Vol. 135: 43-55, 1996 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published May 17

Seasonal and annual variation in abundance of postlarval and juvenile grooved tiger prawns *Penaeus semisulcatus* and environmental variation in the Embley River, Australia: a six year study

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ABSTRACT: We studied the 2-weekly, seasonal and annual variation in abundance of postlarval and juvenile *Penaeus semisulcatus* on a seagrass and an algal bed in the Embley River, Australia, from September 1986 to May 1992. The climate in this region is dominated by the wet and dry seasons, which lead to clear seasonal patterns of salinity, temperature and mean sea level in the estuaries. Similarly, catches of postlarvae entering the estuary and of postlarvae and juveniles in the estuary showed strong seasonal variation; they were highest just before and during the wet season, from September to April each year. Catch rates often had a bimodal distribution each year, but the relative size of each recruitment peak varied considerably between years. Long-term sampling over several years is clearly necessary to identify seasonal patterns in abundance and the range of variation in these patterns for juvenile penaeids. Total catches also varied substantially between years. The bimodal juvenile catch distribution suggests that recruitment to the offshore adult fishery should occur over 2 periods during the year This is in contrast to previous work on adult *P. semisulcatus* in the Gulf of Carpentaria, which found only 1 period of recruitment and has important implications for the management of the fishery. Using multiple regression analysis, the most significant factor in determining the abundance of juvenile *P. semisulcatus* in the estuary was the number of benthic postlarvae that settled on the seagrass and algal beds. Rainfall was the most important environmental variable in the postlarval catch models. Increased rainfall was associated with a lower catch of postlarvae at the seagrass and algal sites but its major influence was through reducing the amount of algal habitat during the wet season. The mean sea level, or the amount of time that the seagrass bed was exposed, was also significant in the regression models for benthic postlarval and juvenile catches; increased exposure of the seagrass bed was associated with decreased catches of *P. semisulcatus*. However, because the proportion of juvenile catch variation explained by environmental variables was low, it is unlikely that predictive models of adult catches can be developed based on environmental factors acting on the estuarine stages of the life cycle of this species.

KEY WORDS: Penaeid · Postlarvae · Juvenile · Environment · Season · Annual variation · Seagrass · Algae

INTRODUCTION

In the past, most penaeid prawn fisheries have been managed on the basis that the spawning stock was not limiting and that any annual variation in recruitment to the fisheries was determined by environmental variation. However, recent studies have challenged this assumption. For example, recruitment of adult brown tiger prawns *Penaeus esculentus* to the fishery in Exmouth Gulf, Western Australia was shown to be related to spawning stock, and management measures were subsequently introduced to protect the spawning stock (Penn & Caputi 1986).

In Australia's Gulf of Carpentaria, commercial catches of 2 species of tiger prawns, *Penaeus semisulcatus* and *P. esculentus*, declined throughout the early 1980s. In the absence of clear evidence for either

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a strong stock-recruitment relationship or a dominant environmental influence on catches, a conservative management approach was adopted, including seasonal closures and a reduction in fishing effort to protect the spawning stock. This management strategy, although appropriate in the short-term, is potentially wasteful in that fisheries income would be needlessly lost if the variation in recruitment was, in fact, not affected by spawning levels.

In order to refine this management strategy, we needed to determine the pattern of recruitment to the fishery as well as the extent to which recruitment is affected by environmental variation. A key problem in this fishery is the uncertainty surrounding the number of recruitment periods. Early studies on adult *Penaeus semisulcatus* suggested that annual recruitment to the offshore fishery was confined to 1 period between December and April (Buckworth 1985). However, another 18 mo study suggested that the pattern of recruitment might vary from 1 to 2 periods per year (Somers et al. 1987). A third study of juvenile *P. semisulcatus* over 1 yr showed 2 equal periods of juvenile abundance on the nursery grounds (Vance et al. 1994). The current management regime, developed in response to declining catches in the 1980s, is based on only a single period of recruitment to the fishery.

Variation in environmental factors, such as rainfall, salinity, temperature and seasonal water currents and levels, have been shown to influence catches of several penaeids. For example, the emigration of juvenile *Penaeus merguiensis* from estuarine nursery areas and the subsequent offshore catch of adult *P. merguiensis* is correlated with rainfall (Vance et al. 1985, Staples & Vance 1986). *P. semisulcatus* is also a commercially important penaeid in many countries throughout the Indo-West Pacific, but, despite its wide distribution and commercial importance, very little long-term research on its biology has been published. Seasonal and annual variations in the abundance of juvenile *P. semisulcatus* have been documented in several countries (e.g. Thailand, Boonruang & Janekarn 1985; India, Babu & Babu 1986; Kuwait, Bishop 1989; Australia, Loneragan et al. 1994), and it has been suggested that environmental variation may have been associated with some of these variations. For example, increased commercial catches of adult *P. semisulcatus* in Kuwait in 1988/1989 may have been due to higher freshwater discharge (Siddeek et al. 1990). The best catches of *P. semisulcatus* in Pulicat Lake, India, seemed to be associated with higher temperatures and salinities (Rao & Gopalakrishnayya 1974). However, most of these studies were too short to confirm the associations statistically.

To provide the information needed to validate or modify the management strategy for the *Penaeus semisulcatus* fishery in the Gulf of Carpentaria, we initiated a 6 yr study of all life history stages of *P semisulcatus* in the Embley River and offshore areas in the northeastern Gulf of Carpentaria. There were 2 major objectives. The first was to identify seasonal recruitment patterns and the range of annual variation in those patterns. The second was to determine whether environmental factors might be controlling recruitment.

Like many penaeids, the life cycle of *Penaeus semisulcatus* involves substantial migrations and the use of different habitats (Dall et al. 1990). The larvae move inshore from offshore spawning grounds and the postlarvae settle in shallow vegetated coastal or estuarine areas. The juveniles then remain on the seagrass or algal beds for up to 3 mo before migrating offshore as sub-adults. This paper focuses on results from the estuarine stage of the life cycle. We have examined the seasonal and annual variation in abundance of postlarval and juvenile *P. semisulcatus* in the plankton and on seagrass and algal beds in the Embley River. 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, the periods of inundation of the nursery areas, and wind.

MATERIALS AND METHODS

We sampled *Penaeus semisulcatus* postlarvae (<3 mm carapace length, CL) entering the Embley River and postlarvae and juveniles (≥3 mm CL) on shallow macrophyte beds within the river. No adults (sexually mature) were caught in our samples. Samples were collected every 2 wk, on spring tides for 6 yr (between September 1986 and May 1992), except for the periods April to August 1990 and June to August 1991, when, as the first 3 yr of the study showed, prawn catches were low. Only 1 sample was taken each month on the macrophyte beds in April and May of 1991 and 1992.

