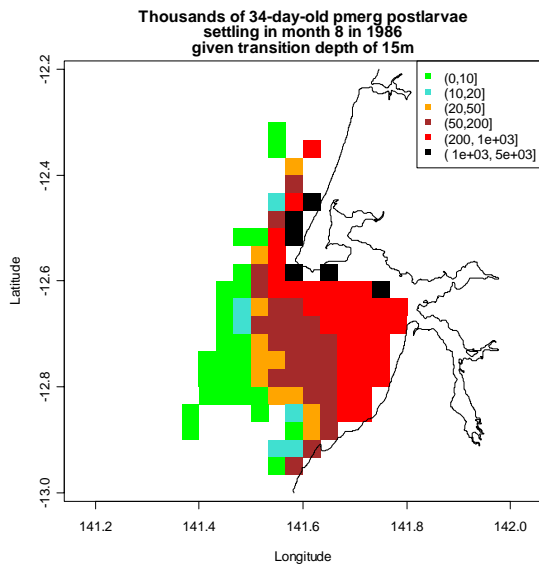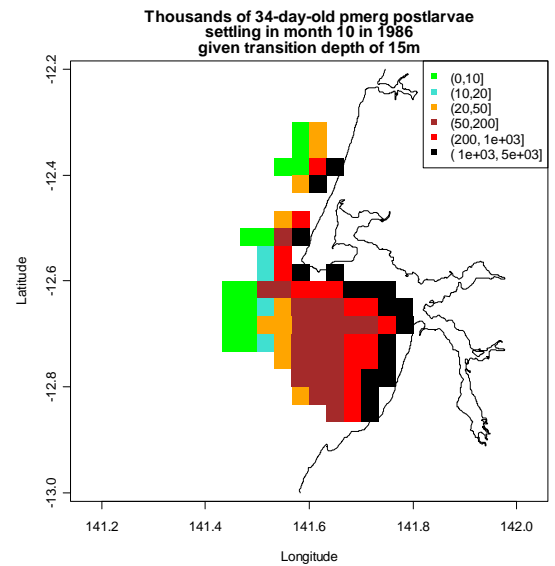
Figure 4.15: Maps of predicted number of *P. merguiensis* nauplii spawned in August (a and c) and October (b and d) 1986 that will settle in estuarine nursery habitat, for transition depths of 7m (top) and 15m (bottom).
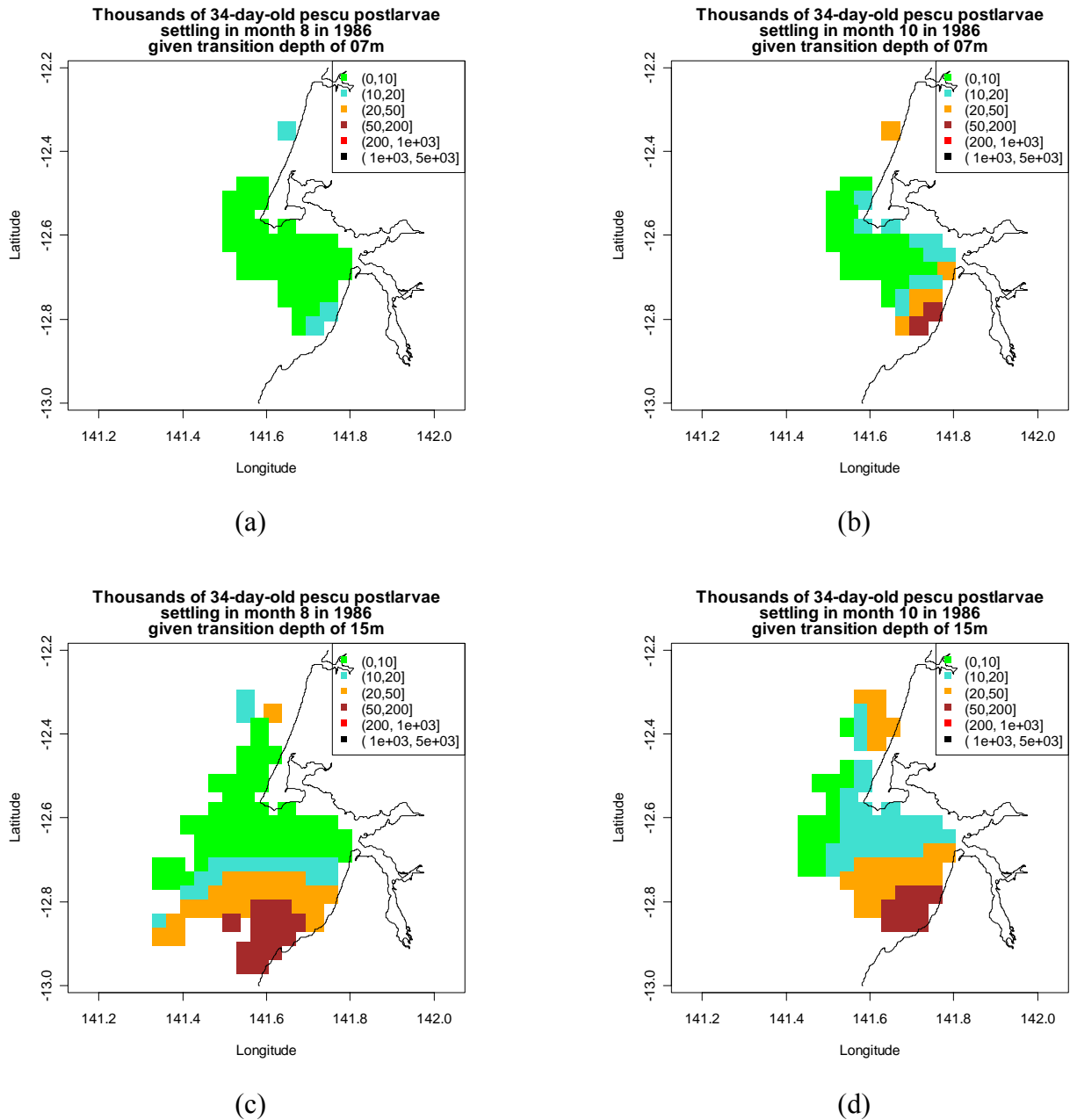
Figure 4.16: Maps of predicted number of *P. esculentus* nauplii spawned in August (a and c) and October (b and d) 1986 that will settle in estuarine nursery habitat, for transition depths of 7m (top) and 15m (bottom).

4.4.6 Trends in spawner and larval indices

The 'PL34' index (which stands for 34-day old Postlarvae) is calculated by summing contributions from all grids, and the trend over months can be seen for the three species in Figure 4.17 (7m transition depth) and Figure 4.18 (15m transition depth). Given the common model used for larval advection (i.e. 1986), spawner abundance for any given year strongly determines the PL34 index. We illustrate this with a high-catch and low-catch year from 1986–1992 and one recent year (2004) which turned out to be exceptionally low for both *P. merguiensis* and *P. esculentus*. There was no survey in December 1989 or July 1991, and there were surveys only in July and October in 2004.
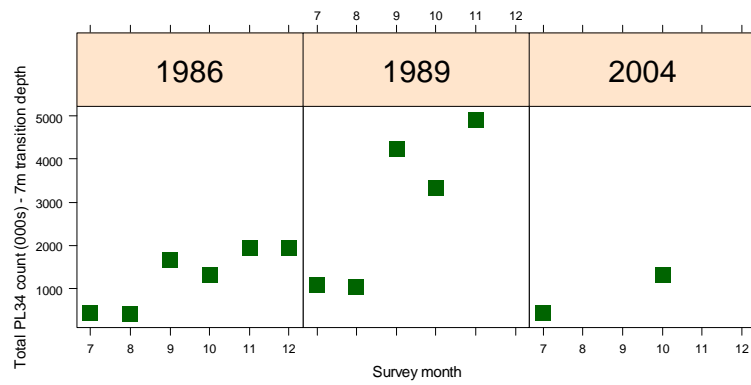
(a)
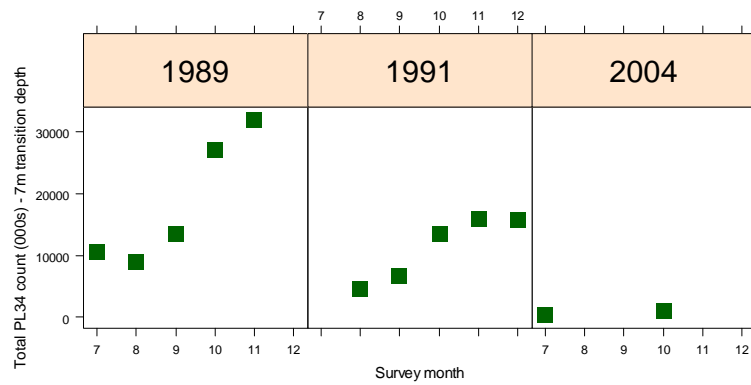
(b)
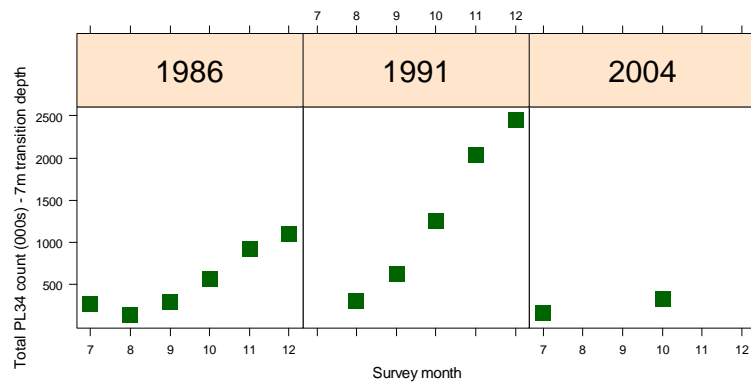
(c)

Figure 4.17: Within-year trends for the PL34 index given 7m transition depth for years with low, medium and high spawner abundance for (a) *P. semisulcatus* **(b)** *P. merguiensis* **and (c)** *P. esculentus*.
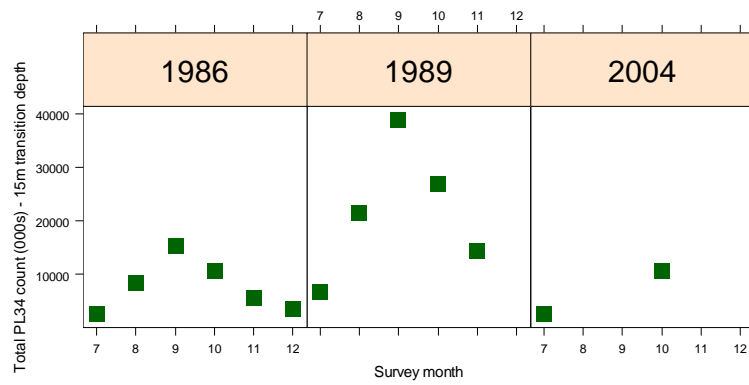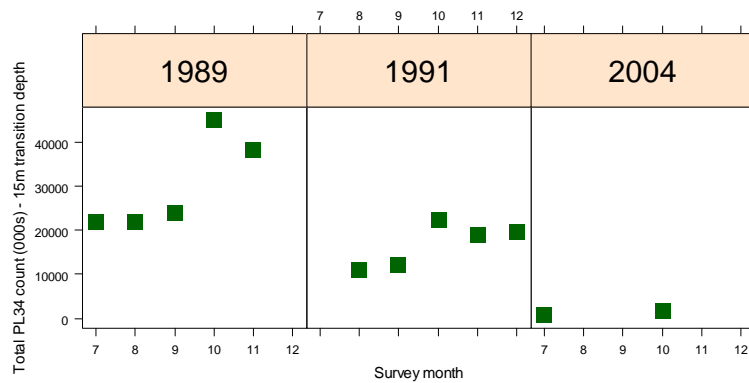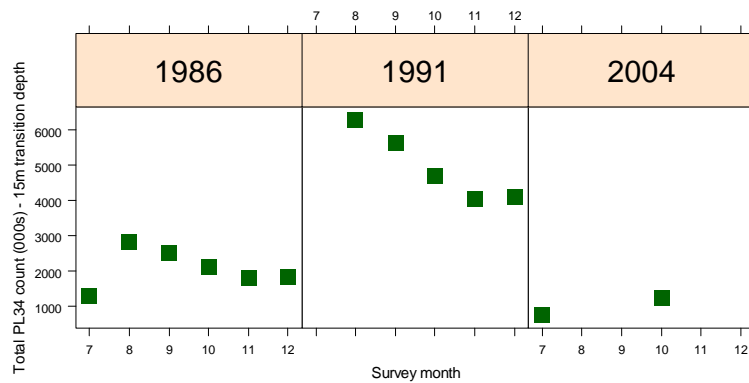
Figure 4.18: Within-year trends for the PL34 index given 7m transition depth for years with low, medium and high spawner abundance for (a) *P. semisulcatus* **(b)** *P. merguiensis* **and (c)** *P. esculentus***.**

For all three species, the PL34 index for the 7m transition depth increased between July and the end of the year. The PL34 index based on the 15m transition depth had a different trend from this: it peaked strongly in September for *P. semisulcatus*; peaked in October for *P. merguiensis*, followed by a slight decline; and peaked in August for *P. esculentus* before a steady decline.

For *P. merguiensis*, the PL34 index is highly correlated with the spawner index for both transition depths (Figure 4.19b), both being low in July/August (squares) and high in November/December (triangles). The PL34 index in October 1989 (the best year – blue circle) was 50 times higher than that of October 2004 (the worst year – brown circle). For *P. semisulcatus* (Figure 4.19a) and *P. esculentus* (Figure 4.19c) the 15m index was less strongly correlated with the spawner index. For both tiger prawn species, the PL34 index for the 7m transition depth was only weakly correlated with the spawner index.

The ratio of total PL34 numbers to total spawner count was high for *P. merguiensis* (427 ± 2 for 15m transition depth; 322 ± 2 for 7m transition depth), reflecting the high density of spawners in shallow inshore waters. For *P. semisulcatus* the ratio was considerably lower (65 ± 1 for 15m; 5.0 ± 0.3 for 7m), and for *P. esculentus* even lower (28 ± 1 for 15m; 3.0 ± 0.4 for 7m).
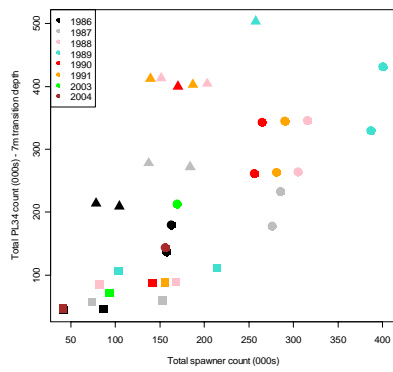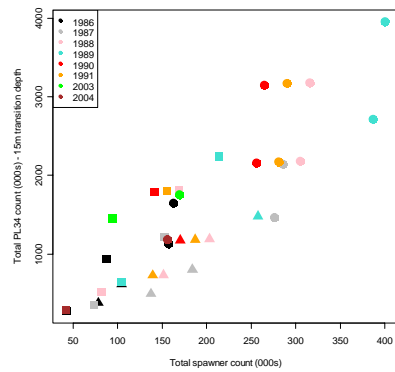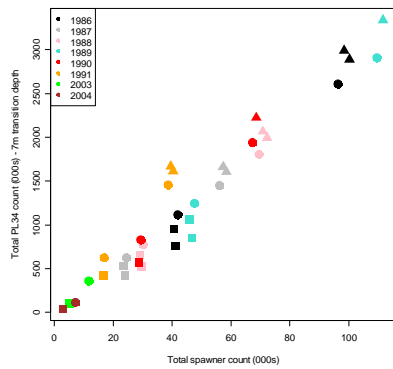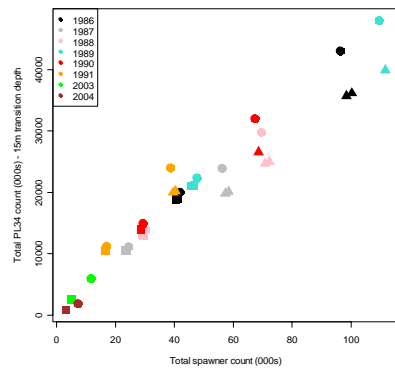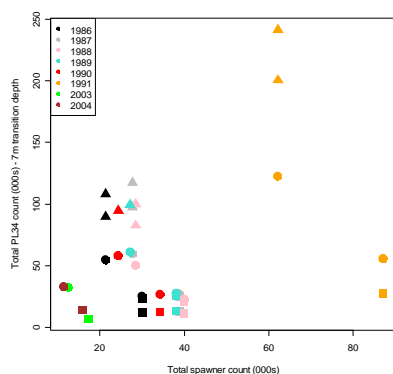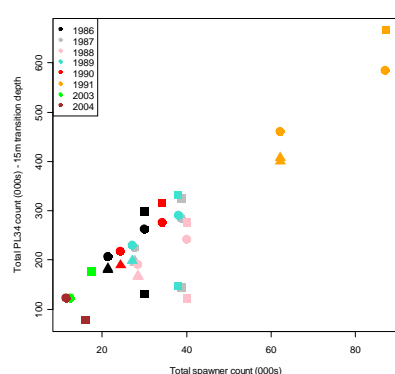
Figure 4.19: Relationship between PL34 index and spawner index for transition depths 7m and 15m for *P. semisulcatus* — (a) and (b); *P. merguiensis* — (c) and (d); and *P. esculentus* — (e) and (f). Squares show July/August indices, circles September/October indices and triangles November/December indices. Year is colour-coded (key on plot).
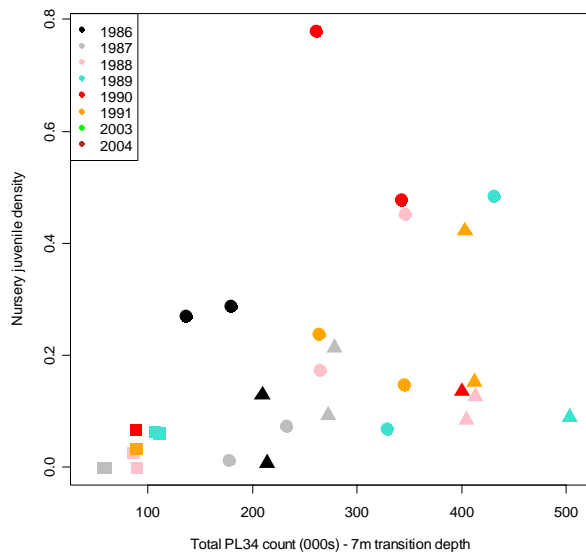
(a)
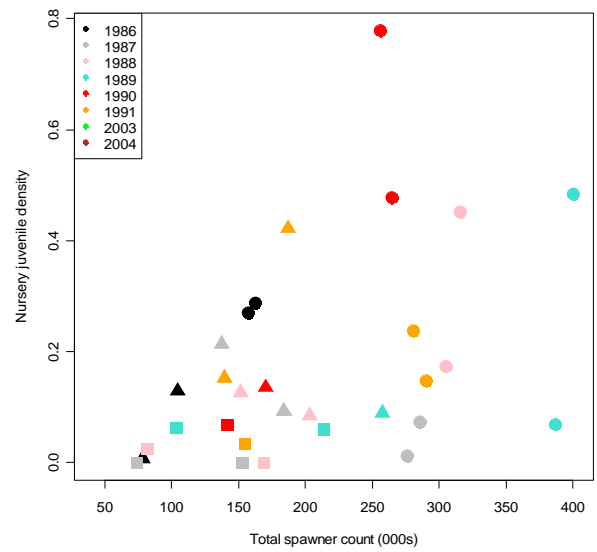
(b)
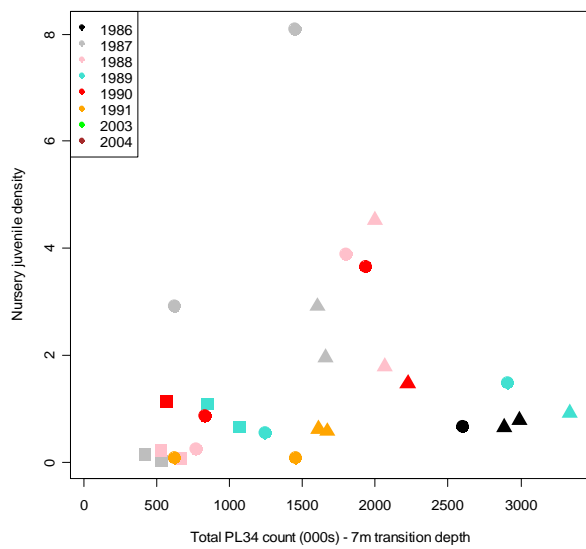
(c)
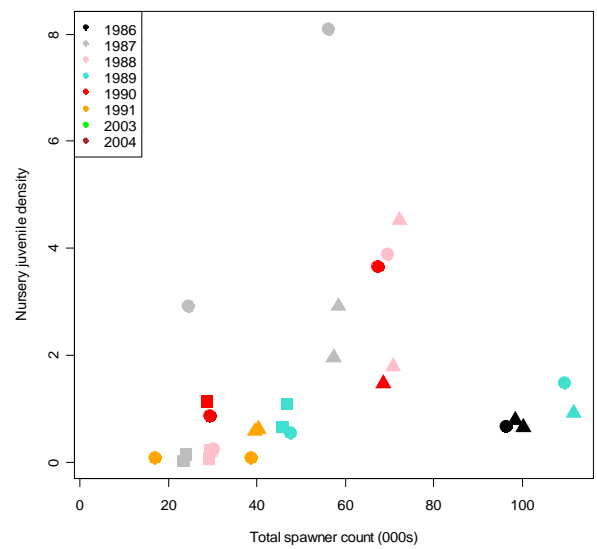
(d)

Figure 4.20: Comparison of PL34 index (7m transition depth) and spawner index with juvenile density in nursery habitat for *P. semisulcatus* – (a) and (b); and *P. merguiensis* – (c) and (d).

