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Field estimates of growth and mortality of juvenile banana prawns (*Penaeus merguiensis*)

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Abstract. Postlarval and juvenile *Penaeus merguiensis* de Man from the Embley River estuary on the north-eastern Gulf of Carpentaria were sampled every 2 wk from September 1986 until August 1989, using a small beam trawl. Settlement of planktonic postlarvae peaked during the pre-wet season (October to December), and declined through the wet season (January to March). Using length-frequency analysis between 12 and 14 cohorts of juvenile prawns were identified each year. Length-frequency analysis and modal progression were used to derive growth rates during the estuarine phase of the life cycle. Growth rates, which could be described by a linear model, ranged from 0.63 to 1.65 mm CL (carapace length) wk^{-1}. Growth rates were positively influenced by water temperature and negatively influenced by prawn density. Salinity had no effect on growth rates. Prawns spent between 6 and 20 wk in the Embley River before emigrating offshore from the estuary. Weekly instantaneous rates of natural mortality (M) ranged from 0.23 to 0.94, and in general were lowest during the dry season (July to September) and highest during the pre-wet and wet seasons. Only temperature significantly influenced mortality rates, with mortality rates increasing with temperature. By projecting juvenile growth rates forward through time, we established which cohorts contributed to the offshore fishery each year. In 1987 and 1988 the April fishery consisted of prawns which had settled in the river before the end of January each year. Slow growth rates during the pre-wet season of 1988 meant that only cohorts that were settled before early December 1988 contributed to the fishery in April 1989. Whether a cohort contributes to the fishery depends on the settlement date, water temperature and prawn density.

Introduction

In Albatross Bay, northeastern Gulf of Carpentaria, Australia, the banana prawn *Penaeus merguiensis* has two peaks of spawning activity: a small peak from September to November and a large peak from February to March (Rothlisberg et al. 1988). The planktonic larvae are moved onshore, with the postlarvae arriving in the Embley River 2 to 3 wk after spawning. They settle in the mangrove-lined sections of the estuary from late September to April, where they remain for between 1 and 3 mo. While there are two peaks of spawning activity each year, there is a single period of emigration of juveniles from the estuary during the wet season (January to March). These prawns recruit to the offshore population from January through to April (Rothlisberg et al. 1985).

Exploitation rates in the *Penaeus merguiensis* fishery are very high, with between 78 and 86% of all recruited prawns being taken by the fishery (Lucas et al. 1979). Recent developments in fishing technology have increased fishing efficiency such that the fishery may last for only 4 to 5 wk following the opening on 15 April. Since the fishery targets adult [>30 mm carapace length (CL)] individuals, and juveniles (≤ 20 mm CL) may still be emigrating from the estuary during March and April, it is likely that only the earlier cohorts leaving the estuary are contributing to the fishery each year. This is because the fishermen have directed their efforts towards other species by the time the late emigrants are recruited offshore.

The *Penaeus merguiensis* fishery is characterised by a high year-to-year recruitment variation (Vance et al. 1985). In the south-eastern Gulf of Carpentaria, the offshore catch of *P. merguiensis* is positively correlated with rainfall (Vance et al. 1985). In the Albatross Bay region, however, the offshore catch does not correlate with rainfall but with the number of emigrating juvenile prawns and, to a lesser extent, with the number of juvenile prawns still in the estuary (D. J. Vance, CSIRO Division of Fisheries, personal communication). The number of juveniles in the estuary will be determined by the timing and magnitude of postlarval recruitment and subsequent growth and mortality. This study examines fluctuations in postlarval recruitment, and growth and mortality of *P. merguiensis* in the Embley River in relation to temperature, salinity and cohort density.

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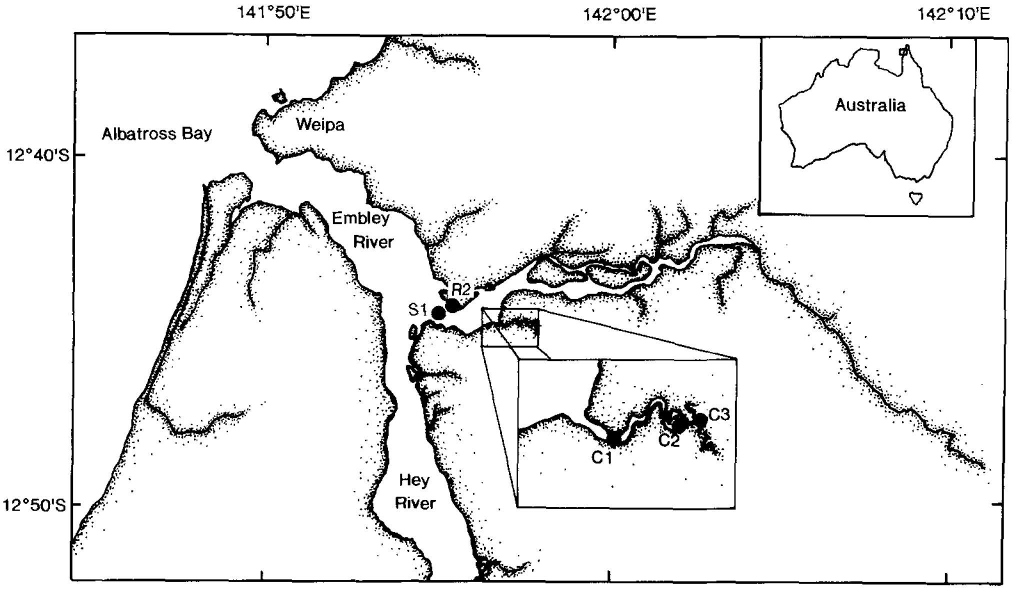

Fig. 1. Sampling sites on Embley River. R2: beam-trawl river site for resident prawns; S1: set-net river site for emigrating prawns; C1-C3: beam-trawl creek sites for resident prawns

Materials and methods

Sampling

During the period that juvenile *Penaeus merguiensis* de Man are resident in an estuary, they disperse through the mangroves at high tide, but at low water are concentrated in a band $\simeq 2$ m from the water's edge, in water <1 m deep (Staples and Vance 1979). When emigrating from the estuary to the sea, they swim downstream on the ebbing tide, close to the surface, and are found in the river channel which may be several hundreds of metres from shore.