Plankton. Postlarvae entering the estuary 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 below the water surface. Each net measured 0.5 × 0.5 m at the mouth and was made of 1 mm mesh. They were set for about 10 min mid-way through a spring flood tide, every 2 wk. 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 on the time of day or night. The volume of water filtered for each sample was measured by a flowmeter

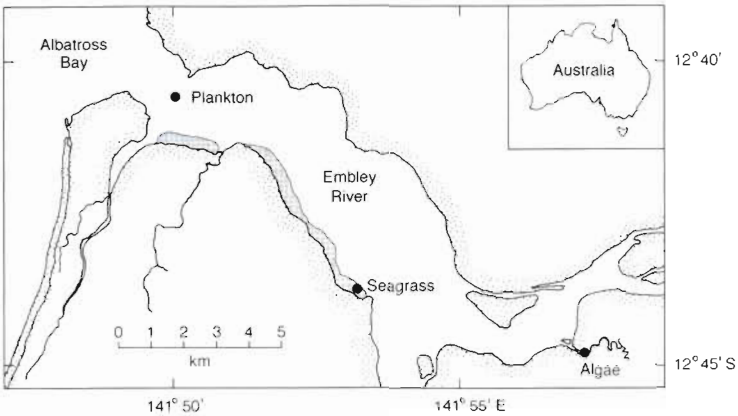

Fig. 1 Map showing the mid-river sampling site for planktonic postlarvae, and the seagrass and algal sites for benthic postlarvae and juveniles in the Embley River, Gulf of Carpentaria, Australia

fixed to the mouth of each net. The mean volume of water filtered by the 3 nets for each sampling period was 3200 m^3 (ranging from 1300 to 4900 m^3).

Benthic prawns. Most of the benthic postlarvae and juveniles were initially collected from 1 intertidal seagrass bed in the Embley River 11 km upstream from the river mouth (Fig. 1). This bed, which was up to 600 m wide, supported the strap-like seagrass *Enhalus acoroides* and 2 very short seagrass species, *Halodule uninervis* and *Halophila ovalis*. Part-way through this study, we found that juvenile *Penaeus semisulcatus* were also present on subtidal algal beds (*Caulerpa* spp.) and from September 1989 onwards, a subtidal algal bed in a small creek 15 km upstream from the river mouth was also sampled (Fig. 1). The biomass of the seagrass and algae and the sediment characteristics of both these sampling sites have been described in Haywood et al. (1995).

Samples at both the seagrass and the algal beds were taken with a small beam trawl towed behind a 4.6 m boat. The mouth of the beam trawl was 1.0 × 0.5 m and the mesh size was 2 mm in the body and 1 mm in the codend. Permanent trawl sites were located between marker posts: 200 m apart at the seagrass site and at right angles to the river bank; 100 m apart at the algal site and parallel to the creek bank, because the creek was not wide enough to allow a trawl at right angles to the shoreline. On each sampling occasion, 2 trawls were made at each site, at night and as close to high tide as possible. Because the catchability of *Penaeus semisulcatus* changes substantially over 24 h (Vance et al. 1994), it is essential to standardize sampling to a particular time of the day-night and tidal cycles if comparisons of abundance over longer time scales are to be reliable. The density of prawns (no. m^{-2}) for each sampling session at the trawl sites was calculated as the mean catch for each pair of trawls. A larger beam trawl, 2.0 × 1.0 m and with 28 mm mesh net, was also used at the seagrass site to check whether the smaller net was adequately sampling the larger prawns. However, catch rates of prawns >10 mm CL for both nets were significantly correlated with each other ($r = 0.48$, $p = 0.0001$, $n = 127$), so only data for the smaller net are presented here.

Prawn identification. The juvenile prawns were identified by their morphological characters (Grey et al. 1983, Heales et al. 1985), whereas the benthic postlarvae were identified by gel electrophoresis (Lavery & Staples 1990). The smaller postlarvae from the plankton were identified by discriminant analysis based on several morphological characters (D. S. Heales unpubl. data). Prawns were measured using a binocular microscope fitted with an ocular micrometer: postlarvae and juvenile prawns from the beam trawls to the nearest 1.0 mm CL, and postlarvae from the plankton nets to 0.1 mm CL.

Environmental data. Water temperature, salinity and light penetration into the water (secchi disc) were recorded with each prawn sample. The stage of the moon phase and the presence or absence of moonlight at the time of each trawl were also noted.

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). The mean of all the hourly tide heights for the 2 wk before each sampling session was calculated from hourly sea levels recorded by an automatic tide gauge near the mouth of the Embley River. Once the approximate sea level at which water left the seagrass bed on each tidal cycle was known, we then calculated the length of time that the seagrass bed was exposed for each 24 h period and determined the mean exposure time for the 2 wk before each sampling session.

Daily wind speed and direction data recorded at 09:00 and 15:00 h at Weipa airport were resolved into 2 components, one at right angles to the coastline (about east/west) — the on/offshore component, and the second parallel to the coastline (about north/south) — the longshore component. A mean value for each component was calculated for the periods between each sampling session and also for 1 mo before each sampling session.

From November 1991 to May 1992, a data logger was operated continuously on the seagrass bed. Accumulated rainfall was logged and mean values of water depth, temperature and conductivity (later converted to salinity) were recorded every 15 min.

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.

Prior to the 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 Inc. 1990). As a result, all the catch variables and rainfall were transformed by taking the 4th root of the variable.

All catch and environmental variables were tested for variation between seasons and years by 2-way ANOVAs. Season and year were treated as class variables using the SAS statistical package (SAS Institute Inc. 1989).

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. Autocorrelation in our data was detected by examining the residuals after regression and by the Durbin-Watson statistic, which was calculated for each regression analysis (SAS Institute Inc. 1989).

