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Seasonal and annual variation in abundance of postlarval and juvenile banana prawns *Penaeus merguiensis* and environmental variation in two estuaries in tropical northeastern Australia: a six year study

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ABSTRACT: We studied the fortnightly, seasonal and annual variation in abundance of postlarval and juvenile *Penaeus merguiensis* in the Embley and Mission River estuaries (northeastern Australia) and of juveniles emigrating from the rivers between September 1986 and March 1992. The climate is tropical with distinct wet and dry seasons, and the pattern of salinity and temperature changes in the estuaries closely reflects this seasonal variation. Postlarval and juvenile prawns were caught for up to 8 mo of the year, from before the wet season to just after the wet season (October to May). There was a weak bimodal distribution of catches during this period but the pattern of variation was quite variable from year to year. There were also subtle differences in the seasonal patterns of abundance between the Embley and Mission Rivers, probably due to different impacts of wet season rainfall on the 2 estuaries. In the rivers, environmental variation explained very little of the variation in catches of planktonic postlarvae, benthic postlarvae and juveniles, but increased emigration of juveniles from the rivers was significantly correlated with increased rainfall. The main factor determining the abundance of juvenile *P. merguiensis* in the estuaries was the supply and successful settlement of postlarvae from offshore areas. The highest densities of prawns caught within the estuaries were near the upper reaches of small creeks rather than in the main rivers. It is likely that these differences are due to differential settlement patterns of postlarvae between the creek and the main river. Although the largest emigration of juvenile prawns from the estuaries occurred during the wet season, lower levels of migration of prawns from the creeks to the main rivers occurred throughout the year. Over the 6 yr of this project, the annual offshore commercial catch of adult *P. merguiensis* was significantly correlated with catches of prawns emigrating from the Embley River during the wet season.

KEY WORDS: Penaeid · Postlarvae · Juvenile · Environment · Season · Annual variation · Estuary · Migration

INTRODUCTION

A major objective of scientists and managers studying penaeid prawn fisheries worldwide is to try and identify causes of annual variation in catches and, in particular, to determine whether the annual variation is due mainly to environmental changes or is related to spawning stock levels. In fact, a clear environmental relationship or stock-recruitment relationship has been demonstrated in only a small fraction of the world's prawn fisheries (Penn et al. 1995, Staples et al. 1995).

The northern Australian fishery for the banana prawn *Penaeus merguiensis* is one fishery where a strong positive relationship between rainfall and subsequent offshore commercial catch of adult prawns has been demonstrated (Vance et al. 1985, Staples et al.

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1995). In the southeastern region of the Gulf of Carpentaria, mean annual commercial catch of banana prawns, calculated over 26 yr, is 923 t (ranging from 34 to 3854 t), and 81% of the annual variation in catch is explained by variation in annual rainfall in that region ($p = 0.0001$) (Vance unpubl. data). However, this relationship is not observed in all regions of the fishery. About 500 km away, in the northeastern Gulf, where mean annual commercial catches of banana prawns are similar (860 t; ranging from 290 to 1920 t), there is no significant relationship between annual rainfall and catch.

The timing of the life cycle may be different for *Penaeus merguiensis* in different regions of the Gulf of Carpentaria (Rothlisberg et al. 1985). *P. merguiensis*, in common with many of the most valuable penaeid prawn species in the world, has a life cycle in which 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. In the southeastern Gulf, postlarval and juvenile *P. merguiensis* that were spawned from August to November settled and survived more successfully in the nursery areas than did prawns from spawnings at other times of the year (Rothlisberg et al. 1985). However, in the northeastern Gulf, postlarvae and juveniles that were spawned from February to May appeared to settle and survive in the estuaries better than prawns spawned from August to November (Rothlisberg et al. 1985).

In most cases where a significant relationship between environmental variation and offshore commercial catch has been observed, the environmental variable acts on early life-history stages before or during the prawn's residence in nursery areas. For example, a 4 yr study in the rivers of the southeastern Gulf of Carpentaria showed that, for *Penaeus merguiensis*, the strong correlation between rainfall and commercial catch was due to an increase in emigration of juvenile prawns that was associated with increased rainfall (Staples & Vance 1986). In the USA (for review see Zein-Eldin & Renaud 1986) and Mexico (Gracia 1989), rainfall and river discharge also influence catches of subadult and adult *Penaeus setiferus*. However, in other penaeid fisheries, different environmental variables have been shown to be important in determining offshore commercial catches or catches of juveniles in estuaries. For example, a model based on the effects of temperature and salinity on the survival of juvenile prawns in the nursery areas was developed to predict commercial catches of *Penaeus aztecus* in North Carolina (Hunt et al. 1980). Catches of *Penaeus duorarum* were also positively related to temperature in North Carolina (Hettler 1992). High seasonal water levels and, therefore, greater inundation of Texas salt marshes were positively correlated with densities of juvenile *P. aztecus* in the USA (Zimmerman & Minello 1984).

In areas where there are large annual differences in population size or in environmental variables such as rainfall, it is necessary to collect long-term data sets to clearly identify the timing of the life cycle and to understand the links between environmental variation and the populations. Although *Penaeus merguiensis* contributes to important prawn fisheries throughout the Indo-West Pacific, very few published accounts of long-term research into catch variation exist. In the northeastern Gulf of Carpentaria, information was needed to identify the timing of the life cycle and the reasons for the apparent differences in environmental effects on commercial prawn catches there compared with those in the southeastern Gulf. We therefore initiated a 6 yr study of all life-history stages of *P. merguiensis* in 2 nearby river systems, the Embley and Mission Rivers, and the adjacent offshore area. In this paper we examine the seasonal and annual variation in abundance of postlarval and juvenile *P. merguiensis* in the plankton and on mangrove-lined mud banks in the Embley and Mission Rivers. We investigated the relationship between catches over the 6 yr and the major environmental variables in the estuary, namely temperature, rainfall, salinity, mean sea level and wind. The importance of the mangrove habitat to juvenile *P. merguiensis* in these rivers has already been described by Vance et al. (1990, 1996a), and growth and mortality estimates based on the first 3 yr of this study have been reported by Haywood & Staples (1993).

METHODS

We sampled *Penaeus merguiensis* postlarvae [<3 mm carapace length (CL)] entering the Embley River and postlarvae (<3 mm CL) and juveniles (≥3 mm CL) within the Embley River and the nearby Mission River (Fig. 1). No adults (sexually mature) were caught in our samples. Samples in the Embley River were collected every 2 wk, on spring tides, for 6 yr (between September 1986 and March 1992), except for the periods April to August in 1990 and 1991, when prawn catches were low (Haywood & Staples 1993). Samples in the Mission River were collected every 2 wk for 3 yr, from September 1986 to September 1989.

Plankton. Postlarvae entering the Embley River were sampled with 3 plankton nets moored in a vertical array in mid-river near the mouth (Fig. 1). The nets fished at depths of 0.5, 2.5 and 4.5 m. Each net measured 0.5 by 0.5 m at the mouth and was made of 1 mm mesh. They were set every 2 wk for about 10 min mid-