Four sites, representing a range of habitats used by juvenile *Penaeus merguiensis* in the Embley River, were sampled at fortnightly intervals (Fig. 1). One site (R2), on a mangrove-lined bank of the river, 8 km from the mouth, was sampled from September 1986 to August 1989. Three sites (C1, C2, C3) on a small creek that drains into the Embley River 10 km from its mouth, were sampled from November 1986 to August 1989. These sites were about 0.8, 2.5 and 3.0 km upstream from the creek mouth, respectively.

Benthic postlarval (<3 mm CL) and juvenile (≥ 3 mm CL) prawns were sampled at the four sites with a beam trawl (mouth dimension 1.0×0.5 m, fitted with a 2 mm-mesh net and 1 mm-mesh cod end). Trawls were completed within 2 h of low water during spring tides because the catchability of *Penaeus merguiensis* is highest at this time (Staples and Vance 1979, Vance and Staples 1992).

One trawl parallel to the bank and four trawls at right-angles to it were completed at each site. Parallel trawls were made as close as possible to the water's edge (within 2 to 5 m) in 0.4 to 0.6 m depth. They were made in the direction of the prevailing current (speed $\simeq 0.5$ m s^{-1}), and were 200 m in length at the river site and 50 m at the creek sites. Right-angle trawls (length = 10 m) from the water's edge towards the middle of the river or creek, were made at random at each site. Temperature and salinity were recorded with a Yeo-Kal salinometer prior to trawling.

Prawns emigrating from the estuary were sampled every 2 wk, using two set nets deployed at the mid-river site S1, which was $\simeq 100$ m from the shore with a bottom depth of 4 m (Fig. 1). One net was 1.0×0.5 m across the mouth and was constructed of 2 mm mesh, while the other net had a mouth of 2.0×1.0 m and 28 mm mesh in the body. These nets fished from the surface to depths of 0.5 and 1.0 m, respectively. A large and a small net were used to ensure that samples reflected the full size-range of emigrating prawns. Both nets were deployed shortly after high water, on the ebb tide, and were recovered just before low water, a period of about 6 h. Only surface nets were used, since over 80% of emigrating *Penaeus merguiensis* can be captured by this method (Staples and Vance 1986).

Measurements and data

Postlarval and juvenile prawns were counted and recorded to the nearest 1.0 mm CL, using an ocular micrometer fitted to a binocular microscope. The mean density (nos. m^{-2}) of postlarval and juvenile prawns was calculated for each sampling session by summing catches from all the right-angle and parallel trawls and dividing by the swept area. Catches from all four benthic sites were pooled to analyse the length–frequency data. This procedure reduces any biases introduced by the migration of juveniles between the river and creek sites (Vance et al. 1990). Catches from both the set nets were summed.

Length–frequency analysis

Pulses of postlarval immigration into estuaries occur during spring tides (Staples and Vance 1985). This generates discrete cohorts of individuals, which can be tracked through time by length–frequency analysis. We used the MIX program of Macdonald and Green (1988) to analyse our data. This program fits a series of component normal distributions to the observed length–frequency distribution of each sample. Each component distribution represents a cohort. MIX provides estimates of the mean CL, standard deviation and proportion of the sample's distribution explained by each component normal distribution.

The number of components in the distribution and initial starting values for the mean, standard deviation and proportion of each component are required as input to MIX. Choosing the number of components by visual inspection of the modes is an unreliable method (Macdonald and Pitcher 1979, Koranteng and Pitcher 1987). In an effort to obtain more objective starting points, the Bhattacharya routine (Bhattacharya 1967) from the ELEFAN package (Gayanilo et al. 1989) was used to provide the initial estimates of the number of components and their parameters. After analysis by MIX, the number of components in the sample distribution was revised if it led to conclusions that were biologically unreasonable. For example, in samples where five or six contiguous size classes contained similar numbers of individuals, the Bhattacharya routine could at times identify only a single component distribution, even though two or more components were clearly visible in samples taken both before and after the sample in question. In these cases we ran MIX again, fitting the number of components suggested by the adjacent samples rather than those suggested by the Bhattacharya routine. As the MIX program failed to resolve the component distributions from one sample (24 August 1988), it was not included in the analyses.

Growth and mortality

The mean CL estimated for each component distribution on each sampling date was plotted against time. The growth of individual cohorts was described by joining the means so that a positive growth rate was maintained and the curves did not cross over. Some scientific judgement was required in following cohorts through time, since the path of an individual cohort was not always clear-cut. Simple linear regression of carapace length on time gave high R^2 values (>0.90) indicating that, over the size range sampled, growth could be described by a linear model. Average growth rates (mm CL wk^{-1}) over the period the prawns were resident in the estuary were calculated from the slope of the relationship between CL and time.

Emigration of prawns from the sampling area results in bias in both growth and mortality estimates derived from length–frequency analysis. This effect was minimised by identifying emigrating cohorts (i.e., when prawns of the same size were present in both the benthic trawls and the set nets on the same sampling date). Growth and mortality were calculated only for the period prior to emigration.

Seasons (each of 3 mo duration) were allocated to suit the tropical climate of the region. These were as follows: wet season = January to March, early dry season = April to June, dry season = July to September and pre-wet season = October to December. Cohorts were assigned to a season according to the mid-point of the period each spent in the estuary. Mean growth and mortality rates were calculated for each season.