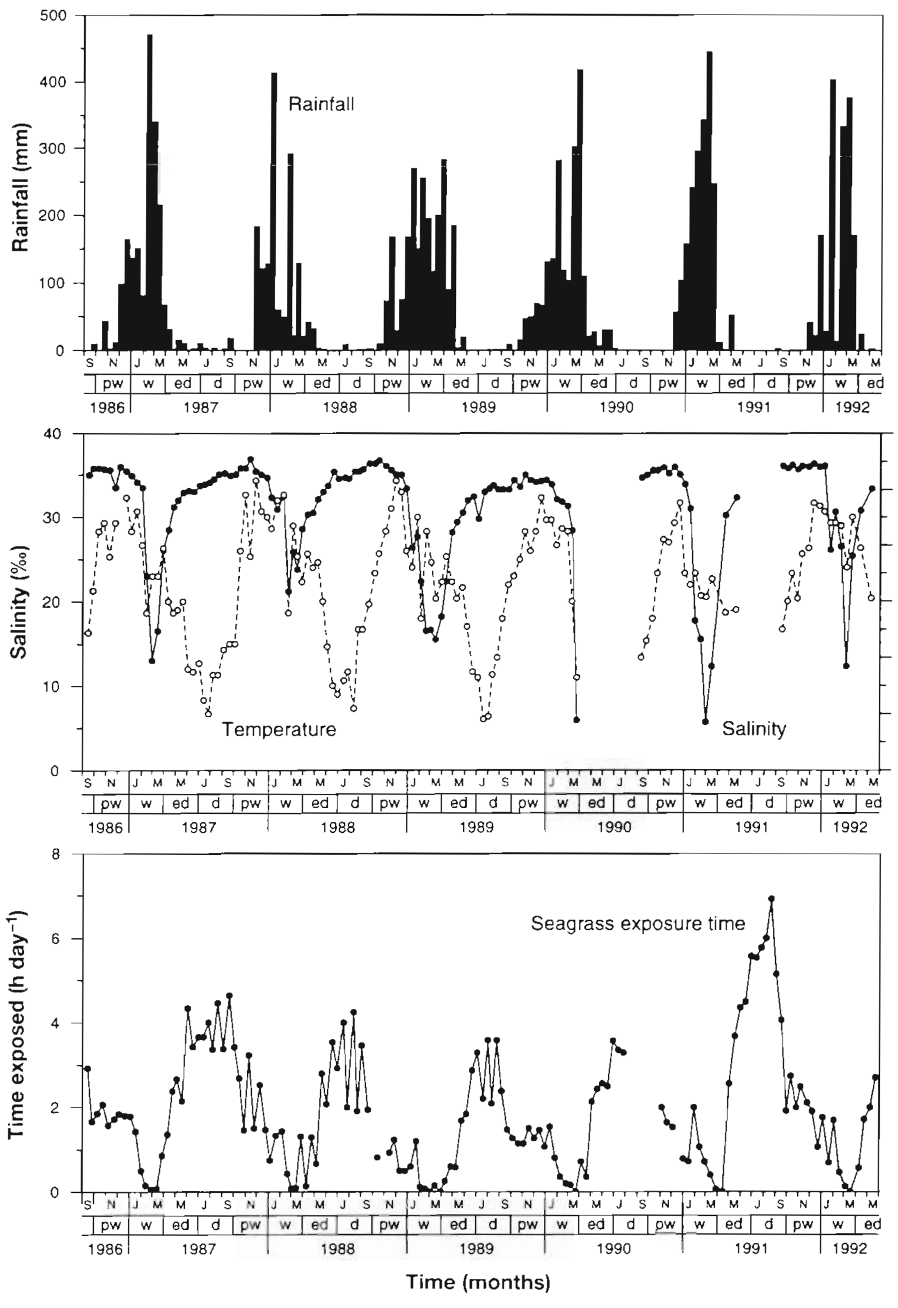

Fig. 2. Rainfall accumulated for 2 wk prior to each sampling, salinity and water temperature at the time of each sampling and mean seagrass-exposure time per day for 2 wk prior to each sampling at the seagrass site in the Embley River from September 1986 to May 1992. pw: pre-wet season; w: wet season; ed: early-dry season; d: dry season

Several approaches were used to minimise the effects of autocorrelation. Because much of this autocorrelation is induced by the seasonality of the data, we regressed continuous variables but included a seasonal class variable (as defined earlier) to remove the effect of season. In many analyses, autocorrelation remained after inclusion of the seasonal variable and in these cases, the significance of regressions was tested with the Proc Mixed module of the SAS statistical package (SAS Institute Inc. 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 the nursery areas. This was tested by regressing catches against environmental variables recorded during the same sampling period. Environmental variation may also have a longer-term effect on the survival of prawns in the nursery areas; this possibility was tested by regressing catches against environmental variables for 2 and 4 wk before each sampling.

RESULTS

Patterns of environmental variation

Water temperatures in this study were lowest in July or August each year, and highest in November or December. They decreased under the influence of the wet season (Fig. 2). The highest water temperature recorded was in November 1987 and 1988 (32.3°C) and the lowest temperature was 23.8°C in July 1989. The mean annual rainfall for the 6 yr of the study was 1886 mm, at least 84% of which fell between November and March each year. Wet season rainfall (January to March) ranged from 1970 mm (in 1988) to 3468 mm (in 1991). The lowest salinities were recorded in either February or March each year (Fig. 2). The highest salinity recorded was 36.9‰ in November 1987 and the lowest salinity was 5.7‰ in February 1991. However, this low varied considerably between years; in 1988, for example, it was 21.2‰ in February. The lowest mean wet season salinity and water temperature were in the highest rainfall year.

Mean sea level also varied seasonally; the highest tides are in February and March each year, at which time the seagrass beds are almost completely subtidal and the seagrass exposure time is close to zero (Fig. 2). The mean daily seagrass exposure time over each 2 wk period ranged from zero in March or April in most years to 6.9 h d^{-1} in August 1991. The length of time that the seagrass was exposed on each day ranged from zero on most neap tides to about 9 h in August 1991. The timing of low tides with respect to the day-night cycle changes throughout the year: the times of longest seagrass exposure are during the day in the winter months of June to August and are mostly at night from October to January.

Although the upstream algal site was sampled only from September to March or May for 3 years, the seasonal variation in environmental variables was similar to the seagrass site. Salinity during the wet season was usually lower at the algal site (on 17 of 20 samples) and ranged from 0.7 to 13.5‰ lower.

A 2-way ANOVA, using all available 2-weekly data, showed that temperature, salinity, mean sea level, mean seagrass exposure time, mean on-offshore wind and the mean rainfall per fortnight all differed significantly between seasons (Table 1). Season had the largest mean square for all variables. Only mean sea level and seagrass exposure time differed significantly between years. However, the finer scale pattern of the changes in rainfall and salinity were not identical for each year. For example, in 1987 the first large decrease in salinity occurred in late January and early February, whereas in 1990, the largest drop in salinity was in March (Fig. 2).

Patterns of catch variation

Catches of planktonic postlarvae, benthic postlarvae and juvenile *Penaeus semisulcatus* varied substantially between 2-weekly samples (Fig. 3). However, indi-

Table 1. *Penaeus semisulcatus*. Mean squares for 2-way analyses of variance of environmental and catch variables between seasons and years using 2-weekly data. Rainfall, planktonic postlarvae, benthic postlarvae and juvenile catches were transformed by taking the fourth root of (variable + 0.5). df = degrees of freedom

Variable	Source of variation (df)			
	Season (3)	Year (5)	Season × Year (10)	Error (93)
Environment				
Temperature	81.78**	1.80	1.52	1.97
Salinity	853.76**	43.64*	22.93	23.31
Rainfall	32.31**	0.91	0.63	0.71
Mean sea level	1.04**	0.18**	0.02	0.02
Seagrass exposure time	31.06**	3.69**	1.15	0.74
On-offshore wind	150.09**	13.71	15.06*	8.25
Prawns				
Plankton postlarvae	0.04**	0.02**	0.01**	0.00
Benthic postlarvae	0.08**	0.08**	0.03**	0.01
Juveniles	0.47**	0.10**	0.13**	0.02

**$p \le 0.001$; *$0.05 < p \le 0.10$

vidual peaks of plankton postlarvae rarely matched exactly with peaks of benthic postlarvae in timing or numbers caught (Fig. 3). Catches of benthic postlarvae and juveniles showed much closer agreement between the timing of peaks of abundance (Fig 3).