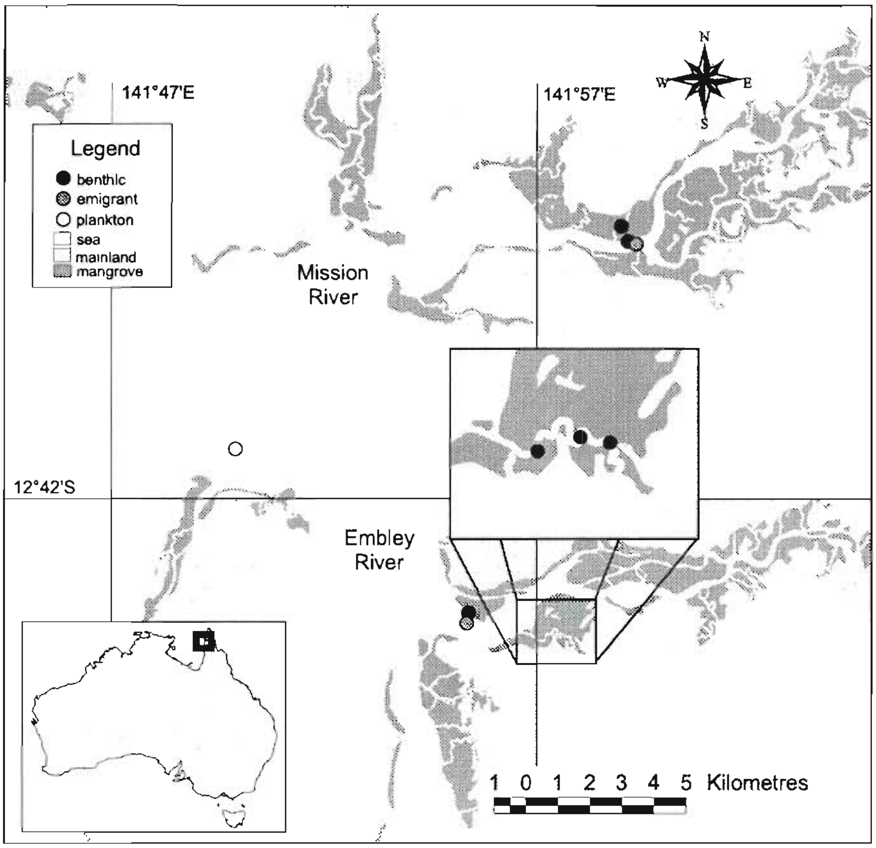

Fig. 1. Mid-river moored-net sampling sites for planktonic postlarvae and emigrating prawns (O, ◎) and river creek trawl sites for benthic postlarvae and juveniles (●) in the Embley and Mission Rivers, Gulf of Carpentaria, Australia

way through a spring flood tide because Staples & Vance (1985) found that the highest catches in the Norman River occurred about midway through flood tides. On most spring tides, there was only 1 flood tide each day but, when there were 2 tides, samples were taken on the largest flood tide of the day or night. Staples & Vance (1985) found that catches of postlarval *Penaeus merguiensis* migrating into an estuary were dependent mostly on the size of the flood tide rather than the time of day or night. The volume of water filtered for each sample was measured by a flowmeter fixed to the mouth of each net. The mean volume of water filtered by the 3 nets for each sampling period was 320 m^3 (ranging from 130 to 490 m^3) and water currents ranged from about 0.3 m s^{-1} to about 1.0 m s^{-1}.

Benthic prawns. In the Embley River, benthic postlarvae and juveniles were collected from 1 site in the main river and 3 sites in a small side creek, 14.0, 17.8, 19.5 and 20.0 km upstream from the river mouth respectively (Fig. 1). In the Mission River, 1 site in the main river and 1 site in a side creek were sampled, 20 and 22 km upstream from the river mouth respectively. All sites were on steeply sloping mudbanks abutting mangrove forests. Samples were taken with a small beam trawl towed behind either a 3.7 m or 4.6 m boat. The mouth of the beam trawl was 1.0 by 0.5 m, and the mesh size was 2 mm in the body and 1 mm in the codend. At each site, 1 trawl parallel to the water's edge and 4 trawls perpendicular to the water's edge were made on the ebb tide within 2 h of low water, which is the time of highest catchability of juvenile *Penaeus merguiensis* (Vance & Staples 1992). Postlarvae tend to concentrate very close to the water's edge (authors' pers. obs.), so perpendicular trawls provide a good estimate of the full size range of the population when prawn abundances are high. However, when prawn abundances are low, catches in the short perpendicular trawls are often zero and a parallel trawl is necessary to provide adequate sample sizes. To maintain a consistent sampling strategy, both methods of trawling were used on all occasions. The parallel trawls were made close to the water's edge in water about 0.5 m deep. Trawls in the river were 200 m long but trawls at the creek sites were reduced to 50 m. The 4 perpendicular trawls, each of 10 m length, were made at random points along the river or creek bank at each site. They were made at right angles to the bank, from the water's edge towards the middle of the river. A mean of catches from the 1 parallel and 4 perpendicular trawls at each site was used to give abundance estimates for each site.

Emigrants. Juvenile prawns emigrating from the rivers were sampled using 2 nets moored in mid-river near the main river trawl site in both the Embley and Mission Rivers (Fig. 1). The nets were set at the water's surface for the duration of the largest ebb tide on the same day that trawls were made at the river sites. One net measured 1.0 by 0.5 m at the mouth with a mesh size of 2 mm, while a larger net, 2.0 by 1.0 m with 28 mm mesh in the body and 12 mm mesh in the codend, was also used to ensure that we adequately sampled the largest prawns. Catches for the 2 nets were added to give estimates of emigration for each sampling period.

All prawns were measured using a binocular microscope fitted with an ocular micrometer: postlarvae and juvenile prawns from the beam trawls and moored nets were measured to the nearest 1.0 mm CL and postlarvae from the plankton nets to the nearest 0.1 mm CL.

Environmental data. Water temperature, salinity and light penetration into the water (measured by secchi disc) were recorded with each prawn sample. The phase of the moon and the presence or absence of moonlight at the time of each trawl were also noted. Tide heights were recorded by an automatic tide gauge near the mouth of the Embley River. Tide range (an estimate of the strength of the ebb tide and the relative volume of water exchanged) for each emigrant sample was calculated as the difference between the observed high and low tide levels for the ebb tide that the nets were set on. Mean sea level was calculated as the mean of all the hourly tide heights for the 2 wk before each sampling session.

The total rainfall for the 2 wk before each sampling session was calculated using daily rainfall data recorded at Weipa airport (about 8 km from the sampling sites). Daily wind speed and direction data recorded at 09:00 and 15:00 h at Weipa airport were resolved into 2 components: an on/offshore component at right angles to the coastline (about east/west), and a longshore component parallel to the coastline (about north/south). A mean value for each component was calculated for the periods between each sampling session (about 2 wk) and also for 1 mo before each sampling session.

Statistical analyses. The climate in the Gulf of Carpentaria is strongly seasonal, with distinct wet and dry seasons. Seasons were defined as follows: pre-wet, October to December; wet, January to March; early dry, April to June; dry, July to September.

Before analysis, each variable was tested for homogeneity of variances, by comparing log-transformed means and variances for each sampling period, and for normality, using the Shapiro-Wilk statistic (SAS Institute 1990). Because the data were non-normal and there were many near-zero values, all the catch variables and rainfall were transformed by taking the 4th root of the variable.

We explored relationships between catch and environmental data by regression analyses, which assume that the error terms associated with adjacent observations are uncorrelated, i.e. there is no autocorrelation in the data. Some autocorrelation was present in our data and was detected by examining the residuals after regression and by examination of the Durbin-Watson statistic, which was calculated for each regression analysis (SAS Institute 1989).

Several approaches were used to minimise the effects of autocorrelation. Because much of this autocorrelation is induced by the seasonality of the data, we repeated regressions using only data from the pre-wet and wet seasons. In these 2 seasons, environmental variables tended to show more variation between adjacent sampling periods and much of the cyclical seasonal variation was removed from the variables. When autocorrelation remained in the full or reduced data sets after these analyses, the significance of regressions was tested with the Proc Mixed module of the SAS statistical package (SAS Institute 1992). Proc Mixed uses the restricted maximum likelihood method to estimate relationships within data sets and can allow for autocorrelation in analyzing the data.

Variation in environmental variables may affect prawn abundances by changing the rate of movement of prawns onto or off of the nursery areas. This was tested by regressing catches against environmental variables recorded at each site at the time of sampling. Environmental variation may also have a longer-term effect on the survival of prawns in the nursery areas; this possibility was tested by also regressing catches against environmental variables for 2 wk and 4 wk before each sampling.

Means were calculated for all catch and environmental variables for the pre-wet and wet seasons for each year, and relationships between these means were tested using correlation analysis (SAS Institute 1990). The total annual offshore commercial catch of adult banana prawns in Albatross Bay was also compared with the estuarine means using correlation analysis.

Analyses were carried out using data from the Embley and Mission Rivers, and in general, results were similar for the 2 rivers, so we have only shown results of analyses using the longer Embley River data set (6 yr).