Cohort densities were calculated by multiplying the mean prawn density for each sampling session by the cohort proportion estimated from the MIX algorithm. Weekly instantaneous rates of natural mortality for each cohort were estimated by regressing the natural logarithm of cohort density against time (Beverton and Holt 1957).

The effects of temperature, salinity and density on both growth and mortality were examined by forward stepwise multiple-regression. The following variables were used for this analysis: mean temperature and salinity over the estuarine life of each cohort; a quadratic temperature term, T_1^2, where T_1 equals temperature minus 28 °C; a quadratic salinity term, S_1^2, where S_1 equals salinity minus 27‰; a temperature × salinity interaction term; and cohort density 4 wk after settlement, as a measure of the average density of each cohort during its estuarine life. The constants used in transforming the quadratic terms T_1^2 and S_1^2 were the mid-points in the temperature and salinity range, respectively, and were used to make the quadratic terms independent of their respective linear terms. Because temperatures for adjacent cohorts are likely to be correlated with each other, mean seasonal temperatures were regressed against mean seasonal growth and mortality rates for each year (i.e., 12 points = 3 yr × 4 seasons).

Results

Physical environment

Temperatures at the sampling sites in the Embley River ranged from 24.3 °C during August 1989 to 31.4 °C in January 1988 (Fig. 2). Over the 3 yr study period, temperatures were highest from October to May (29.5 °C ± 0.1 C°; mean ± SE) and lowest from June to September (25.9 °C ± 0.1 C°).

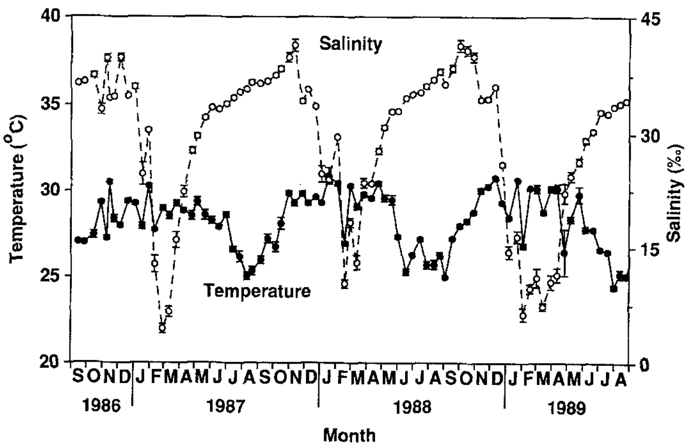

Fig. 2. Mean temperature and salinity (±1 SE) of beam-trawl sites (R2 and C1-C3) from September 1986 to August 1989

Salinity was highest in October and November (36.2 ± 0.1‰), just before the wet season. It decreased rapidly in December and January, reaching its lowest in the last 3 wk of February (9.5 ± 0.5‰). Minimum salinities for each year ranged from 4.4‰ in February 1987 to 10.3‰ in February 1988. After the wet season, salinity increased from March through to October. The period in which salinity remained below 30‰ varied each year: 14 wk during 1986/1987, 18 wk during 1987/1988, and 26 wk in 1989 (Fig. 2).

Postlarval settlement

Most postlarval *Penaeus merguiensis* settled in the Embley River from October to April each year, when water temperatures were highest (Figs. 2 and 3). There were similar levels of postlarval settlement from January to April each year (4.59 ± 0.38 prawns m^{-2}), whereas they varied substantially from October to December each year (8.86 ± 1.06 prawns m^{-2}).

Cohort analysis and growth

In most cases, MIX successfully fitted the component distributions to the sample length–frequency distributions. For example, on 6 January 1989 the sample distribution was composed of four cohorts with means of 3.9, 6.3, 11.5 and 15.7 mm CL, respectively (Fig. 4).

From 2 to 6 cohorts were identified from the length–frequency distribution on any particular sampling date, and 12 to 14 cohorts could be followed in each year (Fig. 5). Cohorts were numbered chronologically from 1 to 38, based on when the postlarvae first appeared in the estuary. For example, Cohort 5 was first captured in the estuary during early January 1987 at a mean size of 2.2 mm CL. By mid-January the mean size had increased to 4.9 mm; by late February its mean was 12.0 mm (Fig. 5 a). Since set-net catches at this time indicated that prawns of this cohort were emigrating from the estuary (Fig. 5 a), the growth and mortality of this cohort were

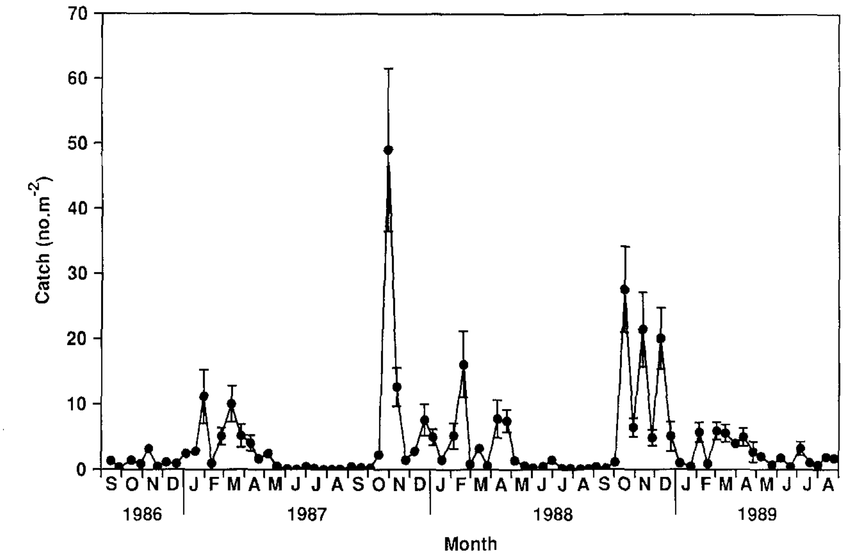

Fig. 3. *Penaeus merguiensis.* Mean fortnightly density (± 1 SE) of postlarvae pooled from river (R2) and creek (C1-C3) sites from September 1986 to August 1989. When smaller than data points, standard errors are not shown.