Catches of postlarvae and juveniles also varied between seasons and years (Table 1). In most years, catches of benthic postlarvae and juveniles showed peaks in both the pre-wet and wet seasons (Fig. 3). In the first 3 yr of the study, when all seasons were sampled, catches were highest in either the pre-wet or the wet season. When data for all 6 yr of the study were combined, the mean monthly catches of planktonic postlarvae showed 1 peak in October to November (Fig. 4). In contrast, benthic postlarvae and juveniles showed 2 peaks in recruitment, in October and April for benthic postlarvae, and in November and March for juveniles (Fig. 4). Catches were low in the early-dry and dry seasons (May to August). It is clear from Fig. 4 that the ratio of benthic postlarvae to juveniles is not consistent throughout the year. From November to March, the catches of juveniles on the seagrass beds were higher relative to the catches of benthic postlarvae, but lower from June to October.

Catches also varied substantially from year to year (Fig. 5). However, the pattern of annual variation was not the same for postlarvae and juveniles: for example, in the pre-wet season of 1990/1991 and 1991/1992, there were only moderate mean catches of benthic postlarvae but very high catches of juveniles. Furthermore, the size of catches also varied substantially between the pre-wet and wet seasons: juvenile catches in the pre-wet of 1991/1992 were the highest for the 6 yr while in the wet season of that year they were the second lowest. The relative height of the pre-wet and wet season peaks also varied between years, which accounts for the significant interaction of season and year in the 2-way ANOVA (Table 1, Fig 5).

Although environmental variation at the algal site was similar to that at the seagrass site, the seasonal pattern of catches of benthic postlarvae and juveniles at the algal site differed markedly (Fig. 6). As at the seagrass site, catches of *Penaeus semisulcatus* at the algal site peaked during the pre-wet each year but, in contrast to the seagrass site, virtually no prawns were caught during the wet or early-dry seasons.

The smallest prawns caught in the plankton or on the seagrass bed were 1.2 mm CL, and 47.6% of all prawns caught on the seagrass were smaller than 3 mm CL. Only 1.3% of all prawns caught at the seagrass site over the 6 yr were larger than 10 mm CL. The length-frequency distributions of all prawns caught on the seagrass and

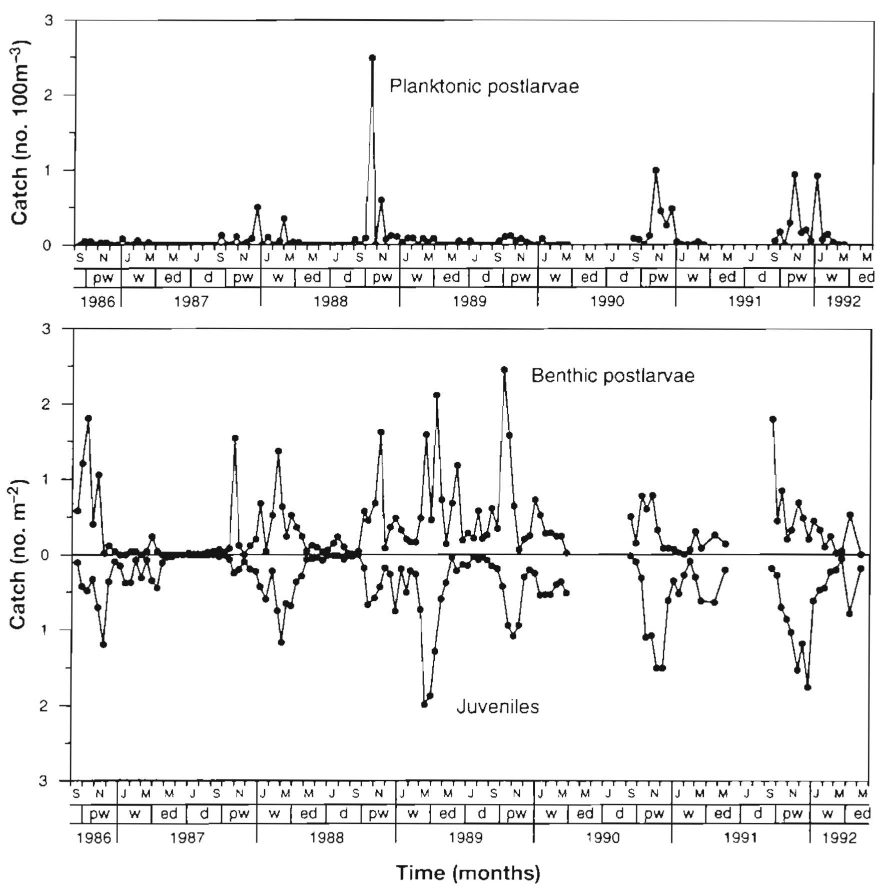

Fig. 3. *Penaeus semisulcatus*. Planktonic postlarvae, benthic postlarvae and juvenile catches at 2-weekly intervals from September 1986 to May 1992. Benthic postlarval and juvenile catches are for the seagrass site. pw: pre-wet season; w: wet season; ed: early-dry season; d: dry season

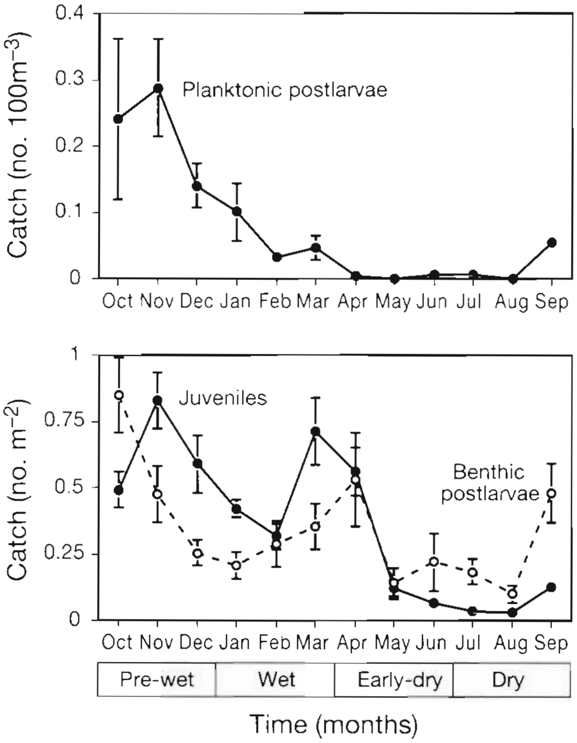

Fig. 4. *Penaeus semisulcatus.* Mean monthly catches (±1 SE) of planktonic postlarvae, benthic postlarvae and juveniles over 6 yr; benthic postlarval and juvenile catches are for the seagrass site. Standard errors less than 0.03 are not shown