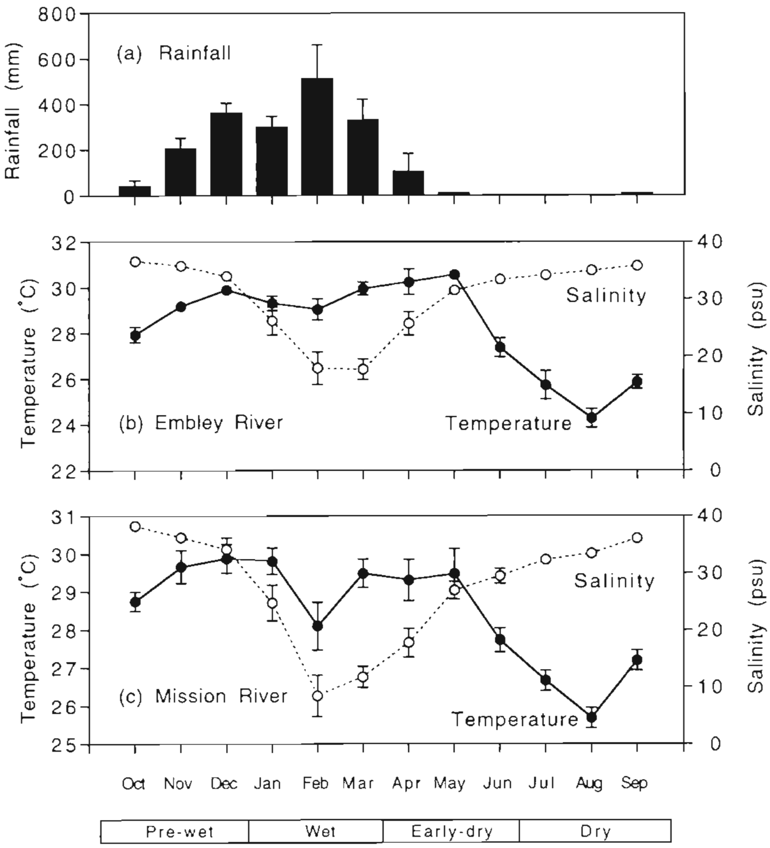

Fig. 2. (a) Mean monthly rainfall (+ 1 SE) recorded at Weipa over 3 yr. (b & c) Mean monthly salinity and temperature (± 1 SE) recorded over 3 yr at the river sites in the Embley and Mission Rivers, Gulf of Carpentaria, Australia

RESULTS

Environmental variation

The climate of the Weipa region is dominated by the strong seasonality of the wet and dry seasons. The mean annual rainfall for the 6 yr of the study was 1876 mm which was close to the 26 yr mean annual rainfall of 1897 mm. At least 84 % of the annual rainfall fell between November and March each year (Fig. 2). Wet season rainfall (January to March) ranged from 761 mm (1988) to 1712 mm (1991).

Patterns of salinity and temperature variation were very similar between the Embley and Mission Rivers, although mean monthly salinities in the wet season were lower in the Mission than in the Embley River (Fig. 2). The highest salinities (recorded at low tide) were in October or November each year, just before the wet season, and the lowest salinities were after rainfall, in February or March each year. In our study, the largest range of salinities in the Embley River was recorded at the upper creek site; the highest salinity recorded was 47.0 psu (October 1988) and the lowest was 0.8 psu (February 1991). The highest and lowest salinities at the main river site for the same sampling periods were 38.1 and 1.3 psu respectively. However, in most years the minimum salinity was much lower in the creek than in the river, e.g. 13.5 psu lower in the creek in 1990 and 1992. The largest difference in salinities (measured during the same sampling period) between the river and upper creek was in March 1990 when the creek salinity was 24 psu lower than the river.

The lowest water temperatures were in June or August each year (23.5°C at the river site in the Embley River in August 1989) and the highest temperatures were recorded between November and May (31.9°C at the creek site in January 1988). The largest difference between temperatures at the river and creek sites for the same sampling period was in January 1992 when the river was 3.7°C higher than the creek.

Catch variation

There was strong seasonality in catches of *Penaeus merguiensis* in the estuary (Fig. 3). Very low levels of planktonic and benthic postlarval catches were taken during the early dry and dry seasons (from May to September) (Fig. 3). Most immigration and settlement was between October and April. However, in the Embley River, catches decreased during the early wet season leading to a strong bimodal distribution of catches of planktonic postlarvae and a weaker bimodal distribution for benthic postlarvae.

A similar pattern of seasonal variation was seen for benthic juveniles, although the bimodal distribution of catches between October and May was more marked in the Embley than in the Mission River (Fig. 3). Prawns emigrating from the river were caught in set nets only from November to March. Maximum emigration occurred from December to February during the early wet season, coinciding with the period of decreased benthic juvenile catches. Although mean monthly catches of benthic postlarvae were similar in the Embley and Mission Rivers for most months, the mean catches of benthic juveniles and emigrants were much higher in the Mission River.

Although the broad seasonal pattern of catches was clear (Fig. 3), catches of planktonic and benthic post-

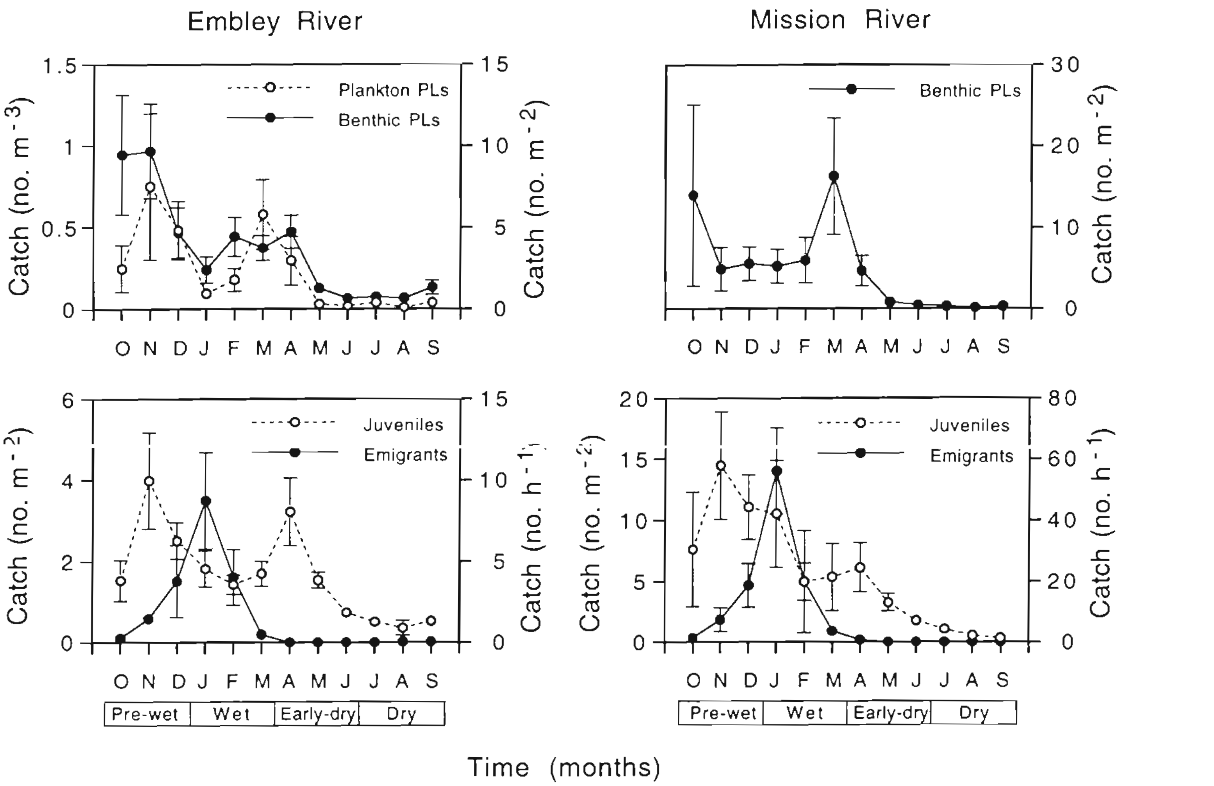

Fig. 3. *Penaeus merguiensis*. Mean monthly catches (±1 SE) of planktonic postlarvae (Plankton PLs; for Embley River only), benthic postlarvae (Benthic PLs) and juveniles (river and creek sites combined) and emigrants over 6 yr for the Embley River and 3 yr for the Mission River. Note the different scales for the 2 river systems

larvae varied greatly between fortnightly sampling periods and also in the pattern of variation between years (Fig. 4). Sometimes there was close correspondence between peaks of planktonic and benthic postlarval catches (for example, in the pre-wet season of 1988/89) but sometimes peaks did not coincide (pre-wet 1987/88). In the Embley River, mean seasonal catches of planktonic and benthic postlarvae tended to be higher in the pre-wet than in the wet season, but the reverse was true in 1986/87 and 1991/92 (Fig. 5). Mean catches of planktonic and benthic postlarvae in the pre-wet season were not always closely related to catches a few months later in the wet season. For example, in 1986/87, the pre-wet season catches of benthic postlarvae in the Embley River were the lowest for the 6 yr while wet season catches were highest for the 6 yr (Fig. 5).