4.4.7 Comparison of spawner and larval indices with juvenile densities in estuaries

The densities of juvenile *P. semisulcatus* and *P. merguiensis* with carapace length 3–4mm in estuarine nursery habitat 30 days after the trawl survey were compared with PL34 and spawner indices derived from that survey. The relationship is not as clear as might have been expected (Figure 4.20), and neither index is better than the other. However, the roughly triangular shape of the graphs suggests that the offshore indices can set an upper limit to the densities in nursery habitat and that

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factors other than larval advection, such as nutrients or weather conditions, modify the survival of incoming planktonic postlarvae. It should be noted that the two high juvenile densities for *P. merguiensis* in 1987 are both interpolated from an exceptionally high peak in juvenile densities in late October of that year (Vance et al., 1998).

4.5 Discussion

We modeled the effect of currents and tides on larval survival in relation to time of year (month) and transition depth for all the years of this study, as hydrodynamic larval advection data produced by Condie et al. (1999) were only available for five of the eight years' offshore survey data. Furthermore, Condie et al. (1999) had found inter-annual variation in advection envelopes was small relative to changes during the course of a year. We used a statistical model to capture the features of the larval advection trajectories supplied by Condie (personal communication) for all months using a 15-m transition depth. Further modeling was carried out to produce estimates of larval advection for all months using a transition depth of 7m, which is considered more realistic in the light of experimental results of Vance and Pendrey (2001).

Using offshore trawl data for the years 1986–1992 and 2003–2004, we modeled the density of nauplii over a region extending slightly north and west of Albatross Bay. We did this for three species of commercial interest: *P. merguiensis*, *P. semisulcatus* and *P. esculentus*. We fitted a common spatial distribution model across years to each species because we had only two surveys in the period July-December in recent years, and the observed catches were generally low due to the focus on females and the fact that banana prawns in particular have been substantially depleted by fishing between April and June.

By combining the larval advection model with the spatial distribution of nauplius density for a given survey, we estimated the number of nauplii that would travel successfully to estuarine habitat in Albatross Bay, and settle by 34 days of age. We assumed that mortality would be highest offshore, decrease on arrival in the estuary and decrease further with residence in nursery habitat. The postlarvae were required to be at least 22 days old before settling, reflecting setting behaviour of postlarval *P. semisulcatus* in seawater tanks containing seagrass (Liu and Loneragan, 1997).

By combining the larval advection model with the spatial distribution of nauplii during a survey and a model of survival that depends on age and location, we were able to estimate the effects of initial location, transition depth, inter-annual and within-year variation on the number of postlarvae that can be expected to recruit successfully to nursery habitat.

Vance et al (1996, 1998) successfully accounted for the density of larger *P. semisulcatus* and *P. merguiensis* juveniles in nursery habitat from earlier cohorts of recently-settled postlarvae (1–2mm). However, they were less successful in accounting for the density of the new arrivals. The predictions of the PL34 index from our effective spawning model were tested against densities of small juveniles (3–4mm).

4.5.1 Effect of initial location on chance of reaching nursery habitat

Not surprisingly, larvae spawned inside Albatross Bay have the best chance of arriving at nursery habitats in time to survive and settle. However, prevailing currents in August and October advected larvae from north of Duyfken Point into the Bay. In fact, our capture region for the 15m transition depth extended slightly further north than the 28-day advection envelopes for 20m transition depth depicted in Rothlisberg et al. (1996), probably due to small differences in the hydrodynamic models.

Larvae spawned further offshore in deeper water, if they reach nursery habitat at all, take appreciably longer. This is likely to reduce their chance of survival: mortality in the offshore phase (Dall, 1990; Preston, 1992) appears to be generally higher than when settled in nursery habitat (O'Brien, 1994; Wang and Haywood, 1999) though this has been observed to be higher in spring than in winter for *P. merguiensis* in estuaries of Albatross Bay (Haywood and Staples, 1993).

4.5.2 Effect of transition depth on larval survival

If the transition depth is really as shallow as 7m, spawners in only a small area contribute effectively to the next generation during the peak months of late winter and spring. The effective spawning area is restricted mostly to waters shallower than 10m in Albatross Bay.

There are temporal changes in the size of the advection envelope over the second half of the year, gradually decreasing from a peak in July/August to a minimum in December/January. In terms of spawning effectiveness, the contributing area is slightly larger in August than in October, mainly because in October southern-bound currents sweep these larvae more rapidly south of Albatross Bay. This confirms earlier findings of the effect of transition depth by Rothlisberg et al (1996), who focused on Albatross Bay, and Condie et al (1999), who included this as one of five regions in the Gulf of Carpentaria.

4.5.3 Temporal changes – year and month

The main mechanism for annual differences in our model is through overall spawner abundance, mediated by the size of the prawns to give an expected nauplius production rate. We did not specifically examine changes in spatial distribution between years, as this tends to be poorly defined in years of low abundance such as those in 2003 and 2004. However, the highly significant differences among years combined with highly significant trends in depth and latitude suggest that the main inter-annual difference in spawner (and nauplius) distribution is in overall abundance rather than the spatial pattern for a given species varying substantially from year to year.

For *P. semisulcatus*, while density rose to a peak in September, the relative spatial distribution showed little change over the second half of the year, even though it is known that mature animals that have migrated far offshore in autumn return in late winter/spring (Crocos and van der Velde, 1995).

For the other two species, the spatial distribution differed to some extent between the winter and spring seasons but the main features of these stayed the same. For example, *P. merguiensis* was consistently most abundant in the shallow waters close to the estuaries while *P. esculentus* was consistently most abundant in mid-shore waters at the southern end of the Bay.

4.5.4 Consequence of transition depth on larval settlement differs among species

A novel aspect of this research is that we can quantify how much the choice of transition depth affects the efficiency of larval transport for the three species, as a consequence of the spatial distribution of the spawners. *P. merguiensis* larvae were transported quite efficiently to nursery habitat in the estuaries, whether the transition depth was 15m (~400 per spawner per month) or 7m (~300). However, even with a transition depth of 15m the tiger prawn larvae were transported less efficiently: ~60 per spawner per month for *P. semisulcatus* and ~30 for *P. esculentus*. Numbers were dramatically reduced, to levels unlikely to be sustainable, when the transition depth was set to 7m (5 and 3 per spawner per month respectively). Admittedly, it is possible that the tiger prawns can settle in seagrass along the coast rather than in the estuary, so that the proportion of nauplii that eventually settle may in fact be better than this. In this respect, however, it is noteworthy that very few *P. esculentus* are found in this region and that densities of both tiger prawns in the Albatross Bay estuaries were appreciably lower here than in embayments of Groote Eylandt (Loneragan et al, 1998).

4.5.5 Implications for stock assessment

This research is essentially a first step in examining the relationship between spawning stock size and recruitment, with a long way to go before we are in a position to develop a specific stock-recruitment relationship for either *P. merguiensis* or *P. semisulcatus* in the Albatross Bay region using these methods.

The poor correlation for both of these species between the new index and juvenile densities in estuarine nursery habitat is disappointing. However, comparison of models at 7m and 15m transition depths suggests that transition depth has little effect on the number of adult *P. merguiensis* that contribute effectively to the next generation as density of this species consistently peaked in shallow waters in the critical spring spawning months. Indeed, a major limitation of our study was our inability to trawl safely in waters shallower than 7-8m where density of *P. merguiensis* was probably highest. This is particularly relevant in the context of the recruitment of juveniles to the fishery the following autumn from the estuaries: Tanimoto et al (2006) found the catch rates of sub-adult *P. merguiensis* in a number of estuaries on Queensland's East Coast decreased in beam trawls after a 30-day period of higher flow while those in offshore otter trawls increased. They speculated that higher river flows increased catchability in the otter trawl fishery rather than productivity of the banana prawn fishery per se. A further consideration for the banana prawn stock-recruitment relationship is that the period of greatest commercial catch is April to June, some months earlier than the most effective spawning period.

The success of *P. semisulcatus* spawning is clearly more susceptible to the barrier presented by the transition depth, given their distribution further offshore in the peak spawning period. The published Ricker stock-recruitment relationship for this species (Dichmont et al, 2006) is very noisy, a situation that is all too common with fisheries data (Hinrichsen, 2001) and prawn fisheries in particular (Ye, 2000).

4.5.6 Future directions

The current approach differs in a number of respects from the approach employed by Crocos and van der Velde (1995), who introduced the concept of effective spawning. They counted only those females identified as 'active' spawners

(ovary stages IV and V), and the number of eggs (hence nauplii) was modelled as a linear function of the spawner's carapace length – in contrast to declining productivity of older females noted by Crocos and Coman (1997) experimentally in seawater tanks. The main difference, however, is that we have directly linked a larval advection model to the data on female prawns from offshore trawls (most of which came from their six-year study). In effect, the indices of postlarval recruitment from the current study draw together the approach of Crocos and van der Velde (1995) and the larval advection modelling in Albatross Bay first attempted by Rothlisberg et al (1996).

One of the fundamental gaps in this research is the lack of detailed larval trajectories for the 7m transition depth at all relevant times – data at this transition depth were only available for one month and the resources of this project did not extend to running the computer-intensive hydrodynamic models for new parameter settings (including larval behaviour), times and locations not covered by Condie et al (1999). It would be desirable to tackle this in future research, preferably running the hydrodynamic model with currents/tides/winds in force at the time of each survey.

A key parameter is larval survival, which is known from field studies to be highly variable both at sea and in coastal areas, and over time due to patchy availability of food and short-term weather patterns that affect the behaviour and movements of prawns. A further aspect that needs more attention is the stochastic component: not all larvae seeded in the same location will follow exactly the same trajectory. This could be tackled by seeding a large number of particles at each seed point.

In using only the larval advection patterns from 1986, we have certainly missed inter-annual changes in the finer scale features of advection. We know, for example, that particles from a larger area north of Duyfken Point were pulled into the Bay in October 1990 than in October 1986.

While it appears that our results are consistent with observations that postlarvae settle in nursery habitat from about 3 weeks of age, we have not examined the extent to which moving them only on night-time flood tides would slow down this process. We have also assumed they become postlarvae within 8 days, then instantly cue into flood tides. These settings are probably optimistic, since larval development and behaviour is likely to vary, depending on their growth in response to available food. For example, less than half of 5-day-old *P. merguiensis* nauplii had reached second protozoeal stage during in situ survival experiments in Albatross Bay (Preston et al, 1992).

It would clearly be beneficial for *P. merguiensis* in particular to collect data on densities of juveniles and adults in waters 2–7m deep in Albatross Bay, probably using beam trawls, in tandem with offshore surveys. Further work on the movement of juveniles in the creeks and estuaries would enhance understanding of both the settlement phase and the recruitment phase. It would be particularly beneficial to have both sources of data covering the same seasons, preferably linked with measurements of river flow. A project that would examine the links between population density and spatio-temporal dynamics of juveniles and river flow during the summer/autumn months in the creeks close to Karumba is planned. Conductivity meters in creeks and estuaries could perhaps be used as a surrogate index of inshore recruits.

4.6 Acknowledgements

4.7 References

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CHAPTER 5: GOOD BANANA PRAWN CATCHES: INCREASED ABUNDANCE OR INCREASED AVAILABILITY?

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5.1 Abstract

The fishery for the banana prawn, *Penaeus merguiensis*, in the Gulf of Carpentaria is characterized by large year to year fluctuations in catch and, in some regions, there is an association between high commercial catches and increased rainfall in the estuarine prawn nursery areas. It has been shown that juvenile banana prawns emigrate from estuaries in response to increased rainfall, probably mitigated through decreased salinity, but it has also been suggested that the offshore distribution of adult banana prawns may be affected by rainfall. In high rainfall years, prawns may move further offshore and become more available for capture by the fishing fleet. If the latter is the case, then years of high catch represent years when a higher proportion of the total banana prawn population is caught which has substantial implications for the size of the spawning stock and therefore the management of the fishery. In this paper we have analysed adult prawn catch data from historical research surveys in Albatross Bay (1986-1992) and at Karumba (1977-78) as well as data from current surveys in the same two regions. We have examined juvenile prawn data from historical research projects in estuaries at Weipa, inshore from Albatross Bay (1986-1992), and at Karumba (1975-1979). We have also analysed estuarine salinity data collected during these past projects and salinity data collected in the current project using data loggers moored in the same estuaries. We have concluded that there is no evidence to support the hypothesis that banana prawns in Albatross Bay or at Karumba are further offshore and therefore more available for capture by the fleet in years of high rainfall and low salinity. This conclusion is least robust for the Karumba region where we had the smallest amount of data and further use should be made of ongoing Northern Prawn Survey data to test this result.

5.2 Introduction

The fishery for adult banana prawns (*Penaeus merguiensis*) in northern Australia is characterized by large variations in catches from year to year (Figure 5.1) (Haine & Garvey 2005). At least some of this variation is thought to be due to environmental variation, particularly to rainfall in the months leading up to the beginning of the fishing season (Vance et al. 1985). Juvenile *P. merguiensis* in the Norman River, Karumba and the Embley River, Weipa have been shown to emigrate from these rivers after heavy rainfall and decreases in salinity (Staples & Vance 1986, Vance et al. 1998). However, it has also been suggested that some of the increased catch of adult banana prawns associated with increased rainfall may be due to increased nutrient levels in the river systems, leading to general increased production and an increased abundance of juvenile and adult *P. merguiensis* (Vance et al. 2003).

It is also possible that the distribution of adult *P. merguiensis* outside the estuaries may be influenced by rainfall or salinity. It has been found in extreme years, e.g. the extraordinary flood of 1974, that banana prawns have been caught much further offshore than is normally the case. However, in less extreme environmental years, it has not been possible to detect this effect from the commercial catch data.

If the inshore/offshore distribution of *P. merguiensis* is affected by levels of rainfall and salinity, there are substantial implications for the management of the fishery. If the prawns are located further offshore in wet years than in dry years, then the prawn population would be more available for capture by the fishing fleet and a larger proportion of the population might be caught in wet years. Since the main spawning population of *P. merguiensis* in the Northern Prawn Fishery consists of prawns that escape capture during the fishing season (Rothlisberg et al. 1985), it follows that, in wet years, a smaller proportion of the initial population remains to spawn and produce next year's recruits. If this is the case, then the spawning stocks are in much greater danger of being over-fished in high catch years.

However, if high rainfall years are actually associated with higher nutrient levels, due to increased runoff from the surrounding land, leading to increased production and therefore a larger banana prawn population, then a high catch in a good rainfall year may represent a similar level of fishing mortality as a small catch in a low rainfall year; i.e. a similar proportion of the initial population probably remains to spawn in both years. Also, industry-based catch rates from this scenario are more likely to reflect prawn biomass than if catch rates are determined by prawns moving more or less offshore and therefore more or less onto the fishing grounds.

In this chapter, we present some analyses of data collected in this and previous projects so that we are able to distinguish between these two hypotheses.
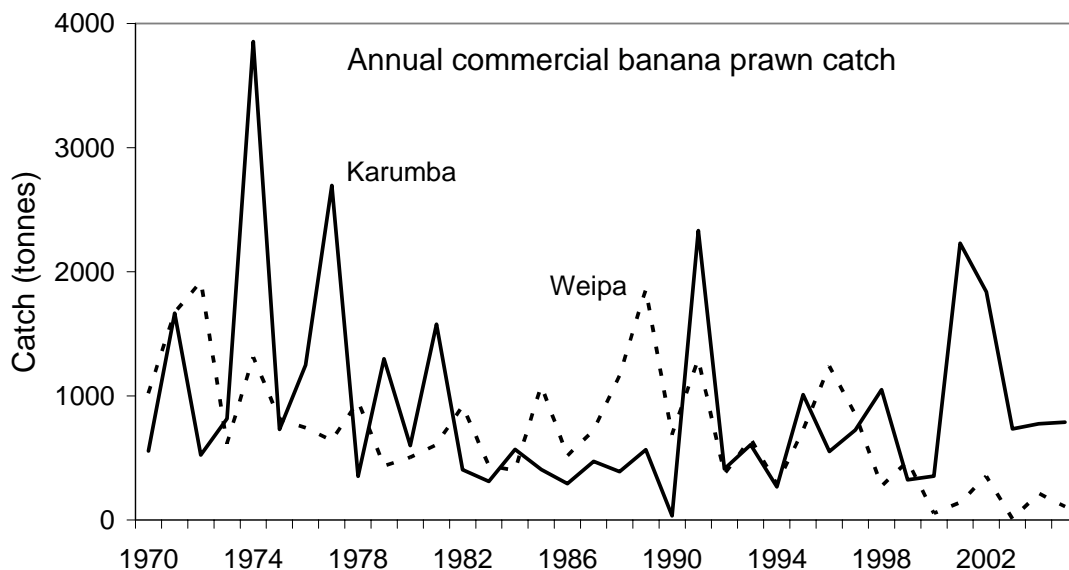
Figure 5.1. Annual commercial catch of adult *Penaeus merguiensis* from Weipa and Karumba in the Gulf of Carpentaria, Australia from 1970 to 2005.