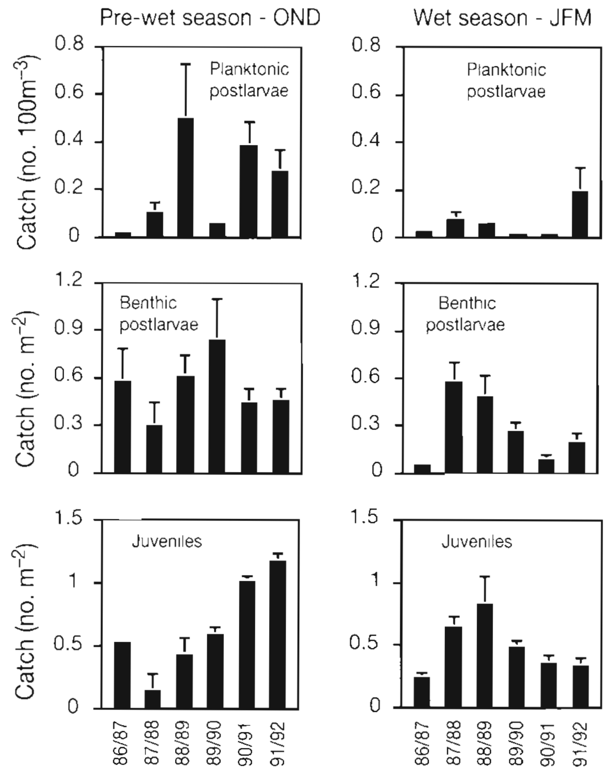

Fig. 5. *Penaeus semisulcatus.* Mean seasonal catches (+1 SE) of planktonic postlarvae, benthic postlarvae and juveniles for the pre-wet and wet seasons from 1986 to 1992. Benthic postlarval and juvenile catches are for the seagrass site. Standard errors less than 0.03 are not shown

algal beds during the study were quite similar, except that the proportion of 2 mm postlarvae was considerably higher on the algal bed than on the seagrass (Fig. 7).

Exploratory multiple regression analysis was carried out and some environmental variables were significantly related to postlarval or juvenile catches (Table 2). However, the proportion of variation explained by most models was quite low, ranging from 18.7% for plankton post-

Relationships between catch and environmental variation

Two-weekly and seasonal variation

All catch and environmental variables showed strong seasonal variation, which made it difficult to identify any causal relationships (Figs. 2 & 3). In some years, catches of postlarvae and juveniles were low at the height of the wet season. However, some postlarval settlement continued during the high rainfall periods. In most years, catches in the pre-wet had begun to decrease before salinity had dropped substantially. Catches were higher at the time of the year when the seagrass bed was less exposed, but there was no clear relationship between peaks of catches and the degree of seagrass exposure.

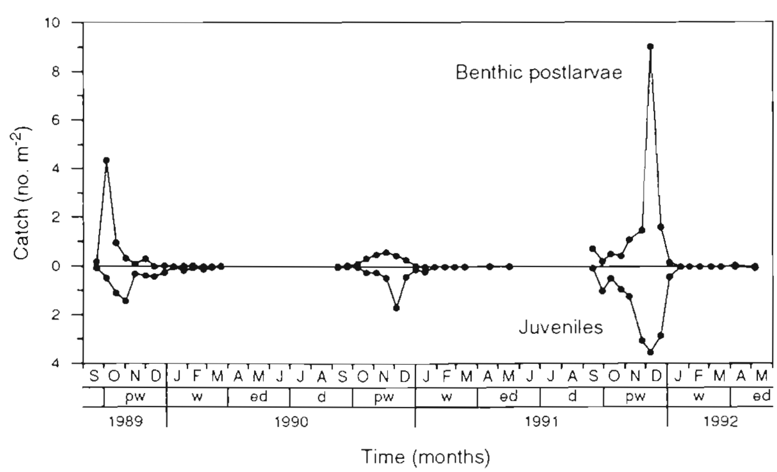

Fig. 6. *Penaeus semisulcatus.* Benthic postlarvae and juvenile catches at the algal site at 2-weekly intervals from September 1989 to May 1992. pw: pre-wet season; w: wet season; ed: early-dry season; d: dry season

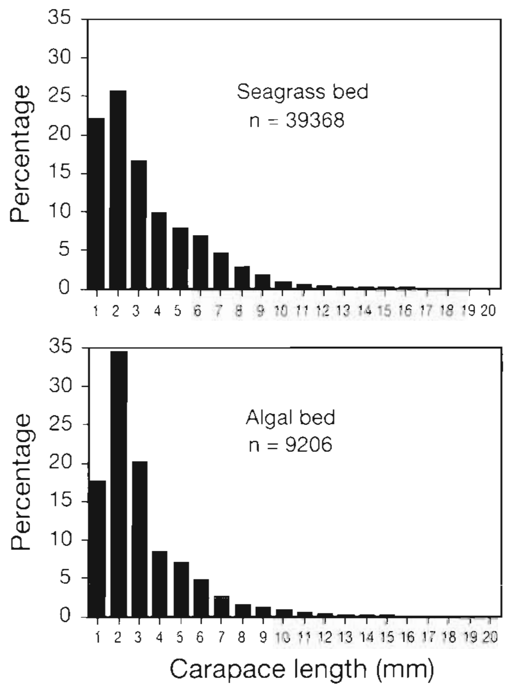

Fig. 7. *Penaeus semisulcatus*. Percentage length-frequency distributions of all prawns caught at the seagrass and at the algal site during the study

larvae with season and rainfall to 39.0% for juveniles at the algal site with benthic postlarvae lagged 2 wk and salinity (Table 2). The season variable was significant in all regression models at the seagrass site.

There was a significant relationship between rainfall and the catches of plankton and benthic postlarvae at all sites (Table 2) and seagrass exposure time was also important in the benthic postlarval model for the seagrass site. Benthic postlarval catch of the previous sampling period was the most significant variable in the juvenile prawn analyses for the seagrass and algal sites; mean sea level was also present in the seagrass model and salinity was significant in the algal model. None of the lagged environmental variables were more significant than unlagged variables in any of the regression analyses.

To test the reliability of the results and confirm that autocorrelation in the data had been effectively removed, we repeated the multiple regressions using data for the pre-wet and wet seasons only, when prawn abundances were highest and catch and environmental variation was greatest. We also combined the data for all variables into seasonal means before analysis. The same variables were again significant in both these analyses and the results confirmed those obtained using all the 2-weekly data.