Fluctuations in fortnightly catches of benthic juveniles between sampling periods were not as marked as for benthic postlarvae (Fig. 6), which is not surprising since the juvenile size group includes some prawns that must have been resident in the estuary for up to 3 sampling periods (about 6 wk, based on size distributions and known growth rates). Mean juvenile catches were mostly higher in the pre-wet than the wet season with the exception of 1986/87 and 1991/92 (Fig. 5).

Although some emigrating prawns were caught in set nets early in the pre-wet season, all the large peaks of emigration were associated with marked decreases in salinity during the wet season (Fig. 6). In 1989/90, when juvenile catches were low and salinity remained high for most of the year, few emigrants were caught. In all years except 1989/90, catches of emigrants were highest in the wet season (Fig. 5). The highest catches of emigrants in the Embley River were in 1988/89 when postlarval immigration and juvenile catches were also high and when salinity began to decrease substantially earlier than in other years (in early December).

The pattern of seasonal mean catches for benthic postlarvae and benthic juveniles was mostly similar, i.e. good catches of benthic juveniles were usually associated with good catches of benthic postlarvae during the same season (Fig. 5). However, the pattern of mean emigrant catches was not so closely related to catches of benthic juveniles. In general, the patterns of variation of seasonal mean catches for all catch groups for the Embley and Mission Rivers were similar for the first 3 yr of the study (Fig. 5). Where there were differences in the relative mean catches for the 2 rivers, the sizes of the standard errors show that the differences were not significant. As the monthly means also showed, catches of benthic juveniles and emigrants were higher in the Mission than in the Embley River for each season and year.

Analyses of catch variation

Using exploratory multiple regression analyses with all fortnightly data and data for the pre-wet and wet seasons only, we found that water temperature was the most significant variable in explaining planktonic postlarval catches, although only 13.8% of the variation was explained (Table 1). Increased temperature was associated with increased catches. When only wet season data were used, rainfall was the most significant variable, explaining 15.0% of the catch variation, and was negatively correlated with catches.

The most significant variable in multiple regression analyses of benthic postlarval catches at each site was the catch of planktonic postlarvae of the same sampling period, with up to 29.5% of the variation in benthic catches explained (Table 2). Mean sea level (positively related) was also significant at 2 of the creek sites, and salinity added to the multiple regression at some sites. Salinity was negatively related to benthic postlarval catches at the river site, not significantly related at the creek mouth and positively related further up the creek.

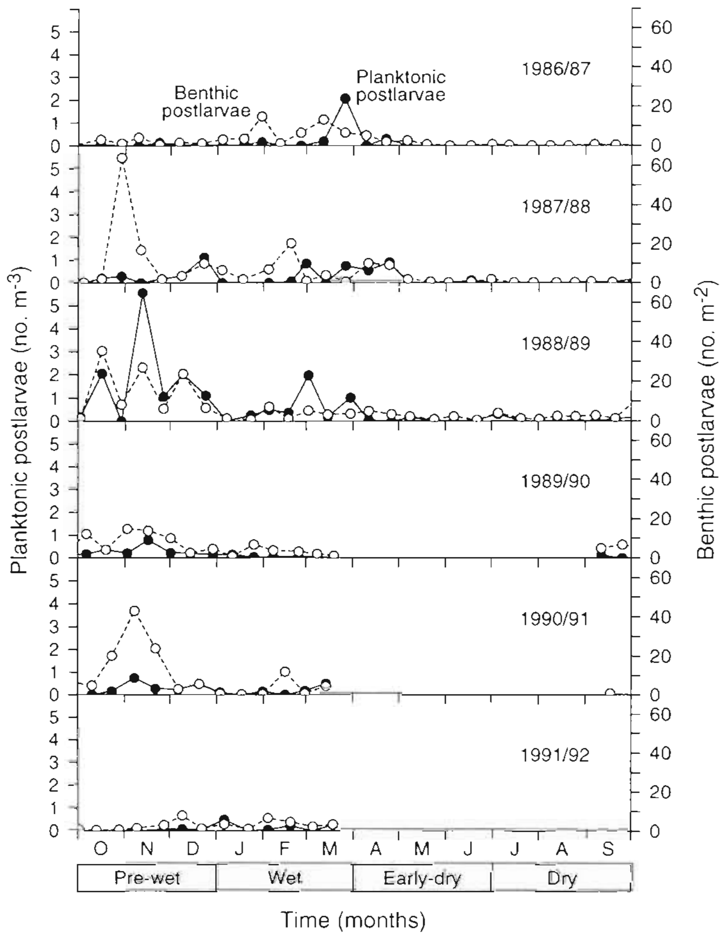

Fig. 4. *Penaeus merguiensis*. Planktonic (●) and benthic (○) postlarval catches at fortnightly intervals from September 1986 to March 1992 for the Embley River. Benthic postlarval catches are means for the river and 3 creek sites

Benthic juvenile *Penaeus merguiensis* catches were most highly correlated with benthic postlarval catches at all sites (Table 2). At the river site, catches of postlarvae at the creek sites 4 wk earlier explained the most variation (45.8%), while at the creek sites, benthic postlarvae of the previous sampling period were most significant. Salinity was also significant in the regressions at some sites, and temperature was added to the regressions at 3 sites. When analyses for benthic postlarvae and juveniles were repeated using data from the pre-wet and wet seasons only, catches of the earlier life stage were again most highly correlated with catches of the later life stage.

Table 1 *Penaeus merguiensis*. Significant sources of variation, mean squares and percentages of the total planktonic postlarval catch variation explained by each variable in multiple regression analyses for fortnightly data in the Embley River. Where necessary, the significance of the regressions was tested with Proc Mixed (see 'Methods') to remove the effects of autocorrelation. The sign of the regression coefficients is shown in parentheses. $^{***}p \leq 0.001$; $^{*}0.01 < p \leq 0.05$

	Source of variation	n	Mean square	Variation (%)
All data	Temperature	116	(+) 0.216***	13.8
Pre-wet and wet	Temperature	66	(+) 0.105*	8.5
Wet	Rainfall	32	(–) 0.057*	15.0

Rainfall was the most significant variable entered into multiple regressions of emigrant catch for all fortnightly data, followed by tide range and the catch of benthic juveniles at all trawl sites for the same sampling session (Table 3). When only data for the pre-wet and wet seasons were analysed, rainfall was replaced in the regression by salinity at the upper

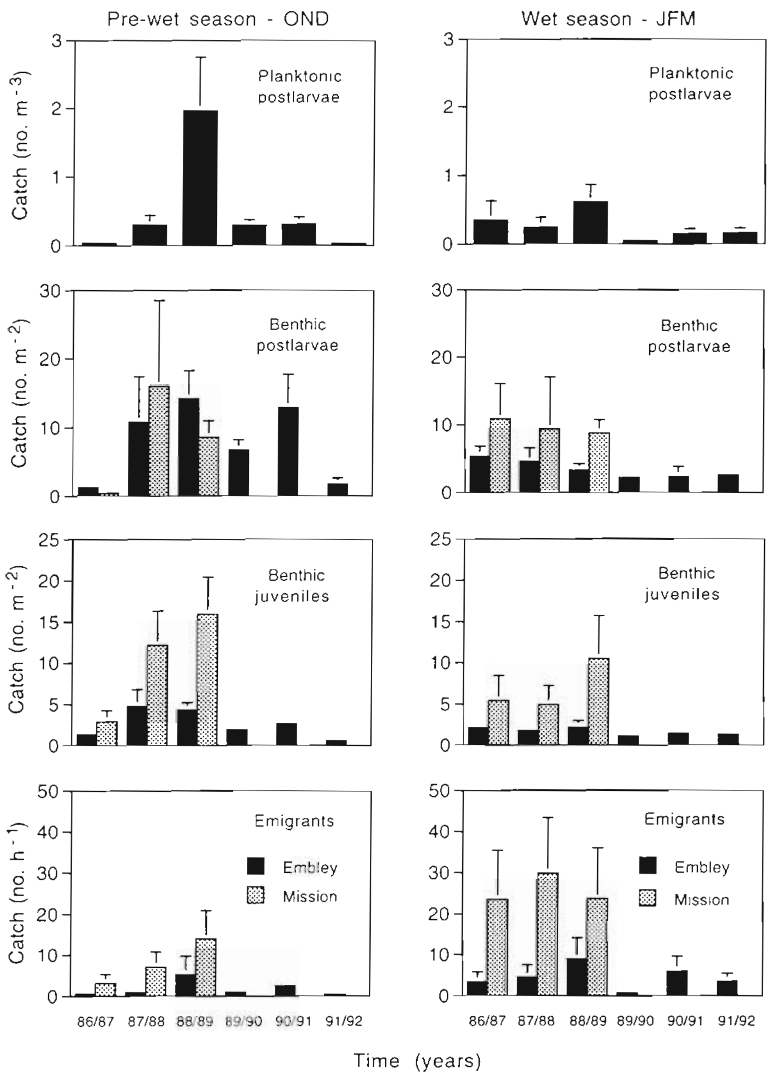

Fig. 5. *Penaeus merguiensis*. Mean seasonal catches (+1 SE) of planktonic postlarvae, benthic postlarvae and juveniles (river and creek sites combined) and emigrants for the pre-wet and wet seasons for the Embley River from 1986 to 1992 and for the Mission River from 1986 to 1989

creek site, but the proportion of variation explained by each variable was almost identical to the analysis for all data.