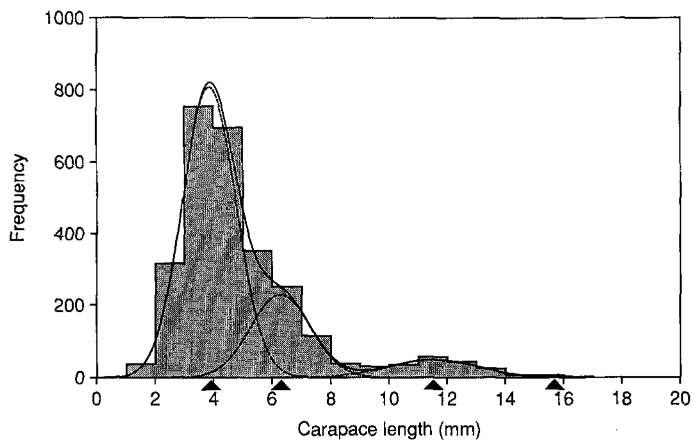

Fig. 4. *Penaeus merguiensis.* Length–frequency distribution (histogram) of total numbers of postlarvae and juveniles caught on 6 January 1989 and its component cohorts as estimated by MIX. Dashed line: component cohorts; continuous line: sum of components. Mean carapace length of each cohort is arrowed

only calculated from early January to mid-February 1987. The growth rate of this cohort was 1.25 mm wk^{-1} during this period (Table 1).

Over the 3 yr, growth rates ranged from 0.63 to 1.65 mm wk^{-1} (Table 1). In 1986/1987 and 1987/1988 they were fastest for cohorts which settled between November and February (1.21 ± 0.08 mm wk^{-1}) and slowest for March- and October-settled cohorts (0.78 ± 0.03 mm wk^{-1}). In contrast, growth rates in 1988/1989 were highest for September- and October-settled cohorts (1.36 ± 0.16 mm wk^{-1}), decreased through to December (0.85 ± 0.09 mm wk^{-1}), and then increased again from February to March (1.21 ± 0.05 mm wk^{-1}).

Cohorts 1 and 2 were omitted from growth and mortality calculations because not all sites were sampled for the first 2 mo of the study. Growth and mortality were not estimated for Cohorts 6, 7 and 26 which were emigrating within a month of settlement. In some cases, modal progression did not reflect growth because of continuous postlarval recruitment during this period (e.g. Cohorts 9 and 23 during the first 2 mo after settlement; Fig. 5a, b). To remove this effect, growth and mortality for Cohorts 9 and 23 were estimated only after 21 April 1987 and 30 June 1988, respectively, when they appeared to be fully recruited. Not all the mean CLs estimated by MIX could be followed over time, which suggests that in these cases the mean CL did not represent a cohort.

Effect of temperature, salinity and density on growth rate

Temperature was the only variable that was correlated significantly with growth rates ($r = 0.55$, $P < 0.05$). However, multiple-regression analysis indicated that density 4 wk after settlement also explained some of the variation after temperature effects were removed. Temperature alone explained over 30% of the observed variation in growth rate, while density 4 wk after settlement accounted for a further 19.6% of the variation (Table 2). Mean seasonal temperature was still significantly correlated with mean seasonal growth rate ($r = 0.60$, $P < 0.05$).

Seasonally, growth rates were fastest during the pre-wet and wet seasons (October to March; Fig 6) and slowest during the early dry and dry seasons (April to September).

Natural mortality

Our estimates of mortality are in fact estimates of natural mortality rates, since prawns are not fished commercially or recreationally until after they have left the sampling sites. Initial settlement densities were highly variable, ranging from 0.01 to 54.06 postlarvae m^{-2} (Table 1). In all cohorts except Cohort 14, densities decreased to less than 10 prawns m^{-2} within 2 wk of settlement, and after 10 wk all cohort densities were very low (< 0.5 prawns m^{-2}), regardless of settlement density (Fig. 7). Instantaneous rates of natural mortality ranged from 0.23 to 0.94 wk^{-1} (Table 1). Low mortality rates were generally recorded in the early dry and dry seasons during all three