Annual variation

Comparisons of yearly means of all catch and environmental variables for the pre-wet and wet seasons showed some significant correlations but some caution is needed when interpreting them, as the number of data points available for the analysis was small (n = 6). Of all the environmental variables, rainfall and seagrass exposure time were most consistently correlated with catch: both were mostly negatively correlated with catch variables (Table 3). Rainfall was significantly correlated with catches of benthic postlarvae in the wet season and with juveniles in the pre-wet season. Seagrass exposure time was significantly correlated with catches of benthic postlarvae in the pre-wet season and with catches of juveniles in the wet season.

Temperature was highly correlated twice in the analysis: negatively correlated with juvenile catches in the pre-wet (when temperatures were highest), but positively correlated with plankton postlarvae in the wet season. The positive temperature correlation in the

Table 2. *Penaeus semisulcatus*. Significant sources of variation, mean squares and percentages of the total catch variation explained by each variable in multiple regression analyses for 2-weekly data at the seagrass site (for 1986 to 1992) and at the algal site (pre-wet and wet seasons only for 1989 to 1992). The significance of the regressions was tested with Proc Mixed to remove the effects of autocorrelation. The sign of the coefficients is shown in parentheses for the continuous variables. Benthic postlarvae lagged = lagged by 2 wk. n ranged from 113 to 117 for the seagrass site and n = 37 for the algal site

Catch variables	Source of variation	Mean square	Variation (%)
Plankton postlarvae	Season	0.03****	16.3
	Rainfall	(–)0.01*	2.4
Benthic postlarvae	Seagrass:		
	Season	0.03*	6.4
	Rainfall	(–)0.06*	4.8
	Seagrass exposure time	(–)0.16***	12.6
	Algae:		
	Rainfall	(–)0.29**	21.4
Juveniles	Seagrass:		
	Season	0.03**	2.5
	Benthic postlarvae lagged	(+)0.52****	15.9
	Mean sea level	(+)0.17***	5.1
	Algae:		
	Benthic postlarvae lagged	(+)0.29****	31.5
	Salinity	(+)0.07*	7.5

****$p \leq 0.001$; ***$0.001 < p \leq 0.01$; **$0.01 < p \leq 0.05$; *$0.05 < p \leq 0.10$

Table 3. *Penaeus semisulcatus*. Correlation coefficients of catches and environmental variables at the seagrass site using seasonal means for the pre-wet and wet seasons. n = 6

Variable	Plankton postlarvae		Benthic postlarvae		Juveniles	
	Pre-wet	Wet	Pre-wet	Wet	Pre-wet	Wet
Plankton postlarvae			−0.07	0.20	0.32	−0.21
Benthic postlarvae					0.20	0.78**
Temperature	−0.21	0.86**	0.30	0.23	−0.73*	−0.1
Salinity	−0.45	0.28	−0.80*	0.17	0.31	−0.19
Rainfall	−0.02	−0.26	0.22	−0.72*	−0.79*	−0.49
Mean sea level	0.55	−0.02	0.61	0.53	−0.17	0.79**
Seagrass exposure time	−0.47	0.16	−0.73*	−0.45	0.05	−0.75**
On-offshore wind	−0.04	−0.01	0.17	0.46	0.01	0.55

**0.01 < p ≤ 0.05; *0.05 < p ≤ 0.10

wet season may well be spurious, as catches of plankton were very low in this season. Juvenile catches were significantly correlated with benthic postlarvae during the wet season but not significantly correlated for the pre-wet season.

Short-term variation in environment between 2 sampling sessions

To demonstrate the effect of extreme, short-term climatic change on prawn catches, we have shown a series of rainfall, salinity, temperature and water-depth data recorded at 15 min intervals by the logger on the seagrass bed during the early part of the wet season in 1992 (Fig. 8). The period covered most of 1 spring-neap-spring tidal cycle from the sampling session of 4 January 1992 to the sampling of 20 January 1992. The salinity was 36.1‰ at the start of the period (4 January) and had decreased to 26.1‰ by the end (20 January). Rainfall during this period was 405 mm, mostly associated with Cyclone Mark, which passed close to the Embley River. In fact, rainfall for 11 January was 167 mm, which was the highest daily rainfall recorded at Weipa during the 6 yr, and rainfall for the 3 d from 9 to 11 January was 325 mm, which was the highest 3 d total in the 6 yr study period. The lowest salinity recorded by the logger was 8.4‰, and occurred several days after the main rainfall. After the cyclone, salinity fluctuated widely throughout some tides: on 12 January, for example, it decreased from 29.6‰ at 00:00 h to 14.6‰ at 07:30 h. Despite such large fluctuations, the mean catch (± SE) of juvenile *Penaeus semisulcatus* only changed from 0.62 (± 0.03) prawns m^{-2} to 0.47 (± 0.09) prawns m^{-2} 2 wk later. However, the size structure of the population changed substantially during this period (Fig. 9). The cohort of postlarvae that was present on 4 January remained in the population but a large proportion of the juvenile prawns larger than 4 mm CL were no longer on the seagrass. No 1 mm CL postlarvae recruited to the seagrass between the 2 sampling sessions.

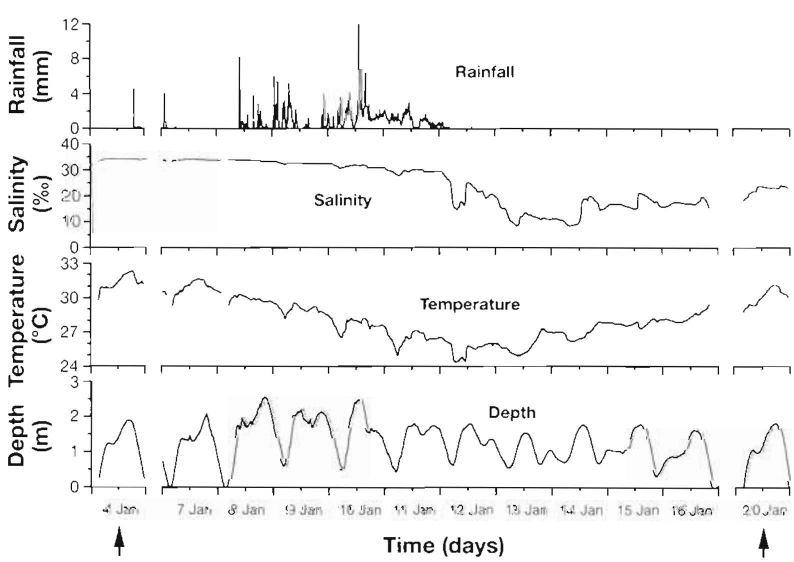

Fig. 8. Rainfall, salinity, water temperature and depth recorded every 15 min at the seagrass site between 4 January and 20 January 1992. Arrows indicate the dates when prawn samples were taken