The multiple regressions using all fortnightly data explained about 14% of the variation in catches of planktonic postlarvae, 16 to 35% of catches of benthic postlarvae, 40 to 48% of catches of benthic juveniles and 40% of catches of emigrants.

Analyses of annual variation

Comparisons of yearly means of catch and environmental variables for the pre-wet and wet seasons produced some significant correlations, but they must be interpreted with caution as only a small number of data points were used in the analyses (n = 6) (Table 4). As for the fortnightly data (Table 2), benthic postlarvae were positively correlated with planktonic postlarvae and benthic juveniles were positively correlated with planktonic and benthic postlarvae. Emigrant catches were positively correlated with benthic juvenile catches. Not all of these correlations were significant.

Temperature was positively correlated with all catch variables, particularly during the pre-wet season. Salinity was strongly correlated only with emigrants during the wet season; decreased salinity was associated with increased emigration. Wind variables were strongly correlated with planktonic and benthic catch variables during the wet season. Increased catches were associated with stronger offshore winds and winds with a stronger southerly component.

Comparisons of creek and main river

Catches of postlarval and juvenile *Penaeus merguiensis* tended to be higher at the creek sites than in the main river, particularly at the upper creek site. At this site, mean monthly catches were higher than in the main river in all months of the year (Fig 7). In fact, catches were higher at the upper creek site than at the river site in 118 out of the 120 samples. However, the difference in catches between the creek sites and the main river decreased towards the creek mouth; catches were higher at the mid-creek and creek mouth than in the main river on 106 and 68 occasions respectively.

A large size range of benthic prawns was caught in the estuary, with values from 1 mm CL at all sites to 20 mm CL at the river site and 18 mm CL in the creek. However, the size distributions of prawns at the river and creek sites were quite different. Newly settled postlarvae (1 mm CL) made up a larger proportion of catches at the river site than at the upper creek site, although the overall abundance of the 1 mm CL size class was higher at the upper creek site than in the main river (Fig. 8). In contrast, the 2 to 5 mm CL size classes were a much higher proportion of total catch at the upper creek site in all seasons

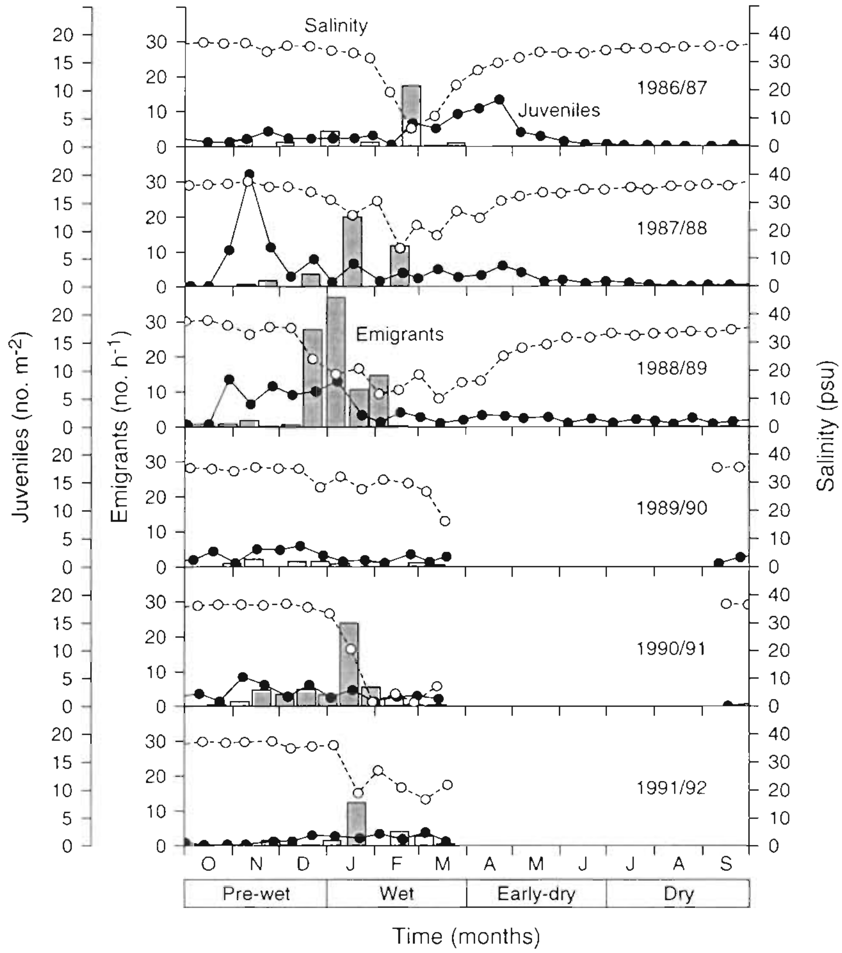

Fig. 6. *Penaeus merguiensis*. Benthic juvenile catches (●), emigrant catches (■) and salinity (O) at fortnightly intervals from September 1986 to March 1992 for the Embley River. Benthic juvenile catches are means for the river and 3 creek sites; salinity was recorded at low tide at the river site. No emigrants were caught between April and July

Table 2. *Penaeus merguiensis*. Significant sources of variation and percentages of the total benthic postlarval and juvenile catch variation explained by each variable in multiple regression analyses for fortnightly data in the Embley River. Where necessary, the significance of the regressions was tested with Proc Mixed (see 'Methods') to remove the effects of autocorrelation. The sign of the coefficients is shown in parentheses. n ranged from 109 to 117. ***$p \le 0.001$, **$0.001 < p \le 0.01$, *$0.01 < p \le 0.05$, ns: not significant

	River	Creek mouth	Creek mid	Creek upper
Benthic postlarvae				
Planktonic postlarvae	(+) 29.5***	(+) 16.5***	(+) 27.0***	(+) 19.6**
Mean sea level	ns	ns	(+) 3.1**	(+) 6.8***
Salinity	(–) 3.4*	ns	(+) 3.6*	(+) 8.2**
Benthic juveniles				
Benthic postlarvae	(+) 45.8***[a]	(+) 28.6***[b]	(+) 31.1***[b]	(+) 46.2***[b]
Salinity	ns	(–) 12.2***	(–) 5.7**	ns
Temperature	(+) 1.5*	ns	(+) 2.8*	(+) 1.5*

[a]Catches of benthic postlarvae at creek sites 4 wk previous
[b]Catches of benthic postlarvae at creek sites 2 wk previous

except during the dry (Fig. 8). Prawns >5 mm CL made up a higher proportion of the catch in the river than in the upper creek (and at each creek site) in all seasons. Over the whole study, 10.2% of prawns caught at the river site were larger than 10 mm CL whereas only 1.0, 0.3, and 0.7% of prawns caught at the upper, mid and mouth creek sites were larger than 10 mm.