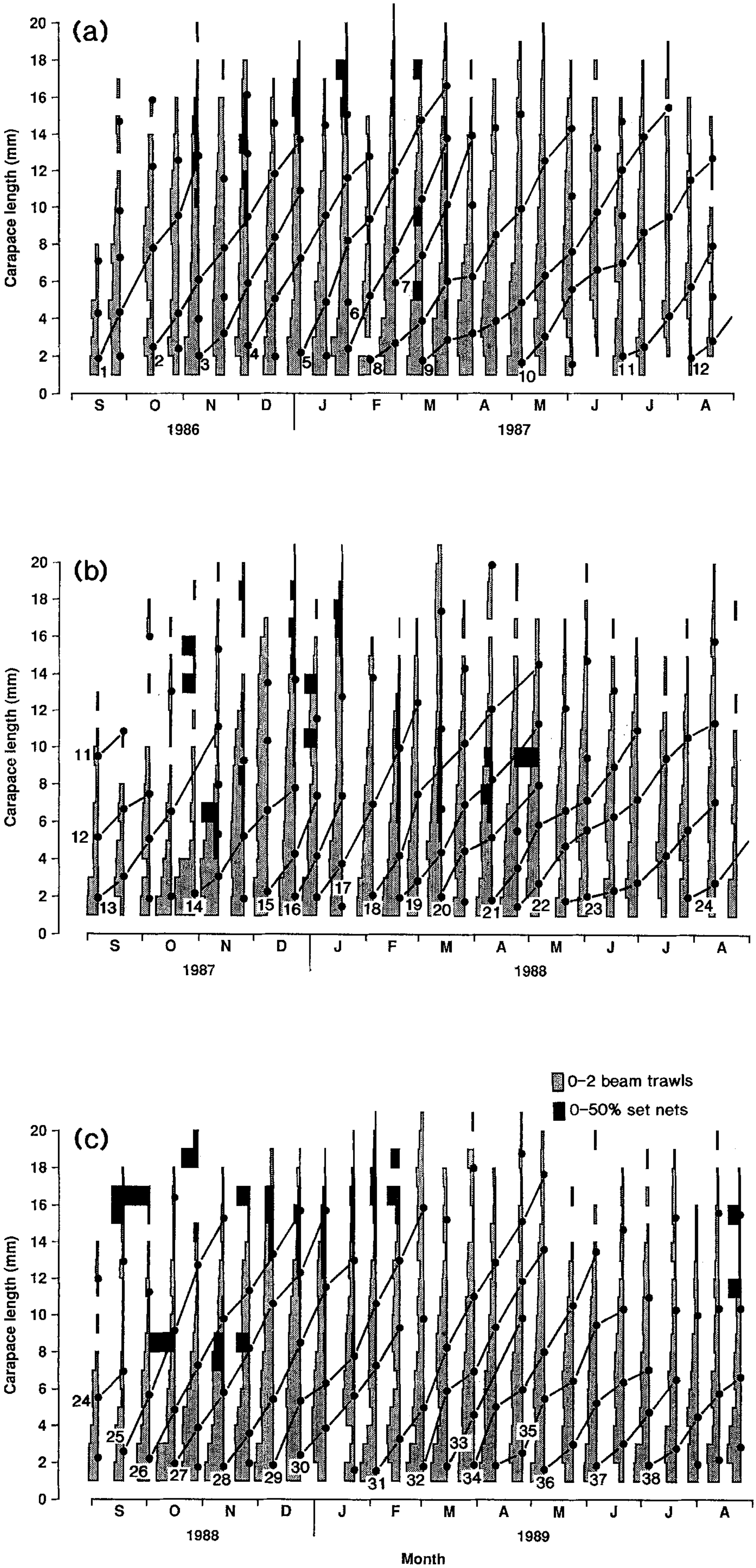

Fig. 5. *Penaeus merguiensis.* Carapace length–frequency distributions from beam trawls at river and creek sites combined (shaded histograms) for (a) September 1986–August 1987, (b) September 1987–August 1988 and (c) September 1988–August 1989. Beam-trawl data are $\log_{10}$-transformed to make relatively small numbers of larger individuals in the larger size classes more conspicuous. Filled histograms are untransformed percentage carapace length–frequency distributions for *P. merguiensis* caught in set nets on each sampling date. Curves connect mean carapace lengths of cohorts on each sampling data (●). Numbers indicate consecutive cohorts

Table 1. *Penaeus merguiensis.* Growth and natural mortality rates of cohorts of juveniles in Embley River estuary between September 1986 and August 1989. *n*: Number of times a particular cohort was sampled before emigration began. –: parameter not estimated because either only river site was sampled (Cohorts 1 and 2) or because members of cohort were emigrating throughout its estuarine phase (Cohorts 6, 7, 29)

Cohort No.	Settlement date	(*n*)	Growth rate (mm wk^{-1})	Initial density (nos. m^{-2})	Natural mortality rate (wk^{-1})
1986/1987					
1	15 Sep. 1986	(4)	–	–	–
2	12 Oct. 1986	(4)	–	–	–
3	08 Nov. 1986	(5)	1.14	3.41	0.27
4	05 Dec. 1986	(5)	1.15	1.37	0.32
5	03 Jan. 1987	(4)	1.38	2.93	0.73
6	28 Jan. 1987	(2)	–	11.59	–
7	24 Feb. 1987	(1)	–	–	–
8	10 Feb. 1987	(9)	0.79	6.62	0.25
9	11 Mar. 1987	(8)	0.88	9.06	0.43
10	05 May. 1987	(9)	0.70	2.28	0.29
1987/1988					
11	30 Jun. 1987	(7)	0.82	0.39	0.38
12	08 Aug. 1987	(5)	0.73	0.01	−0.26
13	06 Sep. 1987	(5)	0.99	0.43	0.31
14	28 Oct. 1987	(5)	0.76	54.06	0.54
15	06 Dec. 1987	(3)	1.40	2.32	0.93
16	21 Dec. 1987	(3)	1.45	8.59	0.94
17	03 Jan. 1988	(3)	1.13	4.69	0.48
18	02 Feb. 1988	(3)	1.47	5.35	0.72
19	17 Feb. 1988	(4)	0.97	15.96	0.52
20	12 Mar. 1988	(4)	0.92	2.20	0.23
21	09 Apr. 1988	(7)	0.73	6.62	0.36
22	23 Apr. 1988	(9)	0.63	7.53	0.26
23	29 Jun. 1988	(4)	0.71	1.62	0.34
24	28 Jul. 1988	(4)	0.69	0.16	0.29
1988/1989					
25	17 Sep. 1988	(5)	1.65	0.36	0.50
26	01 Oct. 1988	(3)	1.31	1.22	0.54
27	15 Oct. 1988	(4)	1.12	27.64	0.74
28	11 Nov. 1988	(3)	0.94	22.55	0.51
29	08 Dec. 1988	(2)	–	20.64	–
30	22 Dec. 1988	(3)	0.75	4.29	0.32
31	03 Feb. 1989	(8)	1.22	5.77	0.43
32	01 Mar. 1989	(6)	1.17	6.46	0.49
33	14 Mar. 1989	(3)	1.34	4.95	0.68
34	29 Mar. 1989	(6)	1.11	3.67	0.49
35	10 Apr. 1989	(6)	0.90	4.95	0.41
36	07 May 1989	(5)	0.69	1.63	0.24
37	05 Jun. 1989	(4)	0.75	1.45	0.38
38	04 Jul. 1989	(5)	0.69	3.17	0.28