5.3 Methods

Data loggers were installed in the Norman River at Karumba in the southeastern Gulf of Carpentaria and in the Embley River at Weipa in the northeastern Gulf. The loggers were attached to wharves at a fixed height above the river bed near the mouth of each river and recorded water conductivity, water temperature and pressure (water depth). Conductivity was later converted to salinity using equations provided by M. Sherlock (CSIRO) and based on PSS78 equations from IEEE Journal of Oceanic Engineering, January 1980.

The loggers were programmed to (a) take 15 measurements over a 1-minute period every 30 minutes, (b) take an average of the 15 measurements and then (c) store the average value for each variable in the logger every 30 minutes. Every one to two weeks, the data was downloaded from the loggers via a modem and telephone to CSIRO Marine and Atmospheric Research, Cleveland Laboratories. The loggers were in place for the wet seasons of 2002/03, 2003/04, and 2004/05 (December to April each year).

To make comparisons with salinity data collected in earlier projects (Vance et al. 1998), a subset of the salinity data was taken as follows: for three days around each spring tide, three consecutive salinity recordings around each low tide were averaged; i.e. a total of nine recordings contributed to each salinity value.

Daily rainfall, temperature and three-hourly wind speed and direction data recorded at Weipa airport and Normanton airport (about 40 km inland from Karumba) were obtained from the Bureau of Meteorology. Daily rainfall was summed for each two weeks between spring tides.

Estuarine data on juvenile *Penaeus merguiensis* for Weipa was extracted from data sets collected in the Embley River, Weipa from 1986-1992. Juvenile prawns emigrating from the river were sampled every two weeks on spring ebb tides using set

nets. Salinity was also recorded at low tide on spring tides at a site about 14 km upstream from the mouth of the river. See Vance et al. (1998) for more details on the methods.

Estuarine data on juvenile *Penaeus merguiensis* for Karumba was extracted from data sets collected in the Norman River, Karumba from 1975-1979. Juvenile prawns emigrating from the river were sampled using set nets at varying intervals, often quite frequently, but only the data collected every two weeks on spring ebb tides were used in these analyses, to allow consistency between years and with data recorded at Weipa. Salinity data recorded at low tide on spring tides was also extracted from the total data set. The sampling site was about 2 km upstream from the mouth of the river. See Staples & Vance (1986) for more details on the methods.

The location of the data logger in the Norman River was within about 1 km of the sampling site used for the data collected in 1975-79. However, the data logger used at Weipa had to be located about 8 km downstream from the site used in 1986-1992. Therefore the salinities recorded during the current project at Weipa are probably higher than if we had been able to record salinities at the original locations.

Offshore catch rates of banana prawns were obtained from surveys carried out at Karumba in 1977-78, Weipa in 1986-1992 and Weipa and Karumba in 2002-2005. See Chapter 2 for more details on the methods of collection.

Surveys carried out in January and March were used for analyses in this chapter. Catch rates (numbers of prawns per ha) were averaged for several depth categories. For Weipa the depth categories were: < 8 m, 8-10 m, 10-12 m, 12-15 m and all depths. For Karumba, the depth categories were: <= 8 m, 8-10 m, 10-12 m, 12-15 m and all depths. To test the inshore/offshore distribution of prawns during these survey periods, we calculated ratios of catch rates in the shallowest depth categories to catch rates in the deeper depth categories. These ratios were then compared with estuarine salinities and rainfall for the same time periods.

5.4 Results

An example of the raw 30-minute logger data for Karumba is shown in Figure 5.2. The progression of the tidal phase can be clearly seen from the plot of depth by time; from neap tides (low tidal range) to spring tides (high tidal range). In early to mid-January, the conductivity dropped in response to rainfall and then fluctuated dramatically during each daily tidal cycle.
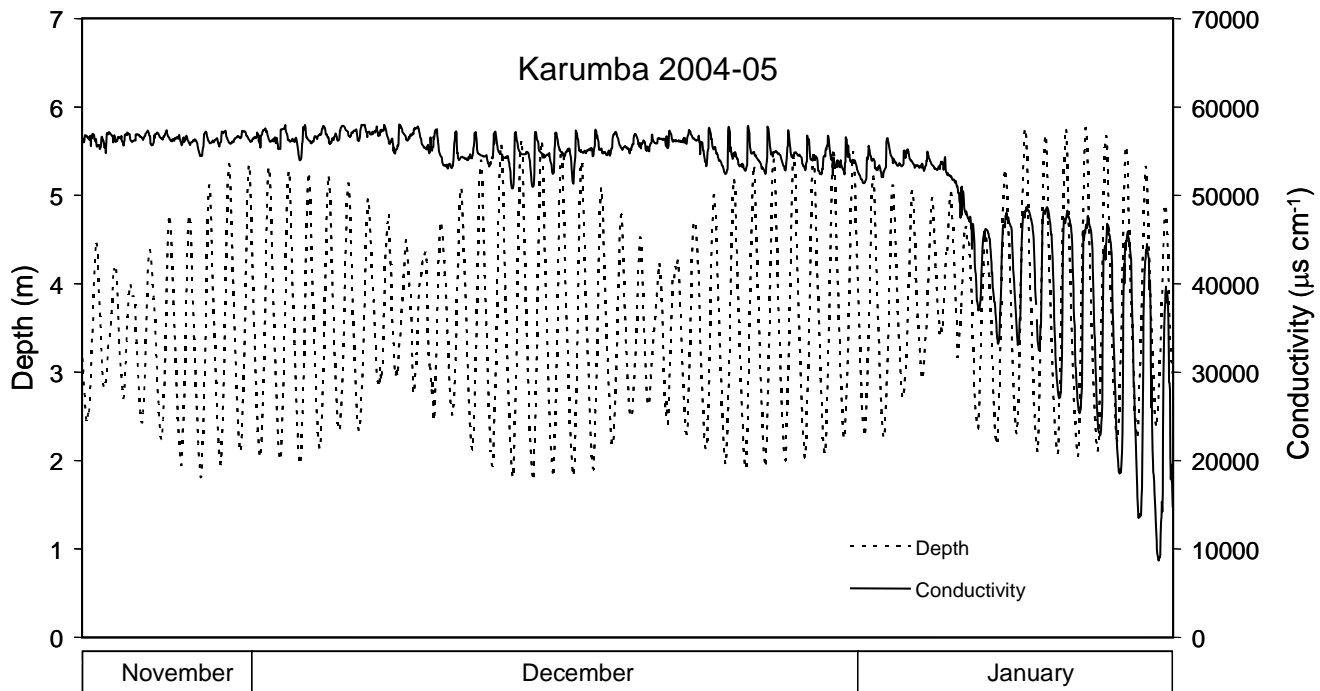
Figure 5.2. Half-hourly records of depth and conductivity recorded at the Raptis wharf in the Norman River, Karumba from 23 November 2004 to 16 January 2005.

The data for January 2005 at Karumba is shown in more detail in Figure 5.3. It can be clearly seen that the conductivity decreases during the ebb tide, reaches a minimum shortly after low tide and then increases again during the flood tide. The decrease is in response to freshwater flowing down from upriver, but this freshwater influence is overcome on the flood tide as high salinity oceanic water re-enters the river.
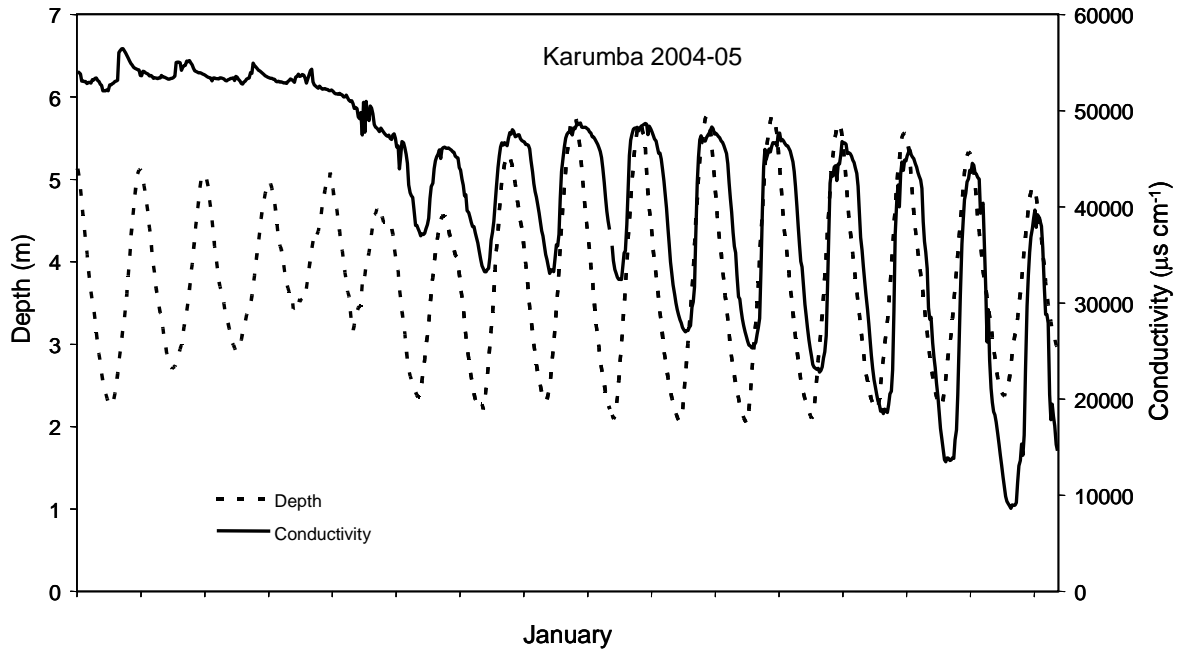
Figure 5.3. Half-hourly records of water pressure (depth) and conductivity recorded at the Raptis wharf in the Norman River, Karumba from 2 to 17 January 2005.
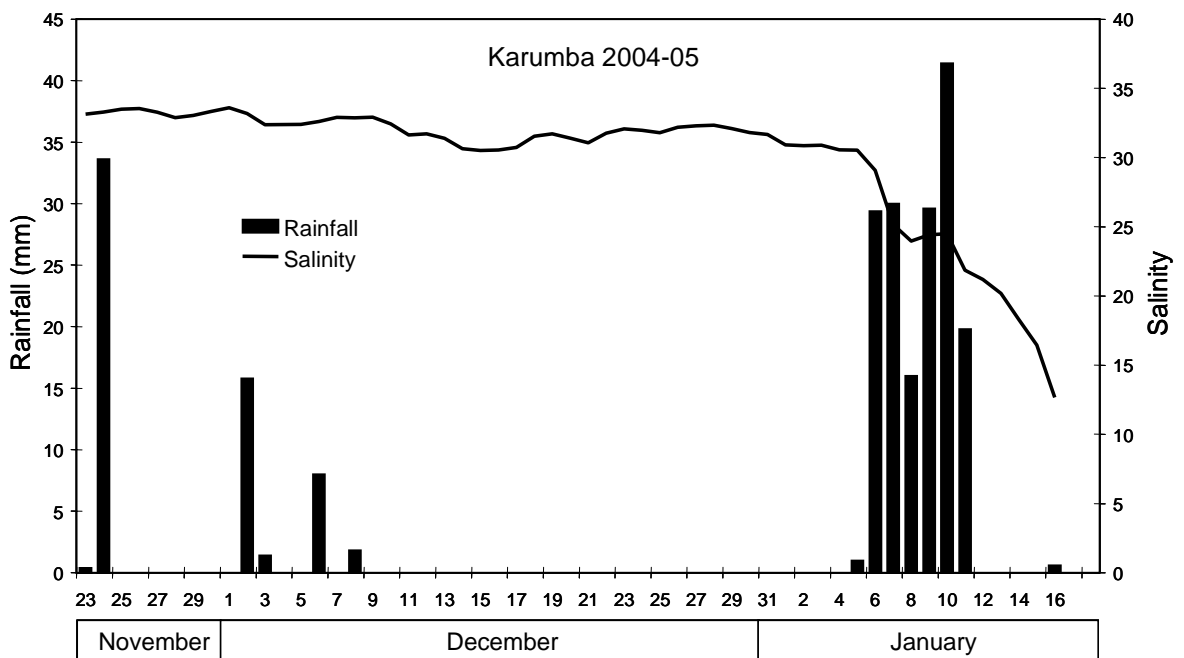
Figure 5.4. Daily summary of salinity recorded at the Raptis wharf in the Norman River, Karumba and daily rainfall recorded at Normanton airport from 23 November 2004 to 16 January 2005.

The 30-minute logger data for Karumba was converted to daily values by simply averaging the data for each variable for each day and then compared with daily rainfall data recorded at Normanton (about 40 km inland) (Figure 5.4). It can be seen that a single day's rainfall of around 30 mm in November has almost no impact on the salinity in the river system near the mouth. However, six successive days of rainfall in early January (minimum 16 mm; maximum 41.4 mm) resulted in a substantial decrease in average salinity; from about 30 to about 13.

5.4.1 Weipa analyses

5.4.1.a Emigrants from river samples vs. rainfall or salinity

Salinity, rainfall and juvenile banana prawn emigration data from the Albatross Bay study of 1986-1992 were compared with data from the current project – 2002-2005 (Figure 5.5). Rainfall levels and salinities recorded in the current project were comparable with those recorded in 1986-92 but salinity was not as low as in early 1991. It must be noted that, because the location of the data logger at Weipa in the current study was downstream from the salinity recording locations used in the earlier study, the salinities recorded during the current project are probably higher than if we had been able to record salinities at the original locations.

There is a significant relationship between mean wet season salinity and banana prawn emigrants over the six years of the earlier study (Figure 5.6). Lower salinities were associated with increased numbers of emigrants from the estuary. The expected numbers of emigrants in 2002-2005, based on the mean salinity levels were in the mid-range of values seen in 1986-92 but the range of expected values was not as great as in the earlier study.

5.4.1.b Banana prawn from trawl surveys vs. salinity and rainfall

We were unable to detect any strong relationship between estuarine salinity and the inshore/offshore distribution of banana prawns in January or March; i.e. before the start of the fishing season. We compared the ratios of the catch rates of banana prawns in inshore waters (< 8 m) to catch rates in a range of other deeper waters with the mean estuarine salinity from December to February each year. In all cases there was a slight negative relation between the ratio of inshore to offshore catches and salinity, but the relationship was not significant, and, in fact, the negative slope was really only due to data from one extreme year (1989) (Figure 5.7). Ratios of all depth categories for January and March were compared and produced similar results to those shown in Figure 5.7.
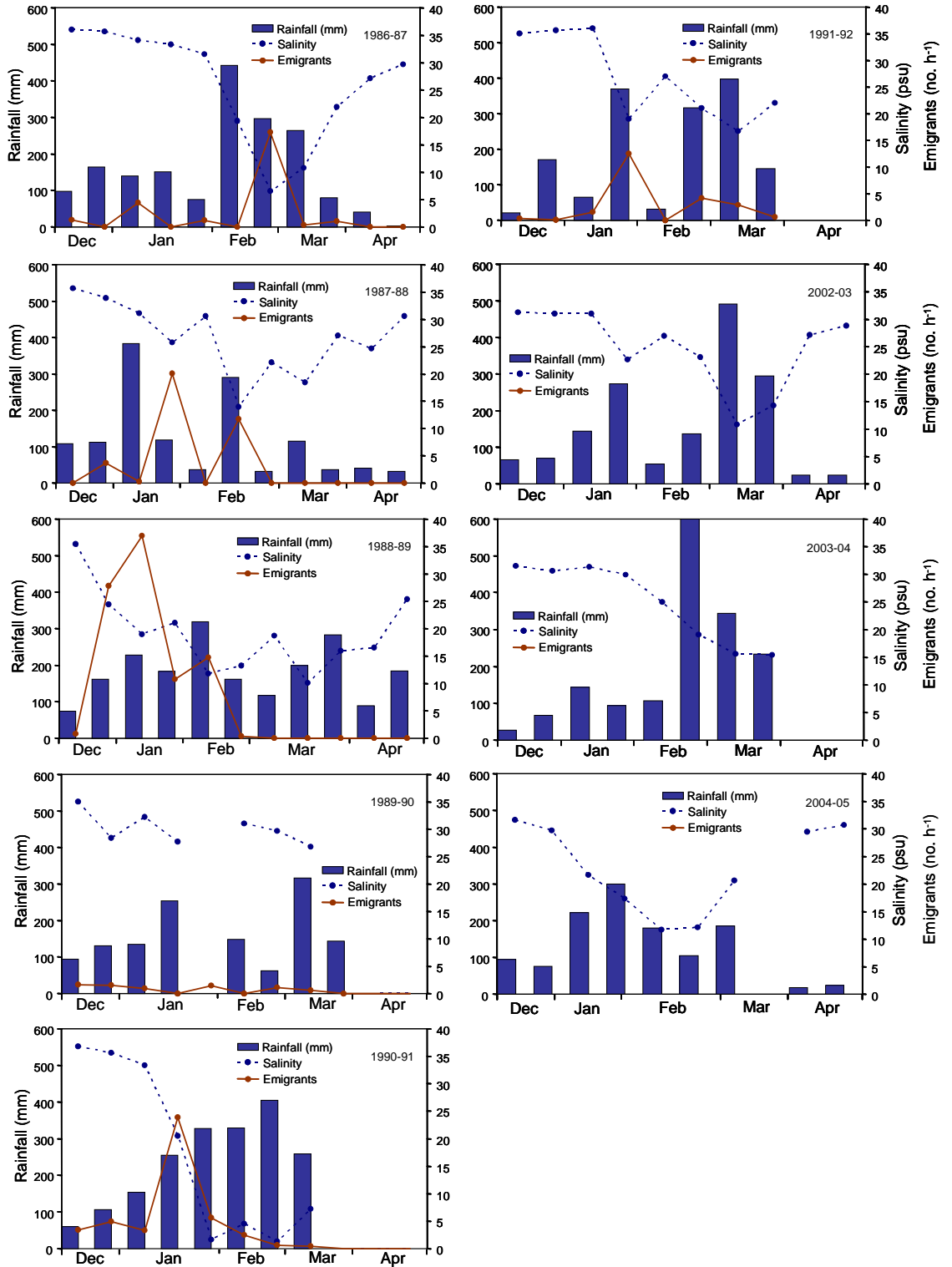
Figure 5.5. Salinity recorded in the Embley River, Weipa at two-weekly intervals and rainfall accumulated over each two weeks between December and April for the years 1986-1992 and 2002- 2005. Emigrating banana prawns recorded at two-weekly intervals for the years 1986-1992.
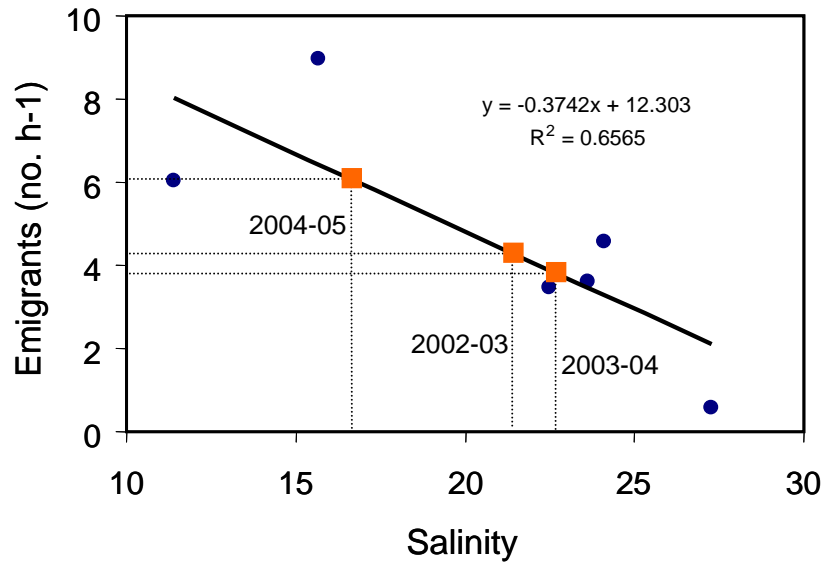
Figure 5.6. Salinity and juvenile banana prawn emigrants in the Embley River, Weipa averaged over December to February each year and the regression line for 1986-1992 (●). Expected values of emigrants for 2003 to 2005 are plotted based on the mean salinity values for those years and assuming emigration follows the regression line based on historical data (■).
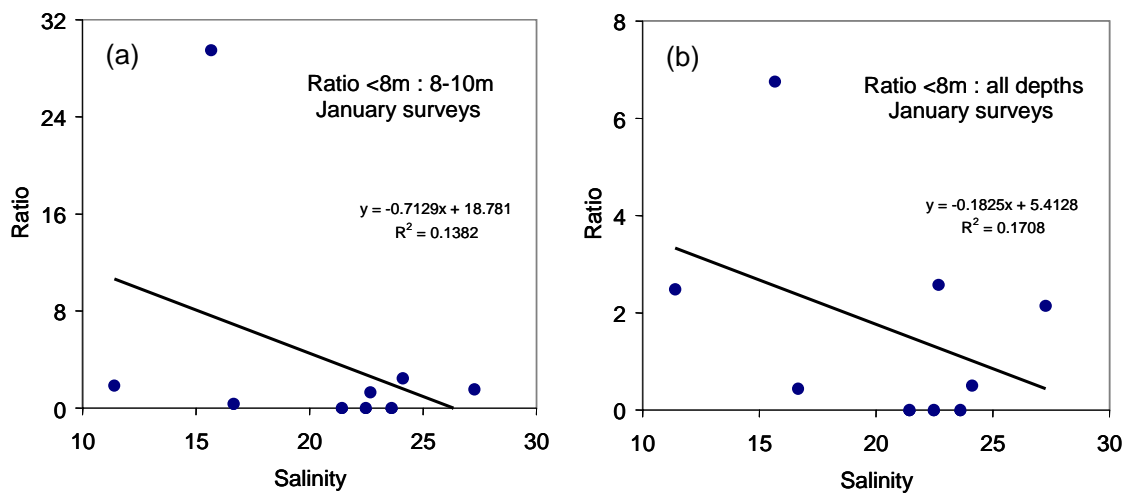
Figure 5.7. The ratio of mean banana prawn catch rates in January survey catches in Albatross Bay, Weipa from less than 8 m of water to (a) catch rates in 8-10 m and (b) catch rates in all depths surveyed plotted against the mean estuarine salinity from December to February each year for 1986-1992 and 2002-2005.