DISCUSSION

Variation in the abundance of postlarval and juvenile prawns occurs at 3 levels: short-term variation between samples, seasonal variation and annual variation. The variation may be caused by factors acting directly on prawns as they enter the nursery grounds, after they reach the nursery grounds or on an earlier life-history stage outside the nursery grounds. For example, heavy

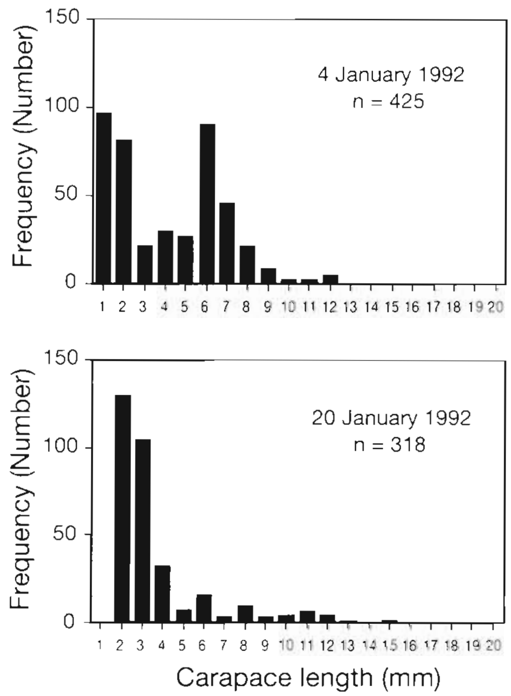

Fig. 9. *Penaeus semisulcatus*. Length-frequency distributions of all prawns caught at the seagrass site before and after Cyclone Mark in January 1992

rainfall in the juvenile prawn nurseries causes juvenile *Penaeus merguiensis* to emigrate from their estuarine habitat (Staples & Vance 1986). Advection of postlarval *P. merguiensis* to estuaries in the southern Gulf of Carpentaria is enhanced by the prevailing currents outside the estuaries during spring but decreased by changing currents in the autumn (Rothlisberg et al. 1983). If these strong seasonal factors are superimposed on the adult spawning patterns, the result is a strong seasonal pattern of juvenile abundance in the estuaries. Any factor influencing abundances over the short-term or between seasons may then lead to annual variation in juvenile prawn numbers.

Catch variation

It is clear that there is a strong seasonal cycle of immigration of postlarval *Penaeus semisulcatus* to the estuary and of postlarval and juvenile abundances on the nursery areas each year; highest catches were always in the pre-wet or wet seasons. Over all years, there is also a bimodal pattern of abundances of benthic postlarvae and juveniles, but this pattern is neither clear nor consistent in each year. In some years, postlarval and juvenile catches were higher in the wet season than in the pre-wet, but for the last 3 yr, the reverse was true (Fig. 5). It is also clear that there is substantial variation in catches between years.

This annual variation in the relative strength of the pre-wet and wet season cohorts has substantial implications for the offshore commercial fishery. Prawns from both cohorts would leave the estuary in time to be caught in the fishery which occurs in Albatross Bay from August onwards. However, the size composition and therefore the value of the prawns in this fishery would be largely determined by the relative strength of the pre-wet and wet season cohorts. For example, if the juvenile prawns leaving the estuary were mainly from the pre-wet season cohort, the fishery would be dominated by older and larger prawns which fetch a higher price on the export market than do smaller prawns. Furthermore, our findings on the 2 cohorts are supported by the conclusions of Crocos & van der Velde (1995), who examined abundances and reproduction of adult *Penaeus semisulcatus* offshore. They found that recruitment to the *P. semisulcatus* fishery in Albatross Bay, offshore from the Embley River, occurs over 2 periods during the year rather than over 1 period, as was previously thought (Somers & Kirkwood 1991). This recruitment pattern will have to be taken into account when examining the stock-recruitment relationship for this fishery as well as in refining the current management measures. A further corollary of the annual variation in catches and the timing of peak catches is that sampling needs to be carried out over several years to clearly identify seasonal patterns.

The bimodal pattern of seasonal variation seen in our study is quite different from that observed by Coles et al. (1993) in Cairns Harbour, on the east coast of Australia and only about 7° south of Weipa. Their mean monthly catch of juvenile *Penaeus semisulcatus* over 8 yr was clearly unimodal with peak catches, on average, in February. It is unlikely that this different seasonal pattern in catches is due to rainfall or temperature variation. salinity ranged from 20 to 37‰ and water temperature at night was between 22 and 33°C during the Cairns study. The shorter period of high catches at Cairns may be due to other factors such as hydrographic variation that affect the advection of larvae and postlarvae onto the seagrass nursery areas.

Biotic factors

The largest amount of variation in 2-weekly juvenile catches at the seagrass and algal sites was explained by the benthic postlarval catch of the previous sampling session (Table 2). Since benthic postlarvae (1 to 2 mm CL) had only recently settled on the nursery grounds (over 99% of the planktonic postlarvae caught in our plankton set nets were 1 mm CL in size), 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. In other words, the most important factor that we were able to identify in determining the abundance of juvenile *Penaeus semisulcatus* at our study sites was the supply and successful settlement of postlarvae.

In all years, catches of planktonic postlarvae were lower in the wet season than in the pre-wet season, and proportionately much lower than benthic postlarval catches. However, this may be a catchability effect rather than a difference in real abundance of plankton. In the Norman River (Australia), planktonic postlarvae of *Penaeus merguiensis* were concentrated in the higher salinity water near the river bottom during the wet season (Staples & Vance 1985), but our plankton nets only fished the top half of the water column in the much deeper Embley River. If *P. semisulcatus* behaves like *P. merguiensis*, then more postlarvae may have entered the estuary during the wet season than were estimated by our plankton nets.

Much of the bimodality in seasonal abundances of postlarval and juvenile *Penaeus semisulcatus* may be due to factors acting outside the estuary. In Albatross Bay, offshore from the Embley River, there was only a slight suggestion of bimodality in the population fecundity index of the adult population; the index was highest in the late dry and pre-wet seasons (Crocos & van der Velde 1995). However, there was strong seasonal bimodality in the offshore larval abundances (Rothlisberg et al. 1988). It is possible that the factors determining offshore larval abundances are responsible for much of the bimodality in postlarval abundances in the estuary.

Abiotic factors

Penaeus semisulcatus has a wide distribution throughout the Indo-West Pacific, between about 30° S and 30° N (Grey et al. 1983). It therefore lives in a wide range of climatic conditions, from temperate to tropical: salinities from 5‰ in South Africa (Forbes & Benfield 1986) to 44‰ in Kuwait (Bishop & Khan 1991); and temperatures from 13 to 34°C, both in Kuwait (Bishop & Khan 1991).

In our study, rainfall was significantly related to postlarval catches. Increased rainfall during the wet season appeared to decrease the abundance of planktonic and benthic postlarvae, either because their mortality increased or because they were avoiding the low salinity estuarine water. In the Norman River, immigration of *Penaeus merguiensis* postlarvae was also lower in high rainfall, and hence low salinity years, than in dry years (Staples & Vance 1985).