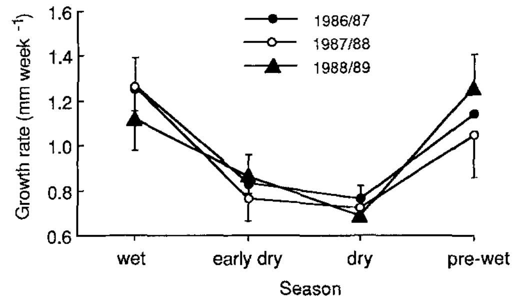

Fig. 6. *Penaeus merguiensis.* Mean seasonal growth rates (±1 SE) of juveniles caught in beam trawls at combined river and creek sites in Embley River for 1986/1987, 1987/1988 and 1988/1989. Wet season = January to March; early dry season = April to June; dry season = July to September; pre-wet season = October to December

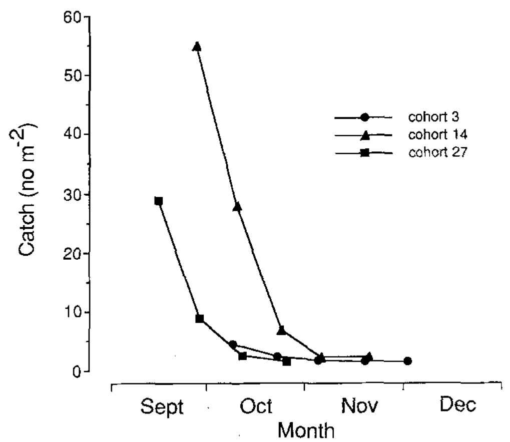

Fig. 7. *Penaeus merguiensis.* Cohort densities exemplified by three cohorts caught in beam trawls at combined river and creek sites in Embley River. Cohort 3 = 1986, Cohort 14 = 1987, Cohort 27 = 1988

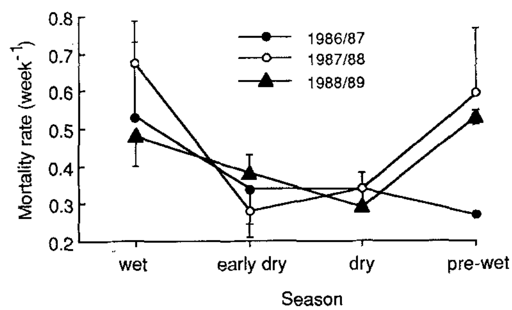

Fig. 8. *Penaeus merguiensis.* Mean seasonal mortality rates (±1 SE) of juveniles caught in beam trawls at combined river and creek sites in Embley River in 1986/1987, 1987/1988 and 1988/1989. Seasons as in Fig. 6

Table 2. *Penaeus merguiensis.* Regression coefficients and their *F* values for significant variables in forward stepwise multiple-regression of growth. Density (4): density 4 wk after settlement, **: $0.001 < P < 0.01$; ***: $P < 0.001$

Variable	Coefficient	*F* value	Model R^2
Temperature	0.192	30.7***	0.306
Density (4)	−0.134	5.7**	0.502
Intercept	−4.247		

Table 3. *Penaeus merguiensis.* Regression coefficient and *F* value for the significant variable in forward stepwise multiple-regression of mortality. **: $0.001 < P < 0.01$

Variable	Coefficient	*F* value	Model R^2
Temperature	0.079	9.01**	0.244
Intercept	−1.782		