5.4.2 Karumba analyses

5.4.2.a Emigrants from river samples vs. rainfall or salinity

Salinity, rainfall and juvenile banana prawn emigration data from the Norman River study of 1975-1979 were compared with data from the current project – 2002-2005 (Figure 5.8). Overall rainfall levels were lower in the current project than for

three of the four years surveyed in the late 1970s. In only 2003-04 did estuarine salinities reach the low levels of 1975-76 and 1978-79, and even then, not for such extended periods.
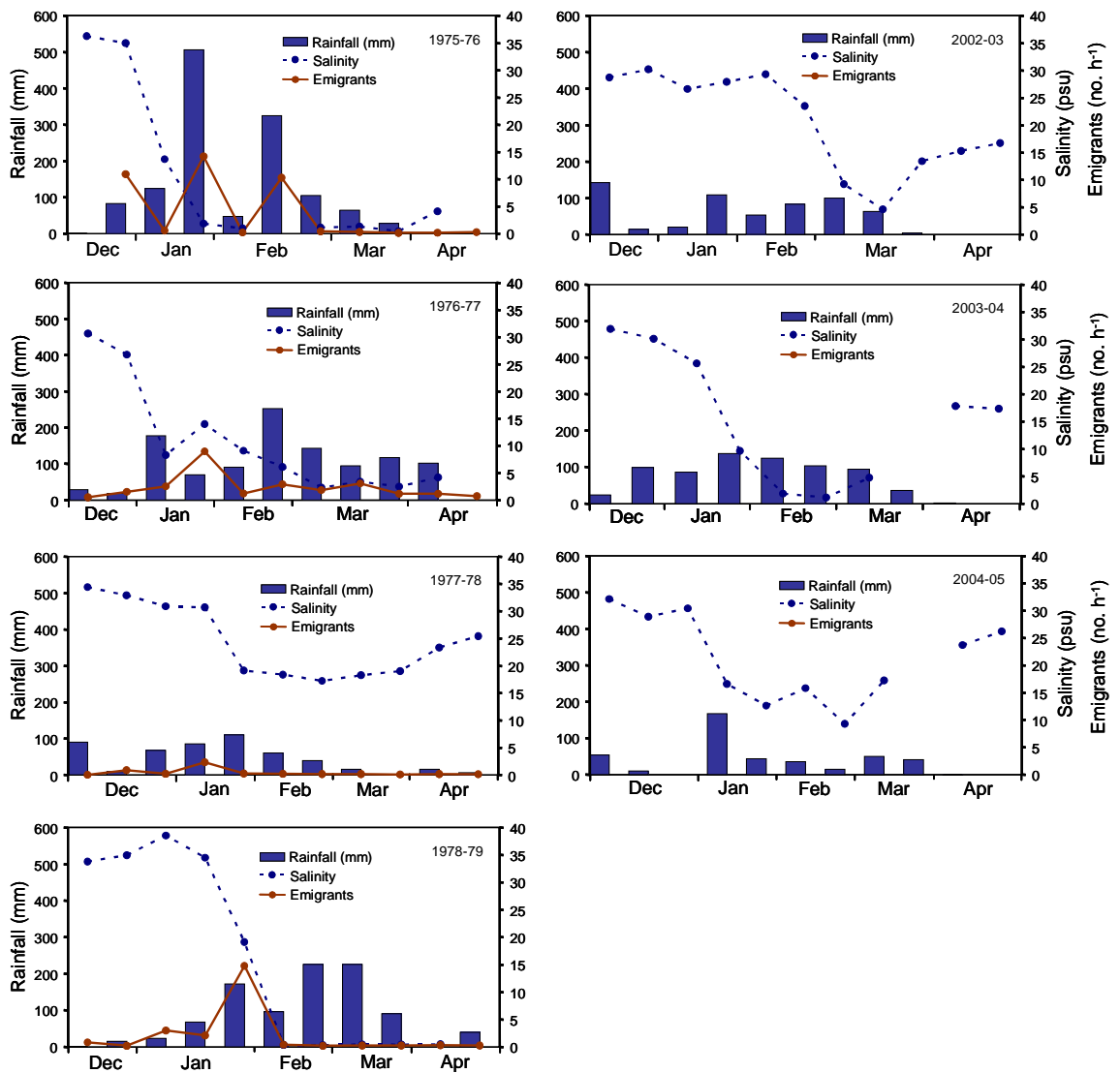
Figure 5.8. Salinity recorded in the Norman River, Karumba at two-weekly intervals and rainfall accumulated over each two weeks between December and April for the years 1975-1979 and 2002- 2005. Emigrating banana prawns recorded at two-weekly intervals for the years 1975-1979. No emigrant data is available for recent years

There is only a weak relationship between mean wet season salinity and banana prawn emigrants over the four years of the earlier study. Lower salinities were associated with increased numbers of emigrants from the estuary, although the relationship was not significant. However, there was a much stronger relationship between total wet season rainfall and banana prawn emigrants (Figure 5.9). The expected numbers of emigrants in 2002-2005, based on the rainfall levels were at the lower end of the range of values seen in 1975-79 and the range of expected values was not as great as in the earlier study.
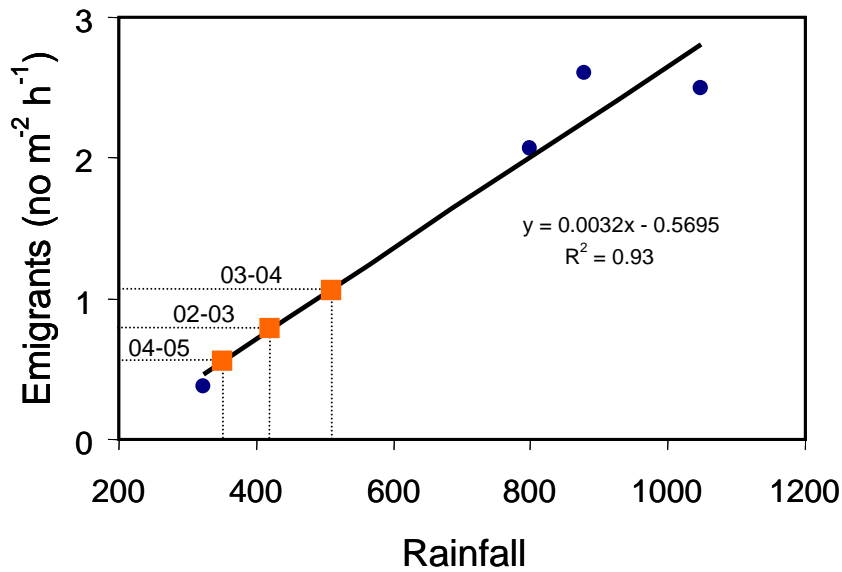
Figure 5.9. Rainfall totals for December to February each year and juvenile banana prawn emigrants in the Norman River, Karumba averaged over December to February each year and the regression line for 1975-1979 (●). Expected values of emigrants for 2003 to 2005 are plotted based on the rainfall values for those years (■).

5.4.2.b Banana prawn from trawl surveys vs. salinity and rainfall

We were unable to detect any strong relationship between estuarine salinity (Figure 5.10) or total rainfall (Figure 5.11) and the inshore/offshore distribution of banana prawns in January or March; i.e. before the start of the fishing season. We compared the ratios of the catch rates of banana prawns in inshore waters (< 8 m) to catch rates in a range of other deeper waters with the mean estuarine salinity and the total rainfall from December to February each year. In all cases there was no significant relationship between the ratio of inshore to offshore catches and salinity or rainfall. Ratios of all depth categories for January and March were compared and produced similar results to those shown in Figure 5.10 and Figure 5.11.
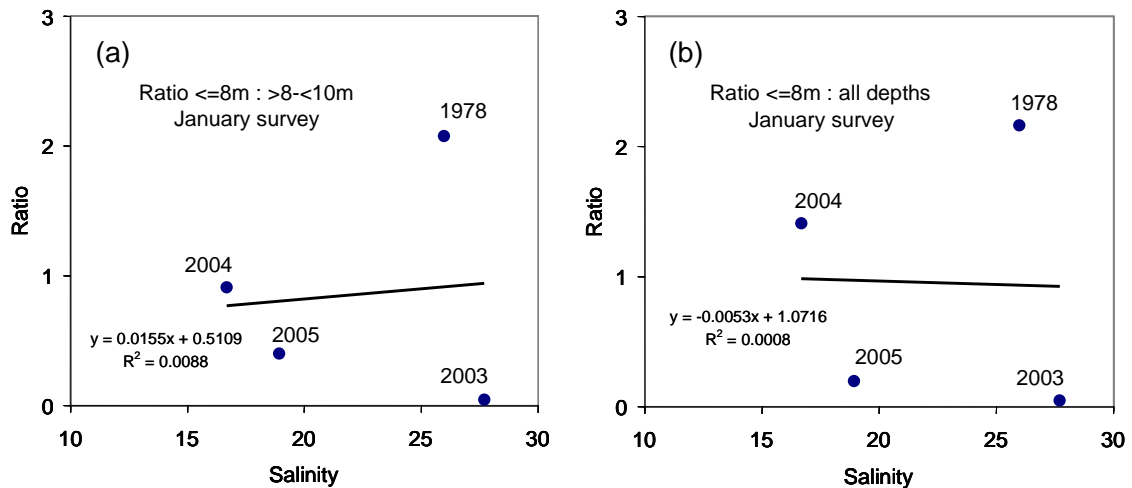
**Figure 5.10. The ratio of mean banana prawn catch rates in January survey catches in the southeastern Gulf of Carpentaria from less than 8 m of water to (a) catch rates in 8-10 m and (b) catch rates in all depths surveyed plotted against the mean estuarine salinity from December to February each year for 1977-1978 and 2002-2005.**
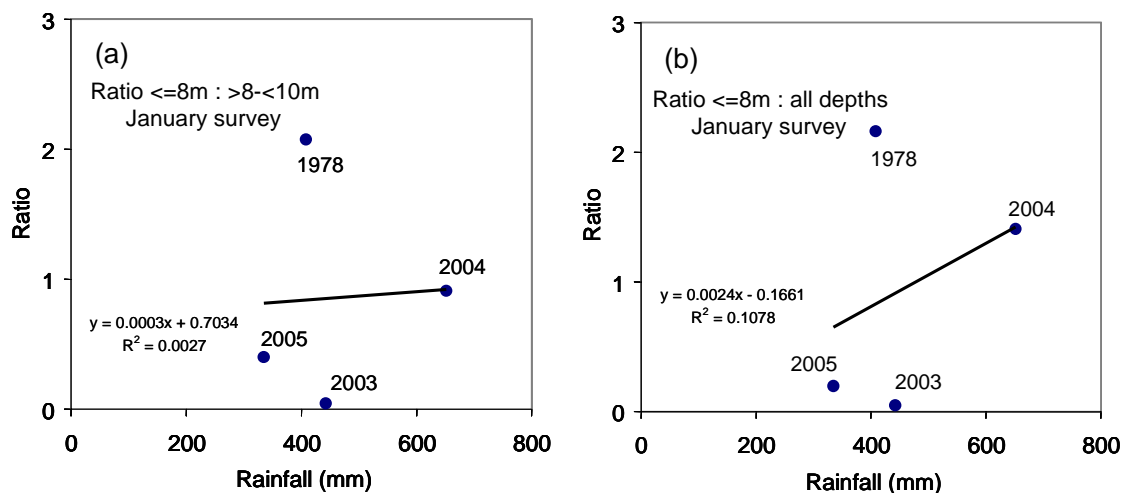
Figure 5.11. The ratio of mean banana prawn catch rates in January survey catches in the southeastern Gulf of Carpentaria from less than 8 m of water to (a) catch rates in 8-10 m and (b) catch rates in all depths surveyed plotted against the total rainfall from December to February each year for 1977-1978 and 2002-2005.

5.5 Discussion

Relationships between rainfall or salinity, and penaeid prawn migrations in many countries have been well documented (Dall et al. 1990). These generally refer to the immigration or emigration of prawns from river systems. In the Gulf of Carpentaria, increased emigration of juvenile *Penaeus merguiensis* from rivers in the Albatross Bay and Karumba regions has been shown to be associated with periods of high rainfall or lower salinities (Staples & Vance 1986, Vance et al. 1998). Significant

positive correlations have also been demonstrated between rainfall and offshore commercial catches of adult *Penaeus merguiensis* in the Karumba region (Vance et al. 1985, Vance et al. 2003) but not for rainfall or salinity in the Albatross Bay region (Vance et al. 2003).

There has been much speculation over many years as to the migration pathways and the distribution of sub-adult and adult *Penaeus merguiensis* after the prawns leave the rivers in the Gulf of Carpentaria, but there has been no formal data available to enable us to clearly understand the distribution of the prawns in the shallow coastal waters. Once prawns reach the deeper offshore waters (> 8 m) they are available for capture by the fishing fleet and prawn distribution in these areas has been better documented, by research surveys and by commercial catch records.

The banana prawn fishery in the Gulf of Carpentaria occurs in April/May each year and targets mainly prawns that have newly recruited to the fishing grounds from inshore areas. Although much spawning does occur in April/May, most of the spawning that gives rise to larvae that will produce next year's population actually occurs later in the year (August – October). Therefore, the critical spawning population of *Penaeus merguiensis* in the Gulf is composed mainly of prawns that are not caught by the commercial fishery earlier in the year. An important question for managers of the fishery to answer is: what proportion of the total prawn population each year is actually caught by the fishing fleet, and consequently, what proportion is left to produce next year's crop?

A corollary of this question is then: what proportion of the prawn population remains inshore of the commercial fishing grounds each year, safe from commercial fishing, and does the proportion vary from year to year in response to rainfall or salinity changes? We have only anecdotal evidence to suggest that there are differences between years, mainly from years of extreme environmental events. For example, in 1974, high rainfall and severe flooding affected many southern Gulf rivers, and caused freshwater to extend out into the Gulf waters. In this year, commercial catches of *Penaeus merguiensis* were made a long way offshore outside the fishery closure line and before the fishing season within the closure began. In other very dry years, fishermen using gill-nets to catch fin fish in the shallow coastal waters have reported seeing and catching large quantities of small adult banana prawns in their gill nets. However, in less extreme years, is there still a relationship between the distribution of adult *Penaeus merguiensis* and rainfall or salinity that is not so obvious but that would still mean that the proportion of the population actually fished by the fishing fleet changes from year to year?

In this project we have not been able to survey as close to the coastline as we would have liked due to limitations imposed by the size of the commercial fishing vessels used for the surveys. However, we have analyzed the available survey data in such a way as to give us some indication of any trends in distribution of the prawns related to rainfall and salinity for the corresponding years.

Our conclusion, based on the data available, is that there seems to be no relationship between rainfall or salinity, and the inshore/offshore dispersion of *Penaeus merguiensis* at Weipa or Karumba. This conclusion is strongest for Weipa, where we had nine years of data to analyze. This conclusion seems consistent with earlier studies of environment and commercial catch at Weipa (Vance et al. 1985, Vance et al. 2003).

Unfortunately, in Karumba, the region where the relationship between rainfall and juvenile prawn emigration is strongest, the results need to be treated with much more caution. In Karumba, we only had four years of data to use in the analysis. Also the variation in rainfall over the three years of the current project has been quite low and there has also not been great variation in survey catches.