Table 3. *Penaeus merguiensis*. Significant sources of variation, mean squares and percentages of the total emigrant catch variation explained by each variable in multiple regression analyses for fortnightly data in the Embley River. Where necessary, the significance of the regressions was tested with Proc Mixed (see 'Methods') to remove the effects of autocorrelation. The sign of the coefficient is shown in parentheses. n = 117. ***$p \le 0.001$, **$0.001 < p \le 0.01$

Source of variation	Mean square	Variation (%)
Rainfall	(+) 3.951***	24.4
Tide range	(+) 1.646***	11.7
Benthic juveniles	(+) 0.437**	3.7

Commercial catch

Annual offshore commercial catch of adult *Penaeus merguiensis* for the 6 yr of this study was highly correlated with the mean catch of emigrating *P. merguiensis* for the pre-wet and wet seasons combined ($R^2 = 0.82$, $p = 0.01$) (Fig. 9). Commercial catch was also significantly correlated with the mean catch of benthic juveniles at the river and creek sites for the same period ($R^2 = 0.71$, $p = 0.03$). Total rainfall for the pre-wet and wet seasons was positively, but only poorly correlated with commercial catch ($R^2 = 0.25$, $p = 0.31$). Mean salinity in the main river was much more strongly correlated with catch than was rainfall; lower salinities were associated with higher offshore catches ($R^2 = 0.56$, $p = 0.09$).

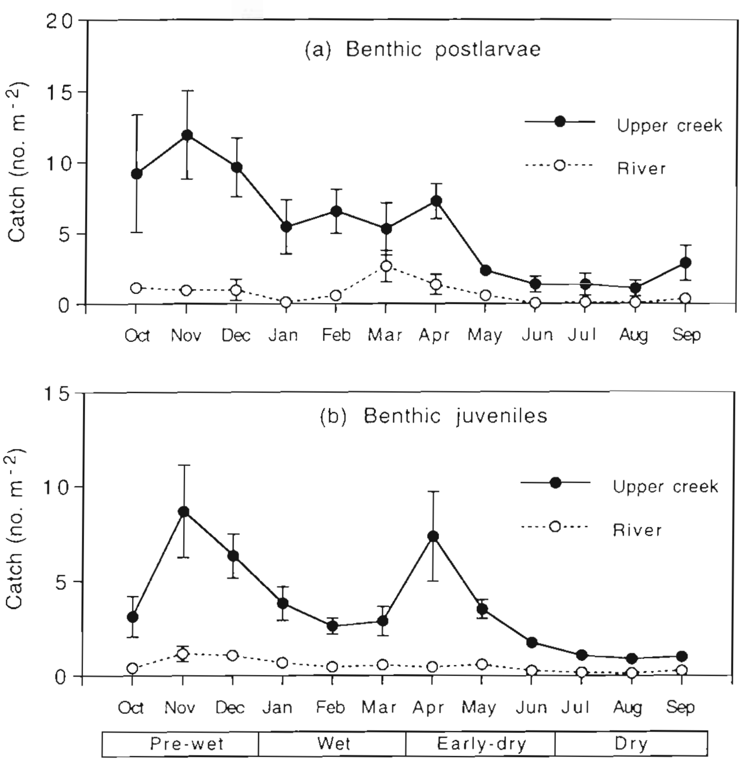

Fig. 7 *Penaeus merguiensis*. Mean monthly catches (±1 SE) of (a) benthic postlarvae and (b) benthic juveniles for the upper creek and river sites in the Embley River over 3 yr

DISCUSSION

Seasonal patterns of catch variation

Rothlisberg et al. (1985) have suggested that the basic life-history scheme for *Penaeus merguiensis* throughout its range consists of 2 populations of approximately equal size (spring and autumn populations) with a life-cycle duration of 6 mo. In some parts of its range, depending on local rainfall regimes, this would result in almost year-round recruitment of prawns to the adult fishery. In the Gulf of Carpentaria, they proposed that this pattern was modified by the short wet season so that the 2 populations were of unequal size and only the autumn or early-dry season population supported the offshore commercial fishery (Rothlisberg et al. 1985).

Other studies have reported a wide range of seasonal abundance patterns of postlarval and juvenile *Penaeus merguiensis*, although the studies have only been 1 or 2 yr long. A pattern of 2 main periods of abundance was found in India by Mohan et al. (1995), although there was substantial variation between the 2 years studied. The main period of abundance ranged from 5 mo in India during the pre-monsoon months (Selvakumar et al. 1977, Achuthankutty & Nair 1982) to 9 mo in Malaysia (Ahmad-Adnan 1994), while postlarvae and small juveniles were caught throughout the year in Indonesia (Noor-Hamid 1976).

Over the 6 yr of this study, we found that peaks in abundance of *Penaeus merguiensis* postlarvae and juveniles in the Embley and Mission Rivers could occur at any time from October to May (8 mo of the year), but the exact timing of the peaks varied from year to year. However, when averaged over all years, the distribution of catches in the Embley River was bimodal, with peaks in the pre-wet and wet or early-dry seasons. The bimodal pattern was much less pronounced in the nearby Mission River. Mean catches in the Mission River were much lower in the wet and early-dry seasons than in the pre-wet season. This may be due to the lower levels of mean salinity in the Mission River from February to April compared to the Embley River. Mean salinity in April was 17.8 psu in the Mission River com-

Table 4. *Penaeus merguiensis*. Pearson correlation coefficients of catches and environmental variables for the Embley River. Annual estimates for benthic postlarvae and juveniles were means for the river and creek sites combined. n = 6. **0.01 < p ≤ 0.05, *0.05 < p ≤ 0.10

Variable	Planktonic postlarvae		Benthic postlarvae		Benthic juveniles		Emigrants	
	Pre-wet	Wet	Pre-wet	Wet	Pre-wet	Wet	Pre-wet	Wet
Planktonic postlarvae			0.60	0.44	0.53	0.90**		
Benthic postlarvae					0.82**	0.77*		
Benthic juveniles							0.58	0.64
Temperature—creek	0.65	0.38	0.74*	0.29	0.77*	0.20	0.76*	0.21
Salinity—creek	0.13	-0.29	-0.06	0.24	-0.14	-0.32	-0.23	-0.85**
Rainfall	0.65	-0.01	0.16	-0.42	0.53	-0.12	0.57	0.37
Mean sea level	0.88**	0.64	0.47	-0.04	0.26	0.35	0.83**	0.31
On-offshore wind	-0.13	0.71	0.55	0.82**	0.23	0.89**		
Alongshore wind	0.51	-0.74*	-0.04	-0.84**	0.04	-0.89**		
Tide range							0.20	0.60

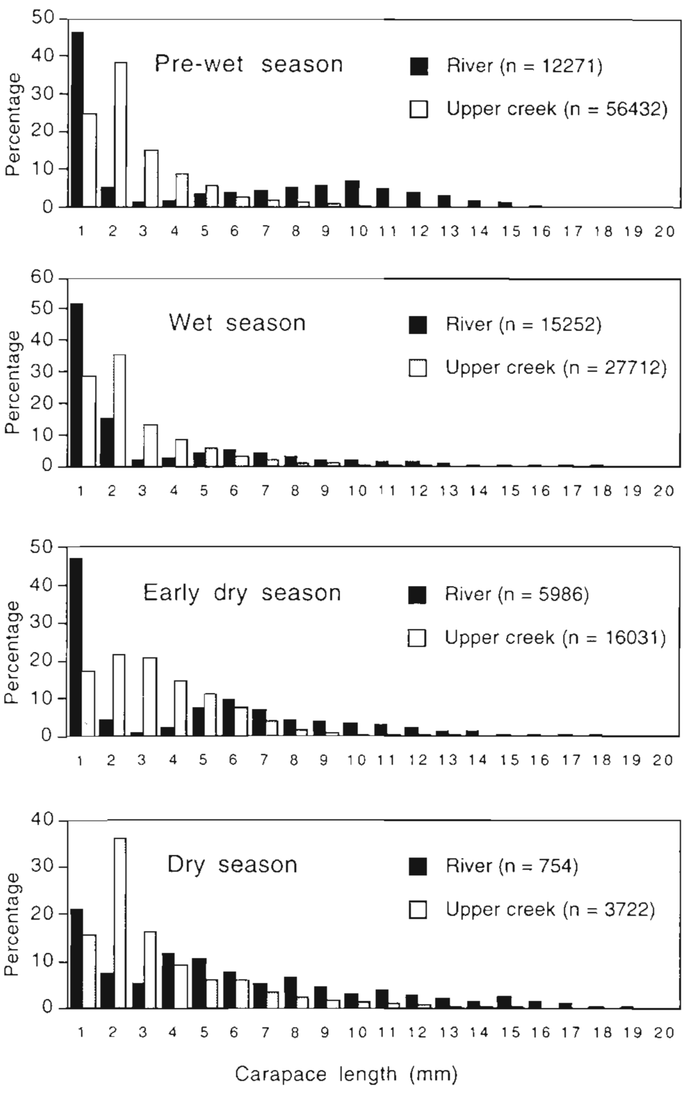

Fig. 8. *Penaeus merguiensis*. Percentage length frequency distributions of all prawns caught at the river and upper creek sites in each of 4 seasons over 6 yr

pared to 25.6 psu in the Embley River (Fig. 2). This lower mean salinity in the Mission River probably inhibited postlarval immigration and settlement, and increased juvenile emigration. The lower salinity in the Mission River is itself due to the river's greater length and the correspondingly larger catchment area (about 1.4 times the size of the Embley River catchment area). It is clear from our study that seasonal abundance patterns vary substantially between years and that data need to be collected for several years to identify the seasonal patterns and the amount of annual variation in those patterns.