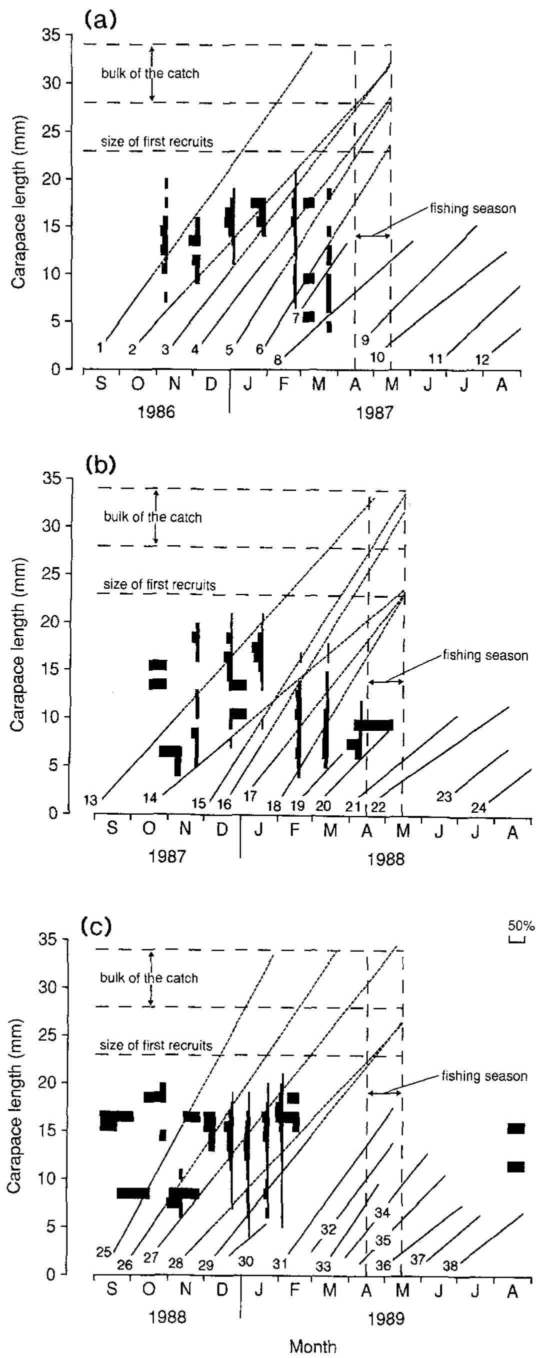

Fig. 9. *Penaeus merguiensis.* Estimated cohort trajectories for (a) 1986/1987, (b) 1987/1988, (c) 1988/1989, and emigrant length-frequencies (histograms). Cohorts numbered as in Fig. 5. Continuous diagonal lines indicate cohorts prior to emigration from estuary, and diagonal dashed lines projected post-emigration growth rates; vertical dashed lines show approximate duration of banana-prawn fishery, which opened on 15 April each year, and horizontal dashed lines size (mm carapace length) at which banana prawns first recruit to the fishery (23 mm CL) and size range of most of commercial catch (28 to 34 mm CL)

years, while mortality rates were generally higher but more variable during the pre-wet and wet seasons (Fig. 8).

Of the variables tested, only temperature was significant in the multiple regression analysis, accounting for 24.4% of the observed variation in mortality rates (Table 3). Mean seasonal temperature was still significantly correlated with mean seasonal mortality rate ($r=0.68$, $P<0.05$).

Emigration

The set-net catches reflected emigration of juvenile *Penaeus merguiensis* from the Embley River sampling sites to Albatross Bay. Small numbers of large prawns (>15 mm CL) were caught in the set nets during the pre-wet season (October to December) each year (Fig. 5), several weeks before the salinity in the estuary reached its highest point (Fig. 2). Smaller prawns were caught in the set nets as the salinity decreased with the onset of the wet season in January each year (Figs. 5 and 2). Set-net catch rates peaked during the wet season, with the highest catch of 306 individuals recorded on 6 January 1989. While no significant numbers of prawns were caught in the set nets after February in 1989 and March in 1987, low numbers of prawns were caught until May in 1988. It seems likely, therefore, that cohorts that settle in the estuary after the end of March do not emigrate from the river until the following wet season.

The amount of time that prawns spend in the nursery area depends upon the time of year in which they settle, relative to the timing of the decrease in salinity. Early in the wet season, provided there is sufficient rainfall, prawns may be stimulated to emigrate after only 2 wk in the estuary, e.g. Cohort 18 (Fig. 5b). However, during the dry season, when there is little rainfall and growth is slower, prawns may spend up to 20 wk in the estuary, e.g. Cohort 9 (Fig. 5a). Not all members of a particular cohort necessarily emigrate from the estuary at the same time; rather, their emigration may be protracted over a month or more, as in the cases of our Cohorts 6, 26, 27, 28 (Fig. 5a, c).

Discussion

Postlarval settlement

During 2 of the 3 yr of this study, *Penaeus merguiensis* postlarval settlement was highest between October and December, with a smaller peak between February and April. The fecundity index of the offshore adult population is also bimodal, but with the highest peak between February and March, and a smaller peak from October to November (Rothlisberg et al. 1988). The arrival of postlarvae in the Embley River during October coincides with the reversal of density gradient currents in the river. This, combined with the vertical migratory behaviour of postlarvae, perhaps facilitates the movement of postlarvae upstream (Heron et al. 1993).

Postlarval recruitment was pulsed during most of the period of this investigation, however there were two periods when continuous recruitment appeared to be occurring (April 1987 and May-June 1988, Cohorts 9 and 23 respectively). We did not detect any unusual environmental conditions which might have explained this phenomenon.

The low postlarval densities between October and December 1986 are probably underestimates, since only the river site was sampled during September and October 1986. It was subsequently demonstrated that postlarval densities in the creek can be up to six times as high as those found at the site in the river channel (Vance et al. 1990).

Growth

The difficulties of using tag–recapture methods with small animals with very high natural mortality precludes their use with juvenile prawns. Length–frequency techniques do not give accurate estimates in open populations, such as those in the Embley River, where prawns are immigrating and emigrating for much of the year. Also, many postlarval penaeids settle in the upper reaches of an estuary and grow as they migrate towards the sea (Dall et al. 1990). Consequently length–frequency distributions measured at a single site along this migration pathway will be biased towards a particular size of individual. In an effort to reduce these biases, we excluded recent immigrants and emigrants from our analyses, and our sampling sites represented a range of habitats, from the upper reaches of a creek where the postlarvae are most concentrated to the main river where larger adolescents predominate.

Penaeid growth follows the typical sigmoidal growth pattern of crustaceans (Dall et al. 1990). However, over the juvenile size range, a linear function is satisfactory to describe growth (Parrack 1979, Staples and Heales 1991). The growth rates recorded during our study ranged from 0.63 to 1.65 mm CL wk^{-1}. Growth rates of juvenile *Penaeus merguiensis* in the Norman River in the southern Gulf of Carpentaria from November to December and February to March averaged 1.2 mm CL wk^{-1} (Staples 1980). Juvenile penaeid growth has been reported elsewhere as ranging from zero in overwintering *P. japonicus* (Doi 1981) to over 4.48 mm CL wk^{-1} in *P. stylirostris* in summer (Menz and Bowers 1980). However, the later value was derived from only two successive samplings in one month.