Inspection of annual commercial catches of *Penaeus merguiensis* in the Karumba region suggests that there may be a negative relationship between high commercial catches and subsequent spawning success. This fishing ground is characterized by large year-to-year fluctuations in banana prawn commercial catches. The years of high catch tend to be associated with high rainfall. However, there is often a year of relatively low catch following a good catch year (Figure 5.1). The reason for these very low catch years may be, at least in part, a result of a lower spawning stock in the previous year, because the high rainfall meant that a larger proportion of the population was available for capture by the fishery. This is contrary to the conclusions stated previously based on the recent survey data at Karumba. This question needs to be revisited in future years when further data has been collected by the NPF Monitoring project.

It is interesting that the largest annual variations in commercial catch of *Penaeus merguiensis* occur in regions where there seems to be a significant relationship between rainfall and commercial catch (Karumba, Mornington, Vanderlins). Commercial catches at Weipa, where there is not a strong rainfall relationship, are much less variable between years.

Clearly, further data and analyzes are needed, particularly for the Karumba region. The Northern Prawn Fishery prawn monitoring series of projects began at about the same time as this project and there has been considerable overlap between the projects. The same sampling sites are used for Albatross Bay, Karumba and Mornington Island. The NPF monitoring surveys will continue into the future, funded largely by the fishing industry so new data on the distribution of prawns in January will continue to become available. The data loggers installed during this project by CSIRO will continue to be serviced and monitored. It is important that catch rates from future January surveys and rainfall and salinity recorded using the loggers should continue to be analyzed to provide further data to help confirm or deny our results.

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CHAPTER 6: IS CATCHABILITY DENSITY-DEPENDENT FOR SCHOOLING PRAWNS?

Is catchability density-dependent for schooling prawns?

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Abstract

Banana prawns, *Penaeus merguiensis*, in the Gulf of Carpentaria, Australia typically form dense aggregations during a fishing season. It has been speculated that catchability decreases significantly as the fishing season progresses and stock size decreases. We used commercial catch effort data from 1987 to 2004 for three stocks in the Gulf to investigate whether density-dependent catchability exists in this species of aggregating penaeid. We developed two stochastic models based on an improved depletion method, one assuming a linear relationship between catchability and abundance and the other assuming a nonlinear power function between catchability and abundance. A stock-specific annual catchability coefficient, initial biomass, and a shape parameter of the power function were estimated using maximum likelihood or hierarchical Bayesian approach (for density-independent catchability models). For the majority of the datasets, the two models result in similar estimates. Although a weak but statistically significant density-dependent catchability, either positive or negative, was detected in about one fifth of the datasets, there is no clear pattern that points to positive density-dependence as suggested by previous studies. With all years and stocks combined, the density-dependent parameter in the second model has an overall mean of −0.03 and a standard deviation of 0.57 from all datasets, and its distribution looks approximately normal. However, a between year negative power function relationship between catchability and abundance appears to exist in this prawn species.
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Keywords: Catchability; Density-dependent; Prawn; Biomass; Binomial distribution; Maximum likelihood; Hierarchical Bayesian

1. Introduction

The catchability coefficient is one of the key parameters for fish stock assessment. This quantity, commonly denoted as q, can be interpreted as the probability of capturing one particular individual from the population by one unit of effort, or the proportion of fish in the population being caught per unit of effort. Catchability has been widely considered as a constant for a particular fishery, although it has been recognized that catchability is determined by availability and vulnerability of fish (Francis et al., 2003), which in turn are affected by many factors such as distribution of fish, abundance, fish behaviour, population biology, environmental conditions, fishing gear efficiency, distribution of fishing fleet, and fishing strategy, etc. (Swain and Sinclair, 1994; Arreguin-Sanchez, 1996; Addison et al., 2003; Salthaug

and Aanes, 2003). Debate on whether q depends on abundance has continued since Paloheimo and Dickie (1964) suggested that catchability would change with abundance. It is conceivable that catchability may not be constant due to such factors as random variation, gear competition or cooperation, and spatial and temporal effects (Quinn and Deriso, 1999). Among the publications that assert that q varies with abundance, the majority of them claim that catchability is a negative power function of abundance, i.e., q increases as abundance declines (Bannerot and Austin, 1983; Shardlow and Hilborn, 1985; Angelsen and Olsen, 1987; Crecco and Overholtz, 1990; Rose and Leggett, 1991; Arreguin-Sanchez, 1996). Because of the importance of this parameter, there has been extensive research on the effect of abundance on catchability. However, the majority of work comes from fish species. There are few studies on the relationship between catchability and abundance of *Penaeus* species (but see Griffin et al., 1997 on the standardization of fishing effort of a shrimp fleet; Perez and Defeo, 2003 on the catchability and CPUE of shrimps; Die and Ellis, 1999 on the depletion of aggregated prawns).

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The Northern Prawn Fishery (NPF) is one of the most valuable fisheries in Australia. The NPF has produced 2157–7245 tonnes of banana prawns (*Penaeus merguiensis*) annually since 1987 (Perdrau and Garvey, 2004). Banana prawns in the Gulf of Carpentaria form dense aggregations that are targeted by trawl vessels. Using logbook data from 1991 and 1992, Die and Ellis (1999) estimated that in the first 3 weeks of the fishing season the number of aggregations decreased by 83% and the average biomass of an aggregation decreased by 93%. Together, they estimated that a decline of 99% of the total biomass occurred in the first 3 weeks. This was considerably greater than the 66% decrease that can be estimated from catch per unit effort data. They suggested that catchability is positively related to stock abundance: catchability decreases significantly as the stock size decreases.

Vance et al. (2003) conducted the first stock assessment analysis for banana prawns in the NPF. Based on Die and Ellis's suggestion of a positive power function between q and biomass, they estimated a positive power function for three of the seven stocks in the NPF. Since the model they used was considered as preliminary, they strongly recommended that further research was needed and identified that the relationship between catchability and abundance is of particular importance.

This paper is motivated by Die and Ellis's research and the quantitative modelling by Vance et al. (2003). Our main objective is to investigate whether catchability changes as abundance declines over the fishing season.

The primary source for our study is commercial logbook data. We use a binomial model to capture the dynamics of the fishable population over time during each fishing season. The model is based on the concept of Leslie and DeLury removal or depletion methods which have been widely applied in fishery research (Mahon, 1980; Farman et al., 1982; Cowx, 1983; Akamine, 1990; Akamine et al., 1992; Hilborn and Walters, 1992; Riley and Fausch, 1992; Maceina et al., 1993, 1995; Rider et al., 1994; Volstad et al., 2000; Burridge et al., 2003; McAllister et al., 2004; Young et al., 2004; Wright et al., 2006). The traditional depletion methods assume that: the population is closed, i.e., there is relatively little emigration and immigration during the fishing period; the catchability and natural mortality are constant throughout the fishing period; a linear relationship holds between catch rate and abundance. In our study, we also assume that recruitment into the fishable population and migration in and out of the fishing grounds are insignificant during the relatively short fishing season. However, because our main interest is to test whether catchability is dependent on population density, in one of our models we assume that the catchability coefficient varies over time as abundance decreases in the season. We did not use the traditional regression approach, rather used more robust maximum likelihood estimation (MLE) (Schnute, 1983; Loneragan et al., 1995) for each stock-year, and used hierarchical Bayesian model (HBM) for meta-analysis of combined data (Liermann and Hilborn, 1997; Adkison and Su, 2001; Harley and Myers, 2001; Su et al., 2001; Rivot and Prevost, 2002; McAllister et al., 2004). Also, instead of modelling catch per unit effort data, we directly modelled the catch as a binomial process, an approach similar to Schnute (1983), Bedrick (1994), Warren

(1994), Loneragan et al. (1995), Wang and Loneragan (1996), and Wang (1999). Further, we expanded the technique by incorporating stochastic fishing processes (Dupont, 1983; Sampson, 1988), natural mortality, overdispersion, and a nonlinear relationship between catchability and abundance into our modelling. However, HBM had difficulties dealing with models that include a density-dependent catchability function. As a result HBM was applied only to density-independent catchability models. Hence, we focused on the MLE results for the density-dependent and density-independent catchability models to examine the relationship between catchability and abundance within each fishing season. We reported the HBM results for the density-independent models only to examine the across-year relationship between catchability and abundance. The detailed comparisons between MLE and HBM for density-independent catchability models will be reported elsewhere (Zhou et al., in review).

2. Methods

2.1. Data

The primary data come from augmented commercial logbook records (personal observations). There are 11 banana prawn stock regions in the NPF. Among these, three major stocks are found in the southeast Gulf of Carpentaria (SE GoC, Stock 9), east Gulf of Carpentaria (E GoC, Stock 10) and Albatross Bay (Stock 11). The E GoC stock includes statistical areas of Keerweer, Edward, and Mitchell as defined by the Australian Fisheries Management Authority (Perdrau and Garvey, 2004). Other stocks typically have too low catches in many years to allow a complete analysis using the model described below. The NPF started in the late 1960s. It was a year-round fishery in the early years. Since 1987, the fishing season for banana prawns has been largely constrained to less than 2 months each year. Such a management practice provides ideal data for depletion analysis. We have a total of 54 datasets from 1987 to 2004 from these three stock regions. However, there were too few fishing days and too little catch on two occasions: the SE Gulf in 1990 and Albatross Bay in 2003 to allow for any analysis. Therefore, we excluded these two datasets.

2.2. Density-independent catchability model

Catch in a fishery can be expressed in a classical form as (Quinn and Deriso, 1999):

$$C = \frac{qE}{z} N_0 (1 - e^{-z}), \tag{1}$$

where C denotes catch, q the catchability coefficient, E the fishing effort, z the total instantaneous mortality, and N_0 is the initial population size of target species. The total mortality $z = F + m$, where instantaneous fishing mortality $F = qE$, and m is the instantaneous natural mortality. From this relationship q is derived as

$$q = \frac{C}{E\bar{N}}, \tag{2}$$

where $\bar{N}$ is the integral average population size over one unit of time.

A prawn's fate on the fishing ground follows a Bernoulli process: either being caught or not. If a prawn is not caught, it either survives or dies due to natural mortality. Let us assume the abundance of a prawn stock is n_i and the observed catch is C_i in fishing time i in days. If $p_{c,i}$ is the probability of a prawn being caught, and $(1 - p_{c,i})$ is the probability of a prawn not being caught, the status of the stock can be described by a binomial distribution:

$$\Pr[C_i] = \frac{n_i!}{C_i!(n_i - C_i)!}p_{c,i}^{C_i}(1 - p_{c,i})^{n_i - C_i}. \tag{3}$$

Because total mortality during period i is $z_i = m(t_i - t_{i-1}) + q_2 E_i$, where q_2 = catchability coefficient (subscript 2 denotes the density-independent model involving 2 parameters), E_i = observed fishing effort (number of boat-days), m = instantaneous natural mortality, and t_i = sequential fishing date, the fraction of catch is

$$p_{c,i} = \frac{q_2 E_i}{z_i}(1 - \exp(-z_i)). \tag{4}$$

Substituting (4) into (3), we get the probability function of the density-independent catchability model:

in the population are mutually independent in responding to fishing process. This condition is hardly met by schooling prawns. Die and Ellis (1999) showed that in the Gulf of Carpentaria banana prawns form dense aggregations during the commercial fishing season. The sizes of aggregations are typically several hundred kilograms, but may vary from 10 to 10,000 kg. Our analysis shows that variance is underestimated if we model the catch in number of animals. This indicates that overdispersion occurs when the model uses raw data. We corrected this overdispersion problem using the following steps. First, we used raw data in model (5) to obtain initial model parameter estimates and a dispersion parameter $\hat{\phi}$:

$$\hat{\phi} = \frac{\chi^2}{k - p}, \tag{7}$$

where k is the number of observations, p the number of parameters, and χ^2 is the Pearson's chi-squared statistic:

$$\chi^2 = \sum_{i=1}^{k}\frac{n_i(C_i/n_i - p_{c,i})^2}{p_{c,i}(1 - p_{c,i})}. \tag{8}$$

Secondly, we divided abundance and catches by this dispersion parameter $\hat{\phi}$ and re-estimated parameters in model (5) and their

$$\Pr[C_i|q_2, n_{02}] = \frac{n_i!}{C_i!(n_i - C_i)!}\left[\frac{q_2 E_i}{m(t_i - t_{i-1}) + q_2 E_i}(1 - \exp[-m(t_i - t_{i-1}) - q_2 E_i])\right]^{C_i}$$

$$\times \left[1 - \frac{q_2 E_i}{m(t_i - t_{i-1}) + q_2 E_i}(1 - \exp[-m(t_i - t_{i-1}) - q_2 E_i])\right]^{n_i - C_i}, \tag{5}$$

where q_2 and n_{02} (the initial prawn abundance from the density-independent model of 2 parameters) are parameters to be estimated. The number of prawns surviving from fishing and natural mortality in one unit of time is

$$n_i = n_{i-1}\exp^{-z_i}. \tag{6}$$

Eq. (6) is the basis of the DeLury depletion model (Hilborn and Walters, 1992). We can obtain the likelihood function by multiplying the fishing process of Eq. (5) over the entire fishing season. In Eq. (5), daily catch C_i, effort E_i, and date t_i are observed data. The instantaneous natural mortality rate, m, is assumed to be 0.05 per week (Lucas et al., 1979). Since 1987 the banana prawn fishing season has only lasted for a few weeks each year, starting in April and ending in May or June. In such a short period the impact of natural mortality on the parameter q and n_0 is not substantial. We tested the impact of natural mortality by changing m from 0.01 per week to 0.09 per week and found that the results remain similar. The log-likelihood function can be maximized to estimate the initial abundance n_0 and the catchability coefficient q.

The binomial model requires that the daily catch C_i and the initial abundance n_0 be discrete numbers of animals. However, the prawn fishery catch is recorded as weight in kilograms. Because the size of banana prawns caught in the fishery does not change during the April–June fishing season (Zhou et al., unpublished data), weight can be converted into number of animals. Theoretically, the binomial distribution requires that n_i animals

associated confidence intervals. The rescaled $n_i/\hat{\phi}$ and $C_i/\hat{\phi}$ are regarded as binomially distributed. After re-fitting we estimated and examined the new dispersion parameter again to ensure that it is close to 1. We recognized that the function obtained by dividing a log-likelihood function for the binomial distribution by a dispersion parameter is not a legitimate log-likelihood function. It is example of a quasi-likelihood function (McCullagh and Nelder, 1989). This technique has been used in a similar manner for prawns species split (Dichmont et al., 2001). Most of the asymptotic theory for log-likelihoods also applies to quasi-likelihoods, which justifies computing standard errors and likelihood ratio statistics using quasi-likelihoods instead of proper log-likelihoods (McCullagh and Nelder, 1989).

2.3. Density-dependent catchability model

In this model we assume catchability is a density-dependent variable. A power function has been found in many fish species and we adopt this in this study, i.e.

$$Q_i = an_i^b, \tag{9}$$

where a and b are parameters to be estimated. To facilitate comparison with q in the density-independent catchability model, we used the following relationship:

$$Q_i = q_3\left(\frac{n_i}{n_{03}}\right)^b. \tag{10}$$

Note because $n_1 = n_{03}$, $Q_1 = q_3$, which can be compared with q_2 in the density-independent catchability model. Also, when $b = 0$, $Q_i = q_3$, exactly as the density-independent catchability model. Accordingly, the probability function of the density-dependent catchability model can be re-written as

calculated as

$$\Delta n_0 \% = \frac{n_{02} - n_{03}}{n_{03}}. \tag{12}$$

$$\Pr[C_i | q_3, b, n_{03}] = \frac{n_i!}{C_i!(n_i - C_i)!} \left[\frac{q_3(n_i/n_{03})^b E_i}{m(t_i - t_{i-1}) + q_3(n_i/n_{03})^b E_i} \left(1 - \exp\left[-m(t_i - t_{i-1}) - q_3 \left(\frac{n_i}{n_{03}} \right)^b E_i \right] \right) \right]^{C_i}$$

$$\times \left[1 - \frac{q_3(n_i/n_{03})^b E_i}{m(t_i - t_{i-1}) + q_3(n_i/n_{03})^b E_i} \left(1 - \exp\left[-m(t_i - t_{i-1}) - q_3 \left(\frac{n_i}{n_{03}} \right)^b E_i \right] \right) \right]^{n_i - C_i}. \tag{11}$$

By taking the logarithm and summarizing the fishing process over the entire season, we can derive a similar likelihood function for the density-dependent catchability model as in model (5). We also applied the dispersion parameter $\hat{\phi}$ obtained from Eq. (7) in this density-dependent catchability model and ensured that overdispersion did not occur in the final model.

2.4. Model comparison

We used the scaled Pearson's chi-square test for assessing the goodness of fit of the density-independent and density-dependent catchability models. We choose $\alpha = 0.05$ as the significance level. The degree of freedom equals the number of fishing days minus the number of parameters in the model (i.e., 2 or 3). We used two criteria to compare the density-independent and density-dependent catchability models and to determine which model fits the data better. First, we used the likelihood ratio test to evaluate whether including a density-dependent parameter in catchability coefficient would improve the model. As the likelihood ratio has a chi-squared distribution, the density-dependent catchability model is considered better if the likelihood ratio statistic is greater than the standard chi-square distribution at $\alpha = 0.05$ with one degree of freedom (i.e., 3.84). Second, we calculated the bias corrected Akaike information criterion to see which model best fits the data (Burnham and Anderson, 2002; Johnson and Omland, 2004). However, since the results are similar to that obtained by the likelihood ratio test, we did not include them in this paper.

We also attempted to obtain the profile likelihood confidence intervals for all parameters in each model. This can be done for most of the parameters of the density-independent catchability model. However, it was very difficult to estimate the confidence intervals for the parameters in the density-dependent catchability model.

2.5. Deviation of estimated initial biomass between the two models

The initial biomass n_0 is a key parameter that is needed for stock assessment and fishery management. Theoretically, the depletion model could estimate "fishable" abundance. The density-independent and density-dependent catchability models may produce different numbers. The relative deviation is

Assuming the density-dependent catchability model is the true one, $\Delta n_0 \%$ is the relative bias of initial biomass when using the density-independent catchability model.