In contrast to the extended period of postlarval and juvenile abundance in the estuary, substantial emigration of juvenile *Penaeus merguiensis* occurred for only a relatively short part of the year (December to February), following rainfall in the pre-wet and the wet season. This phenomenon has also been described for *P. merguiensis* in rivers in the southeastern Gulf of Carpentaria (Staples & Vance 1986).

The results of this study clearly show that the pre-wet season cohort of prawns is at least as abundant and often more abundant in the estuaries than the cohort occurring in the wet or early-dry seasons. This is in contrast to the results of Rothlisberg et al. (1985), who stated that, in the northeastern Gulf of Carpentaria, the second cohort was the most successful. The discrepancy between studies is probably related to the different sampling regimes employed in the 2 studies. The results of Rothlisberg et al. (1985) were obtained from samples taken only at the main river site over 1 yr, whereas our results were taken from the creek and main river sites over 6 yr. In general, catches were much higher at the upper creek sites (Fig. 7) and, therefore,

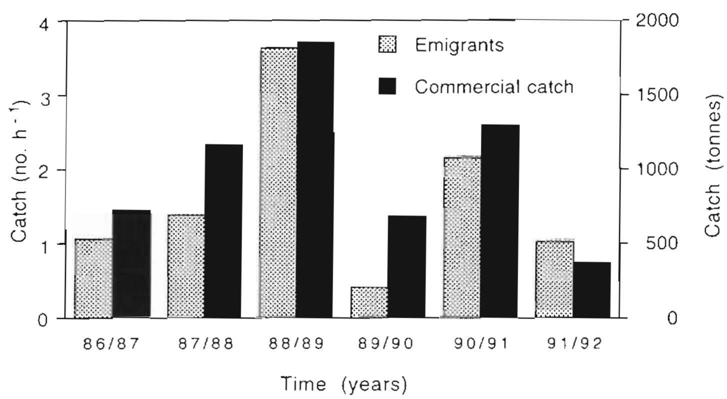

Fig. 9. *Penaeus merguiensis*. Mean catch of emigrants for the pre-wet and wet seasons and annual offshore commercial adult catch over 6 yr

were more important in determining overall abundance in the estuary. In the present study, we have also seen that the pattern of seasonal variation in catches can vary substantially between years. However, our conclusion, that the wet/early-dry season cohort (February to May) is much stronger in the estuaries of the northeastern Gulf than it is in the southeastern Gulf, agrees with that of Rothlisberg et al. (1985). This is partly a result of unfavourable current regimes leading to poor advection of larvae into nursery areas in the southeastern Gulf in the wet season (Rothlisberg 1982) and partly due to salinities in the Norman River (southeastern Gulf) often remaining lower for more extended periods during the wet season than do salinities in the Embley and Mission Rivers (Staples & Vance 1986). The lower salinities would have inhibited immigration of postlarvae into the southeastern rivers during the wet season much more than in the northeastern rivers.

Factors determining abundance

Planktonic postlarvae

Very little of the fortnightly variation in planktonic postlarval catches could be explained by any environmental variation that we could measure. Increased temperature was associated with higher catches, but this may have been due to similar patterns of seasonal variation rather than a causal relationship—the strength of the correlation decreased when only pre-wet and wet seasons were analysed. Temperature may have some effect on offshore spawning and therefore abundance of larvae, and it may also be associated with variation in water movements that might increase advection of postlarvae into the estuary. Mean sea level was significantly correlated with planktonic postlarval catches when annual means were compared; changes in mean sea level may reflect changes in offshore water movements that could affect advection of postlarvae into the estuaries. Rainfall seemed to have a small inhibitory effect on postlarval immigration during the wet season. Some other studies on *Penaeus merguiensis* have also suggested that the abundance of estuarine larvae and postlarvae is decreased during monsoonal wet seasons, but no statistical analyses were carried out (Achuthankutty & Nair 1982, Achuthankutty 1987, Gunaga et al. 1989). Rainfall also seemed to inhibit immigration of postlarval *Penaeus semisulcatus* into the Embley River during the same study period (Vance et al. 1996b).

Overall, only a small proportion of the variation in planktonic postlarval catches could be explained by environmental variation in the estuary and, therefore, much of the variation is presumably determined by factors acting on the offshore spawners or larvae. Interestingly, the mainly bimodal pattern of estuarine abundance is in stark contrast to the seasonal abundance pattern of adult spawners and larvae in Albatross Bay, offshore from the Embley River The major period of offshore abundance was in the wet season (January to March) but very few adults and virtually no larvae were caught during the pre-wet season (October to December) (Rothlisberg et al. 1988, Crocos 1992)—i.e. the highest abundances of prawns in the river (in the pre-wet season) apparently result from only very low densities of adults and larvae.

There are several possible reasons for the discrepancy between offshore larval abundance patterns and estuarine postlarval and juvenile patterns. Increased larval survival in the pre-wet season, as reported by Preston et al. (1992) from *in situ* experiments offshore from the Embley River, may result in larger numbers of postlarvae reaching the estuarine nursery areas. Another possibility is that the offshore water currents in the pre-wet season are more suitable for advecting larvae and postlarvae into the nursery areas than in the wet season. Rothlisberg (1982) has shown that the interaction between the vertical migration behaviour of larvae and the prevailing tidal currents is critical in determining the direction of advection of larvae and that larvae can be advected in quite different directions at different times of the year. It is also possible that the effective adult spawning stock was not adequately sampled, particularly in the pre-wet season. In southeastern Queensland (Australia) adult *Penaeus merguiensis* tagged and released in offshore waters have been recovered within estuaries (Dredge 1985) and, although no sexually mature *P merguiensis* were caught in the Embley River in our study, they may have been just outside the estuary during the dry and pre-wet season. Spawning of these prawns close to the estuary mouth could result in much more effective advection of postlarvae into the estuary than spawning of prawns further offshore. These inshore spawners may then have moved further offshore in response to lower salinities during the wet season, resulting in less effective spawning and lower postlarval recruitment to the Embley River during the wet season.

Benthic postlarvae and juveniles

More of the catch variation was explained by multiple regressions for both benthic postlarvae and juveniles than for catches of planktonic postlarvae. At all sites the single most important factor determining benthic postlarval abundance was the level of immigration of postlarvae into the estuary (i.e. planktonic postlarval catch). Although salinity added only a small amount to the variation explained by the regressions, the salinity relationships provide an insight into the dynamics of postlarval movements within the estuary. Salinity was negatively related to benthic postlarvae in the river, not significantly related at the mouth of the creek and increasingly positively related to postlarval abundance with increased distance up the creek (Table 2). This suggests that, as salinity decreased in response to wet season rainfall, postlarval settlement was inhibited at the upper reaches of the creek leading to lower postlarval abundances there. However, salinity usually didn't decrease quite as much in the main river, and postlarvae that did not settle in the creek were able to settle out in the river, leading to an increased postlarval abundance at the river site.

The largest variation in benthic juvenile catches at all sites was explained by the benthic postlarval catches of the previous sampling period (2 wk previous). The majority of benthic postlarvae would have settled on the nursery areas within the week before sampling, and, although there would have been some mortality of postlarvae after settlement, it is likely that benthic postlarval catches are a reasonable indicator of postlarval supply to the nursery areas. The most important factor in determining the abundance of juvenile *Penaeus merguiensis* in the Embley River was therefore the supply and successful settlement of postlarvae.

A little benthic juvenile catch variation was explained in some regressions by salinity or temperature, but these relationships were neither strong nor consistent. It is surprising that temperature was not more strongly related to juvenile abundance. Haywood & Staples (1993), using cohort analysis on the first 3 yr of this data set, found that temperature explained about 25% of the mortality of juvenile *Penaeus merguiensis*. Their results suggest that increased temperature should result in decreased densities of prawns in the estuary. It is possible that, although increased temperature may decrease the survival of juvenile prawns over the life of a particular cohort, the actual change in density may not be great and that the density of all prawns in the population may be more influenced by the almost continual recruitment of new cohorts to the population.