The seasonal abundance of prawns in the estuary is significantly affected by the amount of available nursery habitat. From about January onwards in most years, there is no algae at the upstream algal site because of the low wet season salinities (Haywood et al. 1995), and almost no juvenile *Penaeus semisulcatus* were caught there. In contrast, vegetation and juvenile *P. semisulcatus* remain on the seagrass bed throughout the wet season. The largest effect of rainfall on *P. semisulcatus* may therefore be in reducing the amount of algal habitat for the juvenile stage.

The relative proportions of benthic postlarvae and juveniles on the seagrass bed were not consistent throughout the year. Juveniles were more abundant than postlarvae from November to March, but less abundant from June to October (Fig. 4) This could be due to postlarvae and small juveniles having a higher mortality rate or emigrating from the seagrass beds more quickly during the early-dry and dry seasons (June to October) than during the pre-wet and wet seasons (November to March).

These differences in mortality or emigration rates may be a consequence of seasonal changes in mean sea level and water temperatures. The longest periods of daytime seagrass exposure occurred in the early-dry and dry seasons. Water temperatures during sampling at high tide at night were often above 32.0°C and would be much higher at low tide during the day. On one occasion in October 1991, the low tide water temperature was above 35°C (Vance et al. 1994). Juvenile *Penaeus semisulcatus* usually remain buried in the seagrass bed at low tide and would therefore be subjected to these high temperatures (Vance et al. 1994). No studies of mortality rates of *P. semisulcatus* in relation to temperature have been reported, but the mortality of *P. merguiensis* and *P. esculentus* increased at 35°C in laboratory studies (Staples & Heales 1991, O'Brien 1994). Preston (1985), however, found only slightly reduced levels of survival of the mysis to postlarval stage of 3 other Australian penaeids at temperatures up to 34°C in laboratory experiments. Reynolds & Casterlin (1979) found that, in the laboratory, some juvenile *P. duorarum* (a species that like *P. semisulcatus* buries during the day) remained in water as warm as 38°C when given a choice of a range of temperatures. However, most *P. duorarum* preferred about 30°C. Even if mortality is not increased by the daytime low tide exposure of the seagrass beds, the juveniles may leave the intertidal seagrass and emigrate to deeper water.

Several other studies suggest that temperature and rainfall may affect *Penaeus semisulcatus* catches, but the results have not been confirmed statistically. Rao &

Kathirvel (1971) reported decreased catches of *P. semisulcatus* in an Indian estuary during seasonally low salinities, and Rao & Gopalakrishnayya (1974) suggested that high temperatures and salinities (and therefore low rainfall) were associated with good growth and survival of *P. semisulcatus*. Siddeek et al. (1990) thought that large commercial catches of adult *P. semisulcatus* in one year in Kuwait may have been due to an increase in rainfall, freshwater discharge and nutrients, and therefore more juvenile nursery habitat. Su & Liao (1987) found an association between low salinities and the emigration of adolescent *P. semisulcatus* from nursery areas using set nets in Taiwan. There was no consistent relationship between rainfall or salinity and size of catches, but catches increased after heavy typhoon rainfall. One laboratory study has shown decreased survival of juvenile *P. semisulcatus* at salinities of 27‰ and less (Harpaz & Karplus 1991).

The proportion of variation in postlarval and juvenile catches that was explained by environmental variables in our study was very low. These results, and the fact that *Penaeus semisulcatus* lives in such widely different environments, suggest that, except in extremes such as cyclone-induced rainfall, environmental variation has little effect on juvenile abundances. It is, therefore, unlikely that predictive models of adult *P. semisulcatus* catches can be developed based on environmental factors acting on the estuarine stages of the life cycle.

Other variation

Although we found some significant relationships between environmental and catch variables, and found that the abundance of juvenile *Penaeus semisulcatus* is clearly influenced by the supply and successful settlement of postlarvae, there is still much unexplained variation in our catch models. Predation is usually thought to be a major cause of juvenile penaeid mortality (Dall et al. 1990), and some of the variation in our catches may have been caused by changes in the levels of fish predation in the estuary. In the Embley River between 1986 and 1988, *P. semisulcatus* was the most commonly eaten commercial penaeid species (Salini et al. 1990). However, the fish sampling was not frequent enough to be able to relate fish abundances and consumption rates to our catches of juvenile prawns.

Conclusions: long-term sampling

The most important factor determining the abundance of juvenile *Penaeus semisulcatus* in the Embley River was the supply and successful settlement of postlarvae. The period of highest abundance of juvenile *P. semisulcatus* in the estuary was found to be quite long (up to 7 mo), but also variable from year to year. Over all years, there was a bimodal distribution in juvenile abundances in the estuary, but the pattern of catches varied substantially from year to year; this would have a substantial impact on the size composition of the offshore adult fishery. The bimodal pattern of juvenile catches also suggests that recruitment to the offshore fishery occurs over 2 periods during the year rather than 1, as was previously thought, and this is important in understanding changes in the fishery and in refining management measures.

It is important to note that the seasonal patterns and the annual variation in those patterns were only identified after several years of sampling. One or 2 yr of sampling would not necessarily have produced the same result. However, the optimum length of a particular study will depend on the level of environmental and catch variation in that study area. At Weipa, more than 3 yr of data were necessary to clearly identify these patterns. There were also substantial differences in seasonal abundance on the seagrass and algal beds, so it is clearly important to sample the full range of juvenile habitat types in the study area. Finally, the seasonal patterns of abundance for juvenile *Penaeus semisulcatus* can vary substantially between locations; there was a much shorter, unimodal period of abundance at Cairns Harbour (Coles et al. 1993) than at Weipa. Therefore, research needs to be carried out in the area where the results will be applied and extrapolation between areas should be treated with caution.

Acknowledgements. We are grateful to Mr Rob Kenyon and Dr Neil Loneragan for assisting in the field. Dr Neil Loneragan, Dr Charis Burridge, Dr Burke Hill and Mr Ian Somers of the CSIRO Division of Fisheries, Cleveland and Dr Vivienne Mawson of the CSIRO Division of Fisheries, Hobart provided helpful criticisms of the manuscript. Dr You-gan Wang of the CSIRO Biometrics Unit, Cleveland helped with advice on the statistical analyses. Daily rainfall and wind speed and direction data were obtained from the National Climate Centre, Melbourne. Hourly sea levels were provided by and with the cooperation of the Beach Protection Authority, Queensland; the Queensland Department of Transport, Marine and Ports Division; and the National Tidal Facility at Flinders University, South Australia. This study was funded by the Fishing Industry Research Trust Account, grants 85/85 and 1989/13.

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This article was submitted to the editor

Manuscript first received: April 24, 1995
Revised version accepted: August 23, 1995