2.6. Hierarchical Bayesian models

Hierarchical Bayesian approach allows sharing information between different datasets. In our study we have three key stock regions where catch and effort comprise the majority of the data in NPF. Each stock region has 18 years of data (1987–2004) when fishing season started in April. We assumed that, within each stock region, fishing process and the prawn behaviour were similar in some respects from year to year. Then simultaneously estimating the parameters of all years of data should result in better estimations. As previously described, we considered the observed daily catch data as a binomial distribution:

$$C_{y,i} \sim \text{binomial } (n_{y,i}, p_{y,i}),$$

where $n_{y,i}$ and $p_{y,i}$ involve two data-level parameters: the annual catchability coefficient q_y^{HB} and the initial abundance n_{0y}^{HB} as in Eq. (5). We assumed that annual parameters q_y^{HB} and n_{0y}^{HB} for a specific stock region share some particular parametric distribution. From preliminary analysis it appeared that catchability tended to be log-normally distributed whereas the initial abundance tended to be normally distributed. Therefore, for this meta-analysis we assumed:

$$q_y^{\text{HB}} \sim \text{log-normal } (\mu_q, \tau_q), \qquad n_{0y}^{\text{HB}} \sim \text{normal } (\mu_n, \tau_n).$$

Parameters μ and τ inside the parentheses are the mean and precision ($\tau = 1/\sigma^2$, i.e., inverse of variance). These parameters are the hyperparameters that come from their own distributions (hyper-prior distribution). We set the hyper-priors as $\mu_q \sim \text{normal}(M_q, T_q)$ and $\mu_n \sim \text{normal}(M_n, T_n)$, where M_q, T_q, M_n, T_n are constants. We chose M_q and M_n to be close to expected μ_q and μ_n while chose small T_q (e.g., 0.01) and T_n (e.g., 1E−12) to make these two prior distributions relatively uninformative but still proper. Many studies have shown that inverse gamma distribution (IG) is appropriate for the priors of the precision parameters τ_q and τ_n (Meyer and Millar, 1999a, 1999b; Millar and Meyer, 2000; Harley and Myers, 2001; Su et al., 2001). In this study we set $\tau_q \sim \text{IG}(a_q, b_q)$ and $\mu_n \sim \text{IG}(a_n, b_n)$, and chose values between 0.001 and 0.01 for these parameters. Combining the hyper-priors, priors, and likelihood, the joint posterior

distribution for all the parameters is

$$P(\mu_q, \tau_q, \mu_n, \tau_n, q_1^{HB}, \ldots, q_Y^{HB}, n_{01}^{HB}, \ldots, n_{0Y}^{HB} | C_{y,i}, E_{y,i}, t_{y,i})$$

$$= P(\mu_q)P(\tau_q)P(\mu_n)P(\tau_n)\prod_{y=1}^{Y}\left(P(q_y^{HB}|\mu_q, \tau_q)P(n_{0y}^{HB}|\mu_n, \tau_n)\prod_{i=1}^{k_y}P(C_{y,i}|q_y^{HB}, n_{0y}^{HB})\right), \tag{13}$$

where $P(C_{y,i}|q_y^{HB1}, n_{0y}^{HB1})$ is as Eq. (5), Y is the total number of years for that stock, and k_y is the number of fishing days in year y.

The hierarchical Bayesian model (13) was applied for each stock region. It used 18 years of data and contained 40 parameters for each stock. This model was run using the WinBUGS software (Spiegelhalter et al., 2003), where the Gibbs sampler, a special Markov chain Monte Carlo (MCMC) technique, was used for sampling from the joint posterior of model (13). This was done by using each of the one-dimensional full conditional posterior distributions in turn to generate a sample from the joint posterior distribution of all the unknown parameters. We set up two Markov chains and ran 5000 iterations of the Gibbs sampler before taking observations. We examined trace plots of the sample values versus iterations to ensure that the simulation has stabilized and convergence has taken place. For statistical reference, we performed the sampling for additional 60,000 iterations and thinned the chain by taking every 10th observation for the two chains.

The overdispersion issue was dealt similarly as in the ML method. First, during the model run a dispersion parameter $\hat{\phi}_y$ was derived as in Eqs. (7) and (8). Secondly, we scaled catches and parameter n_{0y} by this dispersion parameter and re-ran the model (13). A new dispersion parameter was estimated and examined again to ensure that it was close to 1.

3. Results

3.1. Model performance and comparison

We applied density-independent and density-dependent catchability models to 52 datasets from 1987 to 2004 from three stock regions and used MLE to estimate the parameters. For the density-independent catchability models, the MLE and HBM results are similar (Zhou et al., in review). Therefore, we focussed on comparisons of MLE results for density-dependent and density-independent models. According to the chi-squared test both models fit the data well. For the density-dependent catchability model, the optimization process had difficulty in converging for some datasets. Different initial values had to be tested to achieve the possible maximum of the likelihood function to avoid local maxima. The final results show that the chi-squared goodness-of-fit test has a probability < 0.05 for both models in all these datasets. It is difficult to distinguish the two models from either the plots of CPUE over fishing days or CPUE over the cumulative catches (Figs. 1–3). Yet, a likelihood ratio test reveals that the density-dependent catchability model significantly improves the model fit in 11 out of 52 datasets (Table 1).

3.2. Confidence intervals of the estimated parameters

The profile confidence interval for the catchability coefficient q can be estimated for the density-independent catchability model in all datasets (Table 2). However, for the estimated initial biomass this cannot be achieved in some datasets using the density-independent catchability model due to a flat profile of n_0. The results are worse for the density-dependent catchability model. While confidence intervals were obtained for most q_3's and for less than half of the n_{03}'s, we were unable to estimate confidence intervals for any shape parameter b based on the profile likelihood (Table 2). Typically, the confidence intervals extend beyond the range for which the observed data would allow estimating. Also, we had difficulty in attaining the MLE for some datasets using the density-dependent catchability model. The MLE appears to be outside the achievable confidence contour. When the parameter values increase or decrease beyond certain levels, the model breaks down due to the unrealistic estimation (e.g., estimated catch becomes greater than estimated initial biomass).

3.3. Relative deviation of initial abundance between the two models

For the 11 datasets where the density-dependent catchability model is superior to the density-independent catchability model, the relative deviation ($\Delta n_0\%$) of the estimated n_{02} from n_{03} ranges from −25% to 28% with a mean of +4%. If we take all the 52 datasets into account, the relative deviation $\Delta n_0\%$ is between −47% and 28%, with a mean of −0.6% and a standard deviation of 12%, indicating that the mean is not significantly different from 0% (probability > 0.10). If we exclude one extreme value of $\Delta n_0\% = -47\%$ which results from very low catch in 2000 of Albatross Bay stock, the distribution of this relative deviation looks approximately normal where nearly half of the data fall between −5% and 5% (Fig. 4). The large deviations are found in years when the fishing season was short and total catch was low, i.e., SE GoC stock in 1999 ($\Delta n_0\% = -25\%$), Albatross Bay stock in 1992 ($\Delta n_0\% = 28\%$), 1998 ($\Delta n_0\% = 25\%$), and 2000 ($\Delta n_0\% = -47\%$).

3.4. Power function parameter

One of our main interests in this study is the magnitude and property of parameter b in Eqs. (9) and (10). For those 11 datasets where the density-dependent catchability model appears to be better, this shape parameter of the power function ranges from −0.49 to +0.76 with a mean of −0.16. More specifically, 2 out

6

Fig. 1. Observed and estimated CPUE over cumulative catch for SE GoC stock. The solid line is fitted by the density-independent catchability model while the dashed line is fitted by the density-dependent catchability model.

of 11 datasets show positive relationship while 9 datasets show negative relationship. When all the 52 datasets are considered, b ranges from -3.18 to $+1.06$ with a mean of -0.03 and a standard deviation of 0.57. If we consider the distribution of parameter b as approximately normal (Fig. 5), then, statistically, the mean of -0.03 is not significantly smaller than zero at probability > 0.10. Biologically, such a small value also may not be meaningful. This means that although density-dependent catchability may exist in some individual datasets, overall there is no systematic trend toward either a positive or a negative relationship.

Interestingly, among those 11 datasets where including a density-dependent function in the model improves the fitting, the majority, i.e., 8 out of 11 are found in Albatross Bay. This area is in the northeast of the Gulf where strong aggregation behaviour has not been reported and where the "spotter plane" is not useful in finding banana prawn aggregations (see Section 4), perhaps due to water quality. Furthermore, among these 8 years when density-dependent catchability is likely to exist in

the stock of Albatross Bay, only one shows a positive relationship between catchability and abundance.

3.5. Relationship between q and n_0 within season

The results indicate that there is a weak relationship between catchability and abundance within a single fishing season. Since the density-independent and density-dependent catchability models provide abundance estimates over time, we can calculate the daily catchability coefficient q_i using observed catch and effort data. We examined the scatter plots of daily q_i over daily n_i for these three stocks using the output from the density-independent catchability model and an example is given for the E GoC stock (Fig. 6). In general, the catchability coefficient varies greatly at low abundance but stabilizes and becomes an approximate constant when abundance increases. Again, these plots do not show a clear positive or negative relationship between catchability and abundance. Besides the
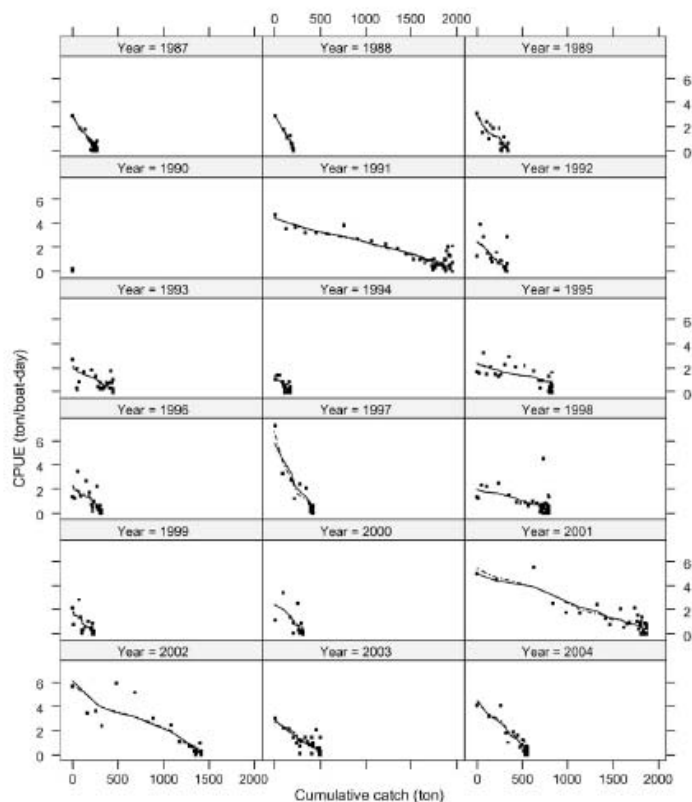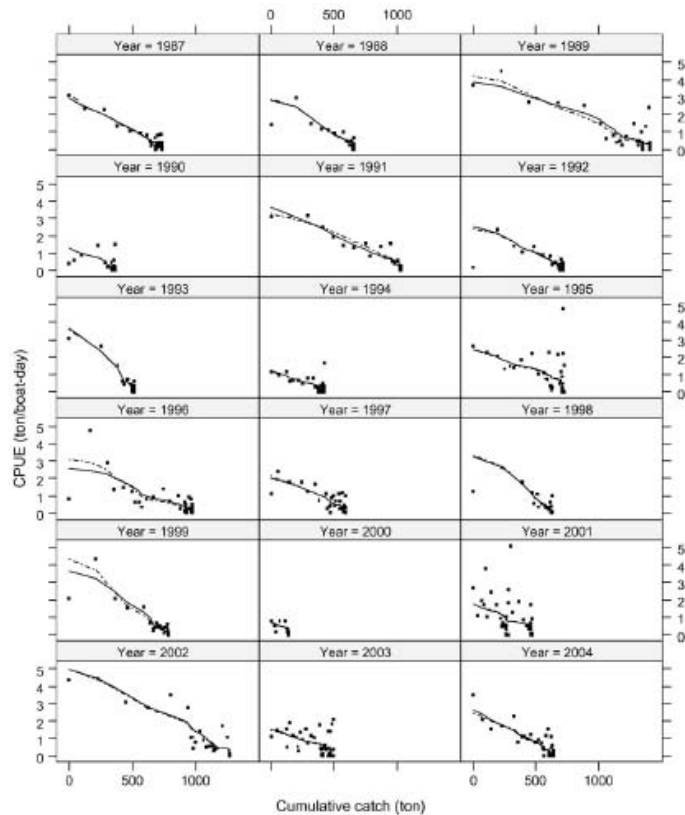
Fig. 2. Observed and estimated CPUE over cumulative catch for E GoC stock. The solid line is fitted by the density-independent catchability model while the dashed line is fitted by the density-dependent catchability model.

changes in behaviour and dynamics of prawns, low fishing effort in the later fishing season, which creates high uncertainty, may have contributed to the high volatility of q at low abundance.

3.6. Relationship between q and n_0 across years

We used the HBM results for examining across-year relationship between catchability and abundance because HBM is a meta-analysis that combines all datasets to improve the estimation. We established a relationship between the estimated q and initial abundance n_0 across multiple years from the density-independent model by combining model results from all stocks and all years. A plot of all the estimated q's and n_0's shows a stronger and clearer density-dependent relationship between q and n_0 between years (Fig. 7). Even when three extremely low abundance years ($n_0 < 100$ tonnes) were excluded, a neg-

ative power function between q and n_0 could be observed. Assuming a normally distributed error structure, we obtained a MLE of the power function as: $q_y = 0.034 n_{0y}^{-0.32}$. The non-linear power function model fit the data well ($\alpha < 0.01$). The 95% profile confidence intervals for b range from -0.566 to -0.076. The 95% confidence intervals for parameter a are between -0.019 and 0.088. When parameter a is removed from the equation, $q_y = n_{0y}^{-0.87}$ (b 95% CI: -0.90 to -0.84). This contrasts to the weak, if any, density-dependent catchability coefficient findings when one compares the density-independent and density-dependent models within each fishing season.

4. Discussion

The removal method has been applied in population studies for over six decades since Leslie and DeLury (Cowx, 1983;
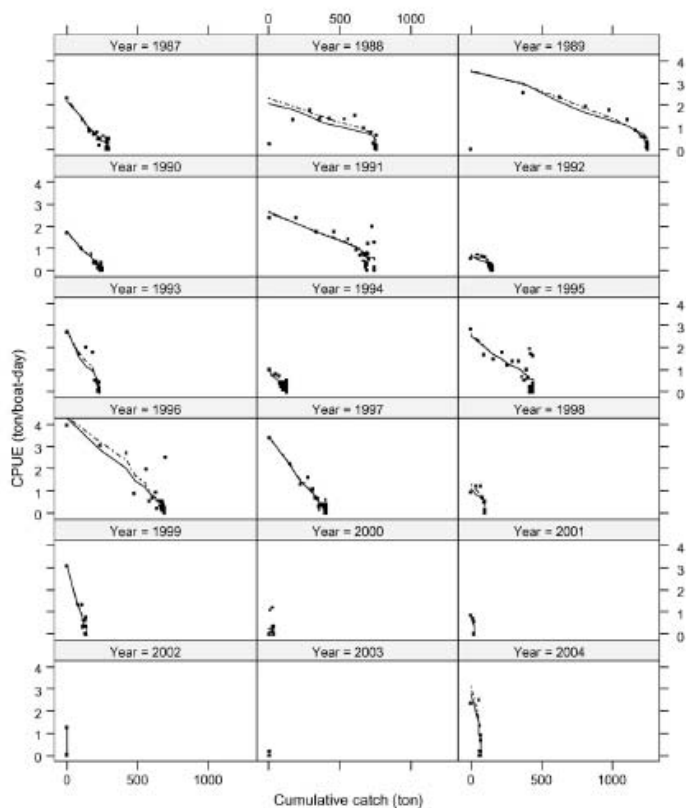
Fig. 3. Observed and estimated CPUE over cumulative catch for the Albatross Bay stock. The solid line is fitted by the density-independent catchability model while the dashed line is fitted by the density-dependent catchability model.

Fig. 4. Relative deviation of n_{02} (initial biomass from the density-independent catchability model) from n_{03} (initial biomass from the density-dependent catchability model) for three prawn stocks from 1987 to 2004.

Fig. 5. Distribution of estimated shape parameter b of the power functions for three prawn stocks from 1987 to 2004.

Table 1

Comparison of model performance and MLE parameters between density-independent and density-dependent catchability models

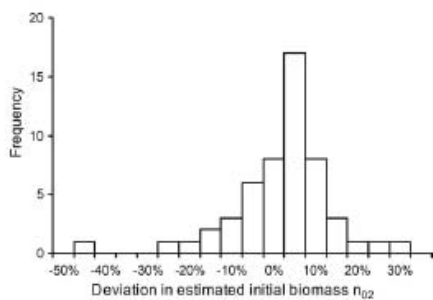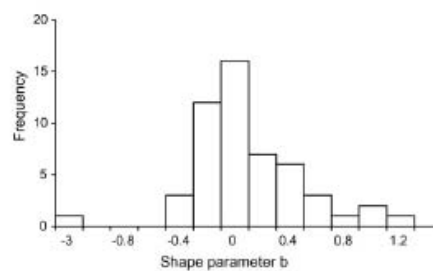| Stock	Year	k	Density-independent model			Density-dependent model				LL ratio
			q_2	n_{02}	LL	q_3	n_{03}	b	LL	
SE GoC	1987	33	0.0081	413.0	−37.6	0.0082	445.1	0.37	−36.5	2.08
SE GoC	1988	17	0.0103	385.9	−29.1	0.0103	368.2	−0.30	−24.5	**9.36**
SE GoC	1989	26	0.0061	566.8	−36.5	0.0059	627.6	0.40	−36.1	0.96
SE GoC	1991	47	0.0018	2595.4	−82.9	0.0018	2599.2	0.07	−82.8	0.27
SE GoC	1992	22	0.0067	374.3	−25.6	0.0077	338.3	−0.23	−25.0	1.07
SE GoC	1993	35	0.0031	668.8	−51.2	0.0029	772.2	0.47	−50.6	1.21
SE GoC	1994	36	0.0056	224.8	−37.8	0.0052	285.8	0.84	−36.9	1.87
SE GoC	1995	42	0.0018	1400.0	−67.4	0.0018	1357.7	−0.04	−67.3	0.23
SE GoC	1996	26	0.0060	408.2	−34.0	0.0064	380.2	−0.38	−32.6	**2.94**
SE GoC	1997	25	0.0102	649.9	−35.6	0.0097	792.8	0.91	−34.7	1.93
SE GoC	1998	62	0.0020	1074.7	−76.0	0.0020	1066.8	−0.03	−76.0	0.03
SE GoC	1999	39	0.0058	357.7	−45.1	0.0049	479.0	1.06	−43.7	**2.82**
SE GoC	2000	28	0.0072	362.7	−27.2	0.0071	370.0	−0.08	−27.2	0.00
SE GoC	2001	50	0.0022	2391.9	−68.9	0.0021	2646.4	0.371	−68.1	1.53
SE GoC	2002	40	0.0036	1854.9	−52.1	0.0035	1842.5	−0.06	−51.9	0.32
SE GoC	2003	42	0.0043	748.1	−58.8	0.0044	698.6	−0.35	−57.9	1.85
SE GoC	2004	37	0.0063	825.2	−55.9	0.0062	810.4	−0.16	−55.3	1.17
E GoC	1987	38	0.0032	1005.3	−57.4	0.0032	1084.9	0.28	−56.7	1.35
E GoC	1988	34	0.0039	739.9	−52.4	0.0039	747.4	0.04	−52.4	0.01
E GoC	1989	41	0.0023	1690.0	−46.3	0.0025	1707.6	0.38	−45.1	**2.42**
E GoC	1990	50	0.0030	433.5	−44.8	0.0031	416.7	−0.11	−44.8	0.02
E GoC	1991	39	0.0030	1288.5	−63.1	0.0029	1200.0	−0.38	−57.2	**11.75**
E GoC	1992	34	0.0032	793.7	−53.1	0.0032	753.0	−0.21	−52.5	1.25
E GoC	1993	35	0.0060	709.4	−40.5	0.0059	706.5	−0.03	−40.5	0.06
E GoC	1994	44	0.0024	499.2	−56.0	0.0025	454.3	−0.23	−55.9	0.24
E GoC	1995	40	0.0021	1206.5	−51.7	0.0024	1045.9	−0.14	−51.6	0.11
E GoC	1996	35	0.0023	1137.5	−50.8	0.0025	1243.0	0.55	−49.6	**2.40**
E GoC	1997	33	0.0026	790.1	−53.7	0.0024	910.2	0.31	−53.6	0.21
E GoC	1998	40	0.0048	678.5	−45.1	0.0048	694.9	0.10	−44.9	0.33
E GoC	1999	36	0.0044	845.6	−47.6	0.0044	998.3	0.76	−45.0	**5.28**
E GoC	2000	24	0.0029	256.7	−29.6	0.0028	270.1	0.17	−29.5	0.14
E GoC	2001	48	0.0024	746.1	−57.6	0.0024	736.8	−0.09	−57.5	0.08
E GoC	2002	42	0.0034	1500.0	−54.5	0.0034	1494.6	0.06	−54.4	0.11
E GoC	2003	43	0.0020	761.3	−61.7	0.0020	730.0	−0.13	−61.6	0.07
E GoC	2004	42	0.0035	769.1	−57.9	0.0034	738.7	−0.19	−57.7	0.47
Alb B	1987	37	0.0051	516.1	−51.2	0.0047	581.7	0.43	−47.6	**7.17**
Alb B	1988	27	0.0021	989.4	−39.4	0.0025	908.9	−0.36	−37.4	**4.00**
Alb B	1989	25	0.0024	1475.5	−40.7	0.0028	1283.6	−0.40	−31.8	**17.73**
Alb B	1990	38	0.0046	532.7	−57.9	0.0046	524.4	−0.07	−57.5	0.86
Alb B	1991	34	0.0023	1321.0	−53.6	0.0023	1294.9	−0.08	−53.5	0.33
Alb B	1992	27	0.0029	281.3	−39.5	0.0043	219.0	−0.43	−33.9	**11.10**
Alb B	1993	21	0.0080	509.1	−27.3	0.0082	482.1	−0.29	−24.4	**5.79**
Alb B	1994	41	0.0055	232.6	−60.0	0.0056	229.5	−0.04	−60.0	0.05
Alb B	1995	27	0.0036	788.7	−43.4	0.0034	850.0	0.15	−43.4	0.06
Alb B	1996	31	0.0047	1127.8	−39.6	0.0048	1127.2	−0.29	−38.8	1.57
Alb B	1997	41	0.0061	734.4	−66.5	0.0059	748.0	−0.04	−2.9	**127.26**
Alb B	1998	17	0.0057	235.9	−22.3	0.0095	189.1	−0.49	−20.1	**4.40**
Alb B	1999	21	0.0123	385.1	−27.7	0.0125	379.1	−0.08	−27.5	0.24
Alb B	2000	16	0.0022	125.8	−11.9	0.0009	236.0	−3.18	−11.4	0.87
Alb B	2001	21	0.0165	79.2	−22.2	0.0203	70.1	−0.25	−21.5	1.41
Alb B	2002	20	0.1360	42.6	−9.3	0.1399	42.6	0.12	−8.8	1.01
Alb B	2004	31	0.0228	168.6	−30.1	0.0297	159.9	−0.31	−26.8	**6.71**
Mean		34	0.0075	782.7	−45.9	0.0079	791.1	−0.03	−43.6	4.74