Emigrants

As was found in the southeastern Gulf (Staples & Vance 1986), the most important factor in regressions that explain juvenile prawn emigration was rainfall for the 2 wk preceding the sampling period. The tide range for each ebb tide and the numbers of benthic juveniles in the river at the time of sampling were also important. These variables were also significant in regressions for the Norman River in the southeastern Gulf, but the abundance of benthic juveniles was more important than tide range in the southeastern Gulf (Staples & Vance 1986).

The relatively short period of emigration and the relatively short wet season in Gulf of Carpentaria rivers are quite different from patterns of rainfall and emigration or offshore abundance seen in other parts of the Indo-West Pacific range of *Penaeus merguiensis*. Gwyther (1982) has suggested that *P. merguiensis* recruits to the offshore fishery in Papua New Guinea for most of the year, recruitment probably being associated with the greater amount and duration of coastal rainfall in the area. In Malaysia, although rain is seasonal to a certain extent, substantial rainfall occurs throughout the year and juvenile and adult *P. merguiensis* are also abundant throughout the year (Staples 1991). It is likely therefore that the seasonal pattern of recruitment of *P. merguiensis* to offshore waters at any particular location throughout its range will be substantially dependent on the amount and pattern of rainfall at that location.

Commercial catch

We found that the mean catch of juvenile *Penaeus merguiensis* caught emigrating from the river during the pre-wet and wet seasons was strongly correlated with the subsequent annual commercial catch of adult prawns in offshore waters. This correlation may have been even stronger if we had been able to sample emigrants more frequently than at fortnightly intervals. Rainfall events occurring between sampling sessions would sometimes have led to pulses of emigration of juvenile prawns that were not completely represented by set net catches in the next sampling session. As rainfall and emigration were quite episodic, it would have been impossible for us to sample all pulses of emigration with equal reliability.

Rainfall - offshore commercial catch relationships

In the southeastern Gulf of Carpentaria there is a strong positive correlation between annual coastal rainfall and the subsequent offshore commercial catch of *Penaeus merguiensis*. However, in the northeastern Gulf there is only a weak relationship between rainfall and commercial catches offshore from the Embley and Mission Rivers (Vance et al. 1985, Staples et al. 1995). Despite this weak relationship, our study has shown that, at the level of fortnightly variation, increased emigration of juvenile *P. merguiensis* from the Embley and Mission Rivers was associated with increased rainfall and decreased salinity, as it was in the southeastern Gulf of Carpentaria rivers (Staples & Vance 1986, 1987). Therefore, the lack of a strong relationship between rainfall and offshore commercial *P. merguiensis* catch in the northeastern Gulf is not due to a difference in response of the juvenile prawns to rainfall in the 2 regions. The difference is much more likely to be caused by differences in rainfall levels and physical characteristics of the river systems in each region.

The most important factor in determining the strength of the correlation between rainfall and offshore prawn catch is probably the size of the river catchment areas; catchment areas draining freshwater into the prawn nursery areas of the southeastern Gulf are about 30 times larger than those draining into the northeastern Gulf (Anonymous 1987). Therefore, heavy rainfall in the northeastern Gulf has an immediate impact on the estuarine prawn nursery areas but, because of the small catchments, the influence of the rainfall is quickly overwhelmed by the high salinity oceanic water. In the southeastern Gulf, heavy rainfall in the larger catchments, which extend for up to 500 km inland, causes a much larger volume of freshwater to flow through the estuarine systems over a much longer time. Consequently, the effects of heavy rain last for much longer and would have a stronger impact on the prawn nursery areas than in the northeastern Gulf. Since rainfall has a much smaller impact on the estuaries in the northeastern Gulf, it is also much more weakly correlated with the offshore commercial catch in the northeastern Gulf.

Comparisons of creek and main river

The results from both Embley and Mission Rivers show that small mangrove-lined creeks are extremely important habitats for juvenile *Penaeus merguiensis*. This agrees with the conclusions of Robertson (1988) and confirms the earlier results of Vance et al. (1990) for the Embley River. The abundance of newly settled postlarvae was higher in creeks in both estuaries, which suggests that the higher densities of juvenile prawns in the creeks were due to higher recruitment and settlement of postlarvae in creeks than in the main river habitats, although postlarvae and small juvenile prawns may also have increased survival rates in the creeks. It is likely that this concentration of postlarvae towards the upper reaches of small creeks results from a combination of hydrodynamic processes and changes in behaviour associated with development stage. Lipcius et al. (1990) suggested that blue crab postlarvae settle on their preferred nursery habitat only when they reach a particular stage of development. Postlarval *Penaeus semisulcatus* in a laboratory study began clinging to seagrass only when they grew to about 1.7 mm CL (Liu & Loneragan 1997). Immigrating *P. merguiensis* postlarvae only move from the substrate into the water column on flood tides (Staples 1980) and probably continue to migrate upstream on flood tides until they are physiologically ready to settle out and adopt a benthic lifestyle. Because their migrations are locked onto the flood tides, once they are inside a small creek, they will become more concentrated at the upstream reaches of the creek. If their cue for settlement was simply the availability of suitable nursery habitat, then the distribution of benthic postlarvae would be more uniform throughout the river and creeks or even concentrated nearer the downstream reaches.

Although the abundance of newly settled postlarvae was higher in the creeks than the rivers, the proportion of 1 and 2 mm CL size groups was not the same. In the main river, 1 mm CL postlarvae were the largest component of the catch in all seasons, whereas 2 mm CL postlarvae were more abundant at the upper creek site (Fig. 8). In other words, there are many more 2 mm CL postlarvae at the upper creek site than at the river site compared with the numbers of 1 mm CL postlarvae present at each site. This may be because of poorer survival of postlarvae at the river site after settlement, or because many of the 1 mm CL postlarvae caught at the river site had not finally settled out from their planktonic lifestyle when they were caught, and continued to migrate further upstream on subsequent flood tides. We were not able to separate these 2 possibilities from the results of our sampling.

Although the major emigration of prawns from the Embley River appears to occur in mid-river after heavy or prolonged rainfall (Figs. 3 & 6), the length frequency distributions of prawns suggest that a lower level of emigration from the creek to the main river continues throughout the year (Fig. 8). In all seasons the proportion of prawns >5 mm CL was greater at the river site than in the creek. There are 2 possible reasons for this difference. If we assume that all initial settlement occurs at size 1 or 2 mm CL, then either prawns suffer higher mortality rates in the creek than in the river, or the larger size groups emigrate from the creek to the river. It is unlikely that prawns in the creek are subjected to higher mortality rates than are those in the river. In fact, predation rates by large fish are likely to be lower at the upper creek because the water is shallower, the channels are narrower and there are more mangroves in relation to the amount of water. Juvenile *P. merguiensis* have been shown to move into the mangrove forests on flood tides and probably gain some protection from predation while in the forests (Vance et al. 1996a). It is more likely that the higher proportion of larger prawns in the river is due to a gradual emigration of those larger prawns from the creek, most likely along the creek and river banks rather than in a mass mid-river migration. Most importantly, this migration appears to occur year round. It is also possible that some of these larger prawns are continuing to migrate gradually out of the Embley River into the coastal areas of Albatross Bay. Some of these larger prawns could be present in the coastal waters as young adults during the later part of the dry season and the pre-wet season. They could then spawn close inshore, thus contributing to the disproportionately large numbers of postlarvae and juveniles caught in the estuary in the pre-wet season (referred to earlier in the 'Discussion').

Conclusions

We found that the most important factor affecting the abundance of juvenile *Penaeus merguiensis* in the Embley River was the supply and successful settlement of postlarvae into the estuary from offshore. We also formed this conclusion for juvenile tiger prawns *Penaeus semisulcatus* that use seagrass and algal beds in the same estuary (Vance et al. 1996b). It is clear from our study that seasonal abundance patterns vary substantially between years and that data need to be collected for several years to identify the seasonal patterns and the amount of annual variation in those patterns. Our study also found subtle differences in seasonal patterns in adjacent rivers (the Embley and Mission Rivers), probably due to differences in the physical characteristics of each river system, and the size of their catchments. Seasonal patterns derived from sampling over only 1 or 2 yr, or from a sampling design that does not adequately represent all the available habitat, may well be misleading, causing incorrect conclusions to be drawn (see also Vance et al. 1996b).

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