k = number of observations, n_0 = abundance in tonnes, LL = log-likelihood value. Alb B = Albatross Bay stock. Bold figures in "LL ratio" indicate that the density-dependent catchability model fits the data better than the density-independent model.

Hilborn and Walters, 1992). One of the key assumptions of the removal method is that the probability of capture remains constant throughout the entire sampling period. We believe our paper is the first to directly incorporate a density-dependent catchability function into the depletion process. We encountered many difficulties in the development of this model. Because of high correlation among the estimated parameters and a flat likelihood profile, global maxima may not have been achieved for

Table 2
MLE profile confidence intervals for the estimated parameters from the density-independent and density-dependent catchability models

| Stock | Year | Density-independent model | | | | Density-dependent model | | | |
| | | q_2 | | n_{02} | | q_3 | | n_{03} | |
		LCI	UCI	LCI	UCI	LCI	UCI	LCI	UCI
SE GoC	1987	0.0061	0.0090	*350.0*	499.7	0.0056	0.0109		
SE GoC	1988	0.0088	0.0119	346.1	431.1				
SE GoC	1989	0.0043	0.0078	455.8	705.0	0.0029	0.0083		
SE GoC	1991	0.0015	0.0021	2322.5	2911.4	0.0015	0.0021	2308.7	
SE GoC	1992	0.0035	0.0085						
SE GoC	1993	0.0019	0.0043	534.7		0.0017	0.0043		
SE GoC	1994	0.0035	0.0072	172.6		0.0018	0.0088		
SE GoC	1995	0.0012	0.0026	1077.5		0.0011	0.0020		
SE GoC	1996	0.0034	0.0087	310.2					
SE GoC	1997	0.0083	0.0121	563.5	748.2	0.0039	0.0131		
SE GoC	1998	0.0015	0.0025	924.4	1273.3	0.0014	0.0026	862.7	
SE GoC	1999	0.0040	0.0075	294.1	438.9	0.0010	0.0075		
SE GoC	2000	0.0044	0.0099	278.7		0.0040	0.0075		
SE GoC	2001	0.0018	0.0026	2113.1	2713.5	0.0007	0.0090		2728.2
SE GoC	2002	0.0030	0.0042	1626.6	2108.4	0.0030	0.0042	1615.5	2097.0
SE GoC	2003	0.0034	0.0053	644.7					
SE GoC	2004	0.0053	0.0073	737.0	924.3	0.0054	0.0072	709.8	914.4
E GoC	1987	0.0027	0.0037	906.1	1115.3	0.0017	0.0038	924.7	
E GoC	1988	0.0033	0.0045	667.1	821.7	0.0029	0.0046	670.0	
E GoC	1989	0.0017	0.0030	1327.3	1948.1	0.0018	0.0033	1407.2	
E GoC	1990	0.0020	0.0040	358.3	536.4	0.0015	0.0032	*360.0*	
E GoC	1991	0.0026	0.0034	1170.1	1418.9				
E GoC	1992	0.0027	0.0037	712.0		0.0028	0.0037	*700.0*	900.0
E GoC	1993	0.0052	0.0067	644.4	781.2	0.0052	0.0068	640.2	787.7
E GoC	1994	0.0018	0.0030	423.6		0.0015	0.0030	*400.0*	
E GoC	1995	0.0014	0.0033			0.0016	0.0034	*800.0*	
E GoC	1996	0.0016	0.0030	949.0		0.0013	0.0036	1022.1	
E GoC	1997	0.0017	0.0036	645.0		0.0016	0.0036		*1000.0*
E GoC	1998	0.0041	0.0055	612.4	752.5	0.0035	0.0055	614.3	
E GoC	1999	0.0037	0.0051		954.0	0.0025	0.0056	804.2	
E GoC	2000	0.0010	0.0050						
E GoC	2001	0.0012	0.0037						
E GoC	2002	0.0027	0.0040	1280.4	1700.7	0.0028	0.0042	1277.4	
E GoC	2003	0.0012	0.0031	571.1	*900.0*	0.0012	0.0032		*900.0*
E GoC	2004	0.0026	0.0044	643.6	918.0				
Alb B	1987	0.0044	0.0058	468.5	569.1	0.0016	0.0057		
Alb B	1988	0.0012	0.0030		1426.2	0.0013			
Alb B	1989	0.0020	0.0028	1323.0	1659.2				
Alb B	1990	0.0042	0.0050	503.8	563.7	0.0043	0.0050	495.0	560.9
Alb B	1991	0.0017	0.0028	1150.5		0.0017	0.0031	986.9	
Alb B	1992	0.0019	0.0039						
Alb B	1993	0.0063	0.0097	440.2		0.0069	0.0090	*450.0*	555.2
Alb B	1994	0.0046	0.0065	207.2	262.5	0.0045	0.0066		
Alb B	1995	0.0025	0.0048	659.4		0.0018	0.0049		
Alb B	1996	0.0039	0.0056	991.1	1284.9				
Alb B	1997	0.0056	0.0066			0.0031	0.0080	581.4	
Alb B	1998	0.0024	0.0088			0.0066	0.0080		215.1
Alb B	1999	0.0103	0.0143	347.5	430.1	0.0094	0.0143	342.6	465.6
Alb B	2000	0.0002	0.0112			0.0002	0.0080		
Alb B	2001	0.0111	0.0213			0.0006			
Alb B	2004	0.0166	0.0286			0.0045			

Figures in italic are the bounds ensuring the optimization could be completed. LCI and UCI are the lower and upper 95% confidence intervals. Other symbols and abbreviations are the same as in Table 1.

some datasets. For the same reasons, confidence intervals based on likelihood profiles are difficult to obtain for some parameters. This is similar to the difficulty in attempting to estimate density-independent catchability, abundance, and natural mor- tality all together (Wang, 1999). As undertaken in Wang (1999), parameter uncertainty was investigated by fixing one parameter at a time. In this study, however, we found that such an exercise had no significant impact on the final results. We also tried to
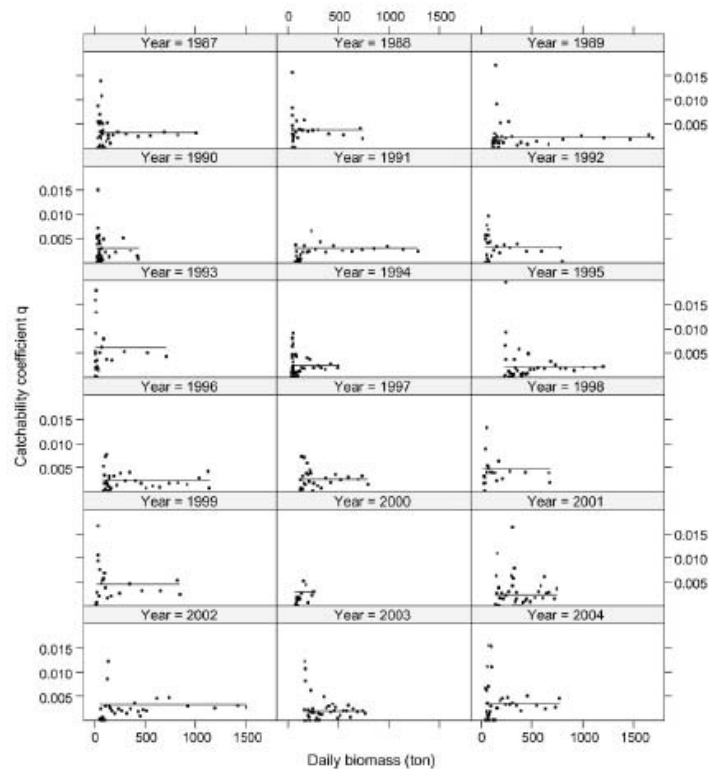
Fig. 6. Relationship between estimated daily catchability coefficient q_i and estimated daily abundance n_i from the density-independent catchability model for the E GoC stock.
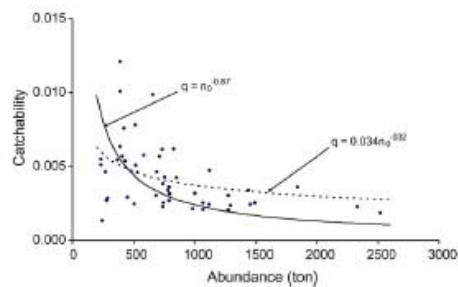
Fig. 7. Between-year relationship between estimated catchability coefficient q_2 and estimated initial biomass n_{02} from the density-independent catchability model for the three stocks from 1987 to 2004. Three data points of extremely low abundance ($n_0 < 100$ tonnes) are excluded.

include fishery independent survey data into the model, which means that all years have to be estimated in a single model. Unfortunately, likelihood estimates are extremely difficult to achieve for the density-dependent catchability model with data from multiple years and multiple sources. This is also the same for the hierarchical Bayesian method. Therefore, in this paper we focused on the single-year analyses using logbook data only, and included only the HBM results for the density-independent model for across-year comparison.

4.1. Is within-season catchability density-dependent?

This question is crucial for fisheries management, as estimates of fishing mortality and population size would be biased if density-dependence is ignored when it exists and *vice versa*. From our analysis of 52 datasets we conclude that there is neither a clear positive density-dependent relationship nor a clear negative density-dependent relationship between q and n_0 within any stock of banana prawns in the regions that we were able

to test. None of the stocks demonstrated a constant positive power function catchability as found by Vance et al. (2003). However, there are a few exceptional years where a significant density-dependent result was demonstrated. Most of these show a negative power function and a few produced a positive power function.

Die and Ellis (1999) compared the changes in daily catch for the entire stock of banana prawns with that of only the aggregating part of that stock in the Northern Prawn Fishery and found that the decrease in biomass of aggregating prawns occurred much faster than the decrease in biomass of the entire stock. Based on the fact that in the banana prawn fishery searching time is the main component of fishing effort, and that the area of the stock remains constant, they showed that as stock abundance decreases the probability of finding an aggregation decreases. In addition, the size of aggregations decreases as stock abundance decreases and the fleet progressively switches from targeting aggregations to targeting the nonaggregated part of the stock. Therefore, they speculated that catchability may decrease significantly as the stock size decreases. We believe that the Die and Ellis hypothesis is viable. According to fishery logbooks, from 1998 to 2004, the average searching time composed nearly 80% of the total fishing effort (searching plus trawling, unpublished data). Searching from airplanes is common in the Gulf of Carpentaria, except near the Weipa area (Albatross Bay stock) because of the low water clarity. Dense aggregations of banana prawns could be visually detected from "spotter planes" or from fishing vessels. In the earlier stage of a fishing season when abundance is high and aggregations are easily spotted by planes or by try-net trawling, low searching effort may result in good catches which results in a high catchability. In contrast, as the fishing season progresses, more effort is required to search and catch small aggregations or a dispersed population. Therefore, we expect a low catchability at low abundance.

We can consider this type of effect of abundance on catchability as indirect because abundance does not directly control the proportion of the stock being caught; rather it affects prawn behaviour and fishermen's searching effort, which in turn affects catchability. On the other hand, mathematically, the catchability coefficient is a function of catch, effort, and mean abundance during one unit of time, as formulated in Eq. (2). In that equation abundance plays a direct role in determining catchability as q is defined as the proportion of fish in the population being caught per unit of effort. Limited fishing capacity of the fleet in a given season may be one major factor preventing a constant proportion of the stock being caught over the entire fishing season. In the beginning of a fishing season when abundance is high, a fleet with the same fishing power will catch a relatively small proportion of the stock because of the limited fishing power and capacity; whereas later in the season when the abundance decreases, the same unit of effort must catch a higher proportion of the remaining smaller stock. Lucas et al. (1979) estimated that in 1971, the fleet caught 90% of the available stock. Our results reveal that on average the banana prawn fishery harvested about 85% of the fishable population in a year from 1987 to 2004 for the three stocks we studied. This means that the abundance decreases dramatically over time, which in turn must have a large impact on catchability. From our findings, one could argue that in most years the influence of abundance on catchability, acting in these two opposite ways, balance each other out and result in a more or less constant catchability with abundance.

Our analysis also shows that density-dependent catchability, both positive and negative, may exist in some years especially in the Albatross Bay area. Aggregations are much harder to find in this region, at least partly due to the turbid water colour, and partly due to fewer aggregations being formed (Vance et al., unpublished data). Competition between direct and indirect effects of abundance may have played an important role in the consequential density-dependent catchability. Note that a positive power function occurs only one out of the 8 years for which a density-dependent relationship may exist. This phenomenon indicates that, more frequently (i.e., 7 out of the 8 years), the direct effect of abundance on catchability (negative power function) has more weight than the indirect effect in this region. This is because the indirect effect assumes that abundance affects prawn behaviour and search effort which in turn affects catchability; high abundance facilitates aggregation and search, which in turn increases catchability. However, the chance of finding dense aggregations is low in the Albatross Bay region. The tendency of negative power function relationship between q and n_0 in this region is consistent with the hypothesis that catchability increases as abundance decreases (Swain and Sinclair, 1994; Arreguin-Sanchez, 1996).

Catchability has long been considered as a complicated parameter (Arreguin-Sanchez, 1996; Quinn and Deriso, 1999; Francis et al., 2003). Eq. (2) states that catchability is the combined result of catch, effort, and abundance. These three variables in turn are affected by many other factors: distribution of prawns and fishing fleet, population biology, environmental conditions, fishing gear efficiency, and fishing strategy, etc. (Swain and Sinclair, 1994; Arreguin-Sanchez, 1996; Addison et al., 2003; Salthaug and Aanes, 2003). For example, nominal fishing effort has significantly decreased over time in the NPF. This has not only reduced sampling size and compromised data quality, but it has also changed fleet composition and made the unit of effort inconsistent. Boat-day has been used as fishing effort in the NPF since the beginning of the fishery in 1970s. This is an imprecise unit because total daily fishing time from 1 to 24 h is all recorded as one boat-day of effort. In combination with these complications and the aggregating behaviour of banana prawns, it is not surprising that in some years catchability diverges and the relationship between catch per unit of effort and abundance deviated from proportionality.

4.2. Is there density-dependent catchability across years?

We have shown that for banana prawns in the NPF there is a strong, and significant, tendency towards negative power function relationship between q and n_0 across years. Many other fisheries have also observed a similar relationship among years (Bannerot and Austin, 1983; Angelsen and Olsen, 1987; Crecco and Overholtz, 1990; Rose and Leggett, 1991; Arreguin-Sanchez, 1996). Because the stock will be depleted more rapidly

in years with low abundance, management should take a more cautious approach with this fishing pattern.

Our models also provide parameter estimates for initial abundance. This is the fishable (available) abundance only and therefore does not include the population outside the fishing ground in the shallow, inshore areas and the nursery grounds. The maximum likelihood method results in reliable estimates for most of the datasets as compared to a hierarchical Bayesian modelling approach (Zhou et al., in review). Of course, the estimates of these parameters contain uncertainty involving both measurement errors and process errors.

First, one major potential source of uncertainty may come from a vague definition of the banana prawn fishery. Because the fishing fleet can fish both banana prawns and tiger prawns during the banana fishing season, when the catch of banana prawns is low, fishermen may turn to targeting tiger prawns at night while still catching some banana prawns during the day. Although the majority of the effort targeted at banana prawns during the banana prawn season and the majority of the catches came from fishing directly targeting banana prawns, there were some banana prawns caught by fishing effort actually targeting tiger prawns.

Second, the data used in this analysis are augmented from fishermen's logbooks (personal observations). We assess that our data in this paper (three stocks from 1987 to 2003, excluding 2004) include 0% to 13% of augmented (i.e., duplicated) records (mean = 3%, S.D. = 3%, n = 51). This practice may have introduced some uncertainty (although may be insignificant compared to other sources of uncertainty) into the final data.

Third, using boat-day (rather than hours) as fishing effort also reduces data accuracy (Zhou et al., unpublished data). As discussed above, reduced fishing effort (i.e., fewer boats remaining fishing banana prawns) in the late season deteriorates data quality and changes fleet composition.

5. Implications for management

Our findings may have important implications in prawn stock assessment and management. To begin with, according to Eqs. (1) and (2), CPUE could be used as a reasonable index of within-season abundance for the banana prawns in the Gulf of Carpentaria, but is not a good one when one compares data across years. Stock assessment models that estimate biomass should either estimate a catchability parameter for each year or estimate a multiple parameter catchability equation that incorporates between-year density-dependence on the catchability parameter.

The fact that our results confirm that a large proportion (about 85%) of the stock in any year is caught is important for the management of this fishery. Although many of the prawns caught during the banana prawn season (April–May) spawn before capture, it has been shown that the spawning that contributes most to the next year's population occurs much later in the year (August–September) (Rothlisberg et al., 1985). Therefore, the proportion of banana prawns that escape capture during the fishery is a critical factor for the long-term sustainability of the

banana prawn fishery and also an important factor in contributing to annual variation in prawn catches.

In terms of estimating fishing mortality, we would recommend testing a model with and without within-season density-dependence. In years where the results significantly point to density-dependence, ignoring this fact could result in significant biases in the estimated initial biomass. However, in the case of banana prawns in the NPF, it seems hard to predict in advance whether within-season density dependence would occur. For pre-season fishery planning, a density-independent catchability should be a default assumption for the banana prawns.

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CHAPTER 7: APPENDIX

The following figures show catch rates (numbers per hour-trawled) of the three main prawn species groups (tiger, banana and endeavour prawns) for each trawl site for eight surveys from January 2003 to October 2004. Some maps include results from sites in the western Gulf of Carpentaria that were taken as part of the NPF Monitoring Project which ran concurrently with this project.

CSIRO Marine Research
NPF Monitoring Cruise - January 2003
Preliminary Results

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CSIRO Marine Research
NPF Monitoring Cruise - March 2003
Preliminary Results

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Australian Fisheries Management Authority

FISHERIES
RESEARCH &
DEVELOPMENT
CORPORATION

Total tiger prawn catch rate (no/hr)
at each site trawled during survey.

Tiger Catch (no/hr)
0
0 - 200
200 - 1000
1000 - 2000
2000+

Gulf
of
Carpentaria

NT

Qld

Total tiger prawn catch rate (no/hr)
at each site trawled during survey.

Tiger Catch (no/hr)
0
0 - 200
200 - 1000
1000 - 2000
2000+

Gulf
of
Carpentaria

NT

Qld

CSIRO Marine Research
NPF Monitoring Cruise - August 2003
Preliminary Results

AFMA Australian Fisheries Management Authority

Total tiger prawn catch rate (no/hr)
at each site trawled during survey.

Tiger Catch (no/hr)
- 0
- 1 - 200
- 201 - 500
- 501 - 1000
- 1000+

Gulf
of
Carpentaria

NT

Qld

CSIRO Marine Research
NPF Monitoring Cruise - October 2003
Preliminary Results

AFMA Australian Fisheries Management Authority

Total tiger prawn catch rate (no/hr)
at each site trawled during survey.

Tiger Catch (no/hr)
- 0
- 1 - 200
- 201 - 500
- 501 - 1000
- 1000+

Gulf
of
Carpentaria

NT

Qld

133

Total tiger prawn catch rate (no/hr)
at each site trawled during survey.

Tiger Catch (no/hr)
0
1 - 200
201 - 500
501 - 1000
1000+

Gulf
of
Carpentaria

NT

Qld

Total tiger prawn catch rate (no/hr)
at each site trawled during survey.

Tiger Catch (no/hr)
0
0 - 200
200 - 1000
1000 - 2000
2000+

Gulf
of
Carpentaria

NT

Qld

CSIRO Marine Research
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Total tiger prawn catch rate (no/hr)
at each site trawled during survey.

Tiger Catch (no/hr)
0
1 - 200
201 - 500
501 - 1000
1000+

Gulf
of
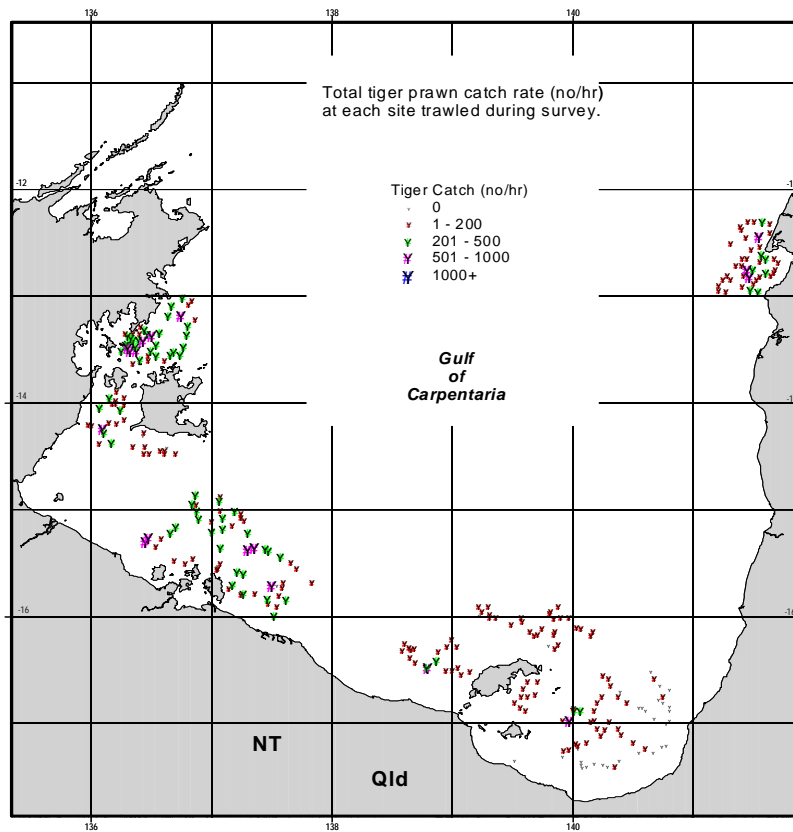Carpentaria

NT
Qld

CSIRO Marine Research
NPF Monitoring Cruise - October 2004
Preliminary Results

Total tiger prawn catch rate (no/hr)
at each site trawled during survey.

Tiger Catch (no/hr)
0
1 - 200
201 - 500
501 - 1000
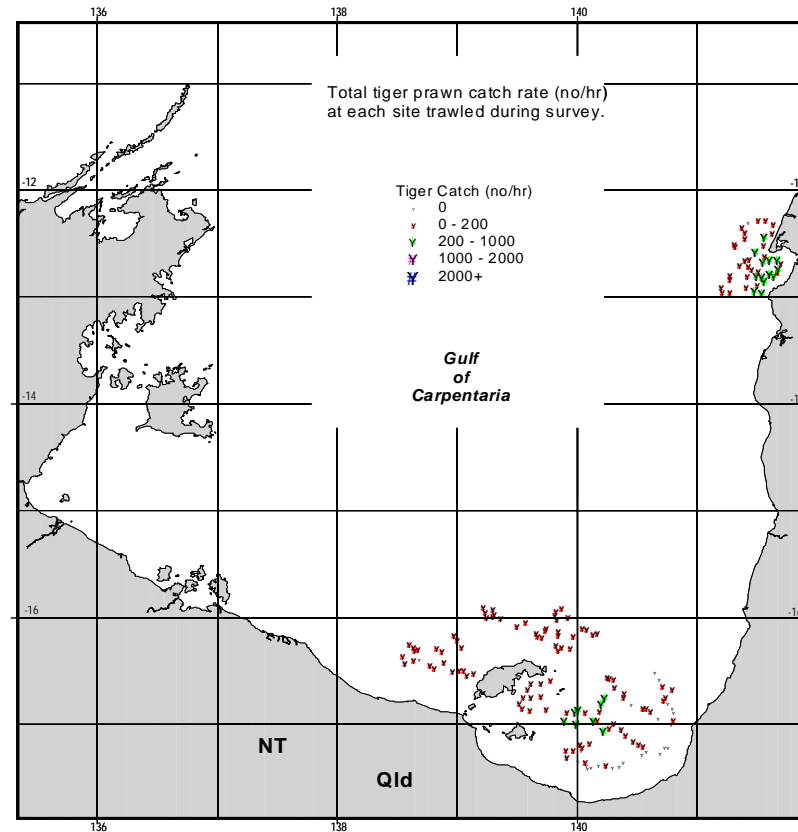1000+

Gulf
of
Carpentaria

NT
Qld

CSIRO Marine Research
NPF Monitoring Cruise - January 2003
Preliminary Results

Australian Fisheries Management Authority

Total banana prawn catch rate (no/hr)
at each site trawled during survey.

Banana Catch (no/hr)
- 0
- 0 - 200
- 200 - 1000
- 1000 - 2000
- 2000+

Gulf of Carpentaria

NT

Qld

CSIRO Marine Research
NPF Monitoring Cruise - March 2003
Preliminary Results

Australian Fisheries Management Authority

Total banana prawn catch rate (no/hr)
at each site trawled during survey.

Banana Catch (no/hr)
- 0
- 0 - 200
- 200 - 1000
- 1000 - 2000
- 2000+

Gulf of Carpentaria

NT

Qld

CSIRO Marine Research
NPF Monitoring Cruise - August 2003
Preliminary Results

AFMA Australian Fisheries Management Authority

Total banana prawn catch rate (no/hr)
at each site trawled during survey.

Banana Catch (no/hr)
- 0
- 1 - 200
- 201 - 500
- 501 - 1000
- 1000+

Gulf
of
Carpentaria

NT

Qld

AFMA Australian Fisheries Management Authority

AFMA Australian Fisheries Management Authority

Total banana prawn catch rate (no/hr)
at each site trawled during survey.

Banana Catch (no/hr)
0
1 - 200
201 - 500
501 - 1000
1000+

Gulf
of
Carpentaria

NT

Qld

Total banana prawn catch rate (no/hr)
at each site trawled during survey.

Banana Catch (no/hr)
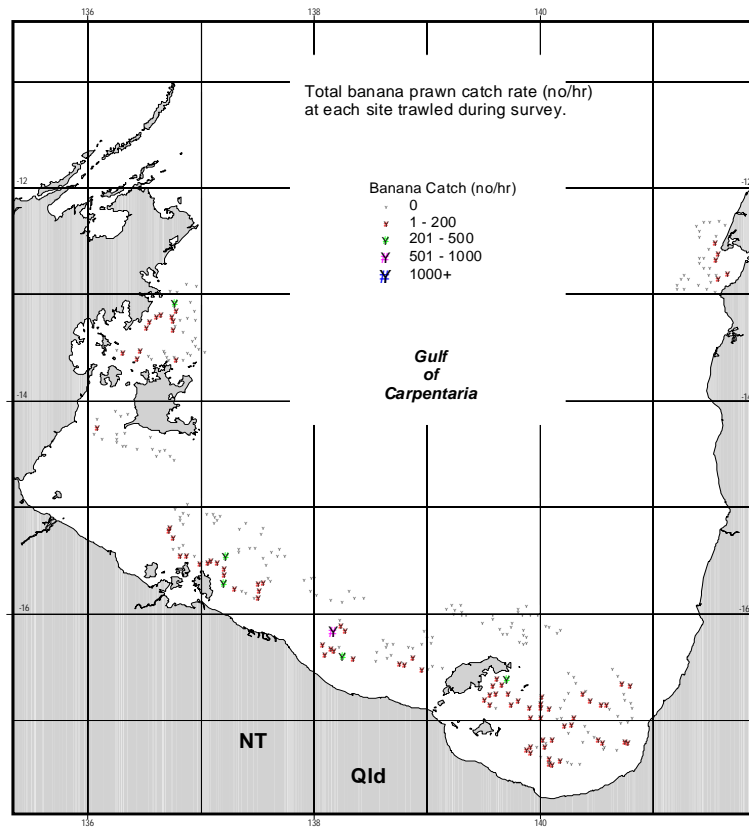0
0 - 200
200 - 1000
1000 - 2000
2000+

Gulf
of
Carpentaria

NT

Qld

138

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Preliminary Results

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Total banana prawn catch rate (no/hr)
at each site trawled during survey.

Banana Catch (no/hr)
0
1 - 200
201 - 500
501 - 1000
1000+

Gulf
of
Carpentaria

NT

Qld

CSIRO Marine Research
NPF Monitoring Cruise - October 2004
Preliminary Results

CSIRO MARINE RESEARCH

AFMA Australian Fisheries Management Authority

FISHERIES RESEARCH & DEVELOPMENT CORPORATION

Total banana prawn catch rate (no/hr)
at each site trawled during survey.

Banana Catch (no/hr)
0
1 - 200
201 - 500
501 - 1000
1000+

Gulf
of
Carpentaria

NT

Qld

CSIRO Marine Research
NPF Monitoring Cruise - January 2003
Preliminary Results

Australian Fisheries Management Authority

Total endeavour
prawn catch rate (no/hr)
at each site trawled during survey.

Endeavour Catch (no/hr)
- 0
- 0 - 200
- 200 - 1000
- 1000 - 2000
- 2000+

Gulf of Carpentaria

NT

Qld

CSIRO Marine Research
NPF Monitoring Cruise - March 2003
Preliminary Results

Australian Fisheries Management Authority

Total endeavour
prawn catch rate (no/hr)
at each site trawled during survey.

Endeavour Catch (no/hr)
- 0
- 0 - 200
- 200 - 1000
- 1000 - 2000
- 2000+

Gulf of Carpentaria

NT

Qld

CSIRO Marine Research
NPF Monitoring Cruise - August 2003
Preliminary Results

Total endeavour prawn catch rate (no/hr) at each site trawled during survey.

Endeavour Catch (no/hr)
0
1 - 200
201 - 500
501 - 1000
1000+

Gulf of Carpentaria

NT
Qld

CSIRO Marine Research
NPF Monitoring Cruise - October 2003
Preliminary Results

Total endeavour prawn catch rate (no/hr) at each site trawled during survey.

Endeavour Catch (no/hr)
0
1 - 200
201 - 500
501 - 1000
1000+

Gulf of Carpentaria

NT
Qld

CSIRO Marine Research
NPF Monitoring Cruise - January 2004
Preliminary Results

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AFMA Australian Fisheries Management Authority

FISHERIES RESEARCH & DEVELOPMENT CORPORATION

Total endeavour prawn
catch rate (no/hr) at each site
trawled during survey.

Endeavour Catch (no/hr)
- 0
- 1 - 200
- 201 - 500
- 501 - 1000
- 1000+

*Gulf
of
Carpentaria*

NT

Qld
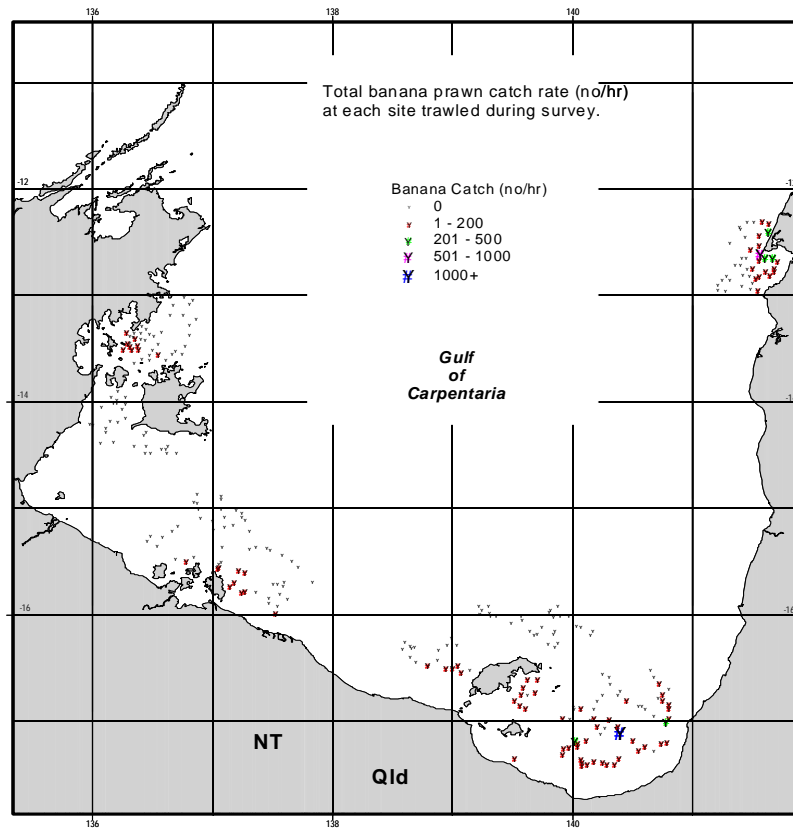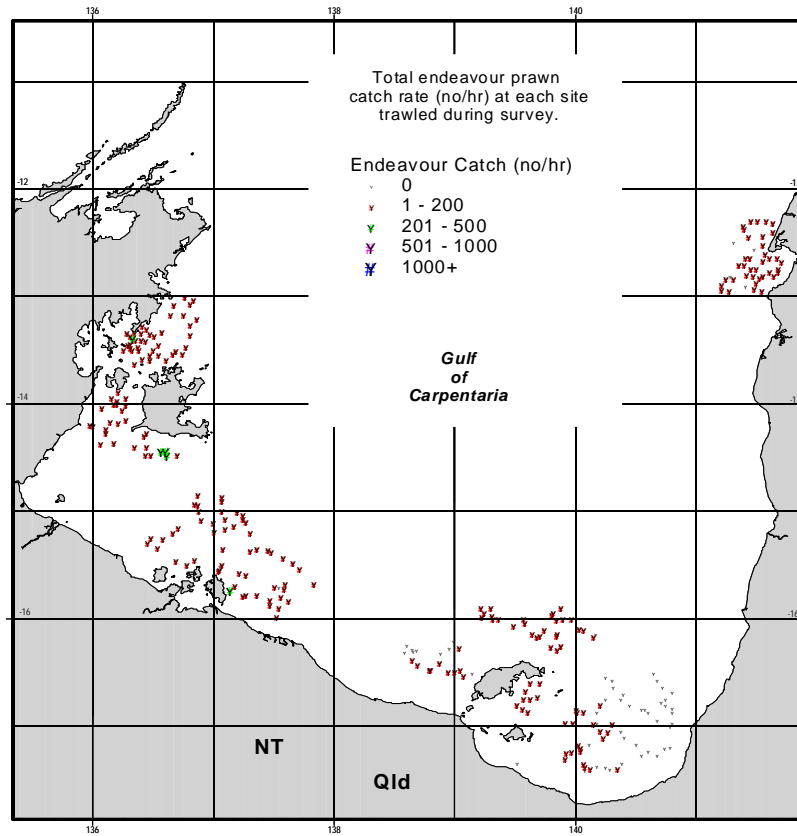
CSIRO Marine Research
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AFMA Australian Fisheries Management Authority

FISHERIES RESEARCH & DEVELOPMENT CORPORATION

Total endeavour prawn
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- 0
- 0 - 200
- 200 - 1000
- 1000 - 2000
- 2000+

*Gulf
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Carpentaria*

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Qld

CSIRO Marine Research
NPF Monitoring Cruise - August 2004
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- 1000+

Gulf of Carpentaria

NT
Qld

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- 501 - 1000
- 1000+

Gulf of Carpentaria

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Qld