Of the factors tested, temperature was the most important in explaining variation in growth rates, with increasing temperature resulting in faster growth. Similarly, in a field study in South Africa, the growth rate of *Penaeus indicus* was found to be positively correlated with temperature up to 26.5 °C (Benfield et al. 1990). A curvilinear (quadratic) temperature term did not significantly improve the fit of our model. In contrast, Staples and Heales (1991) were able to incorporate a quadratic temperature term in their model of the growth of juvenile *P. merguiensis* under laboratory conditions. Staples and Heales, however, used a wider temperature range (15 to 35 °C) than occurs in the Embley River, and the growth response in the same temperature range as recorded in this study (24.4 to 30.9°C), was essentially linear.

Multiple regression analysis suggested that after temperature effects were removed, growth of individual cohorts was to some extent density-dependent, with slower growth at higher densities. Using cages, Edwards (1977) demonstrated suppressed growth in *Penaeus vannamei* at densities greater than 2.5 m^{-2}. Maguire and Leedow (1983) also reported an exponential decrease in the growth of pond-reared *Metapenaeus macleayi* when stocking densities were increased from 6.1 to 21.2 prawns m^{-2}.

Salinity had no detectable effect on growth during this investigation. While this accords with laboratory studies of *Penaeus aztecus* (Zein-Eldin and Aldrich 1965) and *P. vannamei* (Edwards 1977), a laboratory study of *P. merguiensis* found growth to be significantly influenced by salinity (Staples and Heales 1991). The salinity estimates used in our field study had been averaged over the estuarine life of each cohort, whereas in the above laboratory experiments, prawns were maintained at extreme salinities for long periods (up to 9 wk in the Staples and Heales study), which does not happen in the field.

Mortality

Our estimates of the natural mortality of juvenile *Penaeus merguiensis* ranged from 0.23 to 0.94 wk^{-1}, and so are considerably higher than the rate for adult *P. merguiensis* (0.05 wk^{-1}) estimated by Lucas et al. (1979). The few field estimates of juvenile penaeid natural mortality in the literature are all high, although several different methods were used to derive them, e.g. 0.57 wk^{-1} for marked *P. vannamei* kept in enclosures (Edwards 1977); 0.3 to 0.76 wk^{-1} for *P. aztecus* and 0.01 to 0.62 wk^{-1} for *P. setiferus* from length–frequency analysis of trawled individuals (Laney 1981); and 0.19 to 0.41 wk^{-1} for *P. aztecus* from length–frequency analysis of individuals captured by drop trap (Minello et al. 1989).

Abiotic factors such as hypoxia and extremes of temperature and salinity, or biotic factors such as predation, disease or limited food supply, may contribute to the natural mortality of juvenile penaeid prawns. Multiple-regression analyses indicated that of the variables examined, only temperature was significant in influencing mortality of juvenile *Penaeus merguiensis* in the field. Under laboratory conditions Staples and Heales (1991) found high mortality of juvenile *P. merguiensis* at temperature extremes (15 and 35 °C) at 20 and 35‰ salinity. However, there also appeared to be an interaction between temperature and salinity: at 30 °C and 35‰ mortality was relatively high, but at 30 °C and 20‰ it was low.

Over the three years of the present study, water temperatures were always above 24 °C and salinity was only at 20‰ for a few days each year. Since the optimum conditions for growth and survival for juvenile *Penaeus merguiensis* in the laboratory are 20 °C and 20‰ (Staples and Heales 1991), the Embley River population of juvenile *P. merguiensis* may never be growing under optimal conditions. However, as mentioned earlier, prawns in the laboratory study were kept under constant temperature and salinity for periods of up to 9 wk. In the field, temperature and salinity are changing over each tidal cycle. In addition, the prawns in the laboratory experiments were collected from central Queensland at 23 °S and may have different optimal growth conditions from those in the Embley River estuary (12°40′S).

Within the range of values experienced in the Embley River, salinity was not important in determining the natural mortality rate of juvenile *Penaeus merguiensis*. This result is not unexpected, since natural populations of juvenile *P. merguiensis* in the Gulf of Carpentaria are found in salinities ranging from 0 to 40‰ (Staples and Vance 1987). Density 4 wk after settlement did not have a significant effect on mortality either. Similarly, Edwards (1977) found mortality of juvenile *P. vannamei* to be independent of density.

Predation is usually considered to be the most important factor contributing to mortality of juvenile penaeid populations (Minello et al. 1989, Dall et al. 1990). A concurrent study of fish predation identified 20 species of fish that ate commercially important prawns, including *Penaeus merguiensis* (Salini et al. 1990). Predation on prawns was highest just before and during the wet season (October to March), and lowest during the dry season (July to September), which parallels the seasonal pattern of juvenile *P. merguiensis* mortality found in this study.

Some of the most important penaeid predators identified by Salini et al. (1990) were also species that are targeted by commercial fishermen, e.g. barramundi (*Lates calcarifer*) and queenfish (*Scomberoides commersonianus*). However, the Embley River estuary is closed to commercial fishing, and in other Gulf of Carpentaria rivers where commercial fishing is permitted these important penaeid predators may be less abundant, resulting in lower natural mortality rates of the resident juvenile *Penaeus merguiensis* populations.

Mortality in the nursery area is high and variable, which may have marked effect on recruitment to the fishery. The natural mortality of adults offshore is considerably lower than that of the estuarine juveniles in the Embley River. If juvenile mortality is also lower offshore than in the estuary, it would be advantageous for a cohort to emigrate relatively early, away from the area of high mortality. In 1988/1989, the high early rainfall resulted in large numbers of prawns emigrating early in the wet season and a high commercial catch subsequently. Increased survival because prawns moved out of the estuary relatively early may have contributed to the high commercial catch this year.

Cohorts that contribute to the fishery

To determine which cohorts are contributing to the offshore fishery, we need to know the growth rates of prawns after they leave the estuary. These data are not available for the Weipa region, but by projecting juvenile growth trajectories forward through time we can estimate which cohorts may be important in the fishery. Growth rates probably decrease as the prawns get older, however, and so this technique may overestimate the number of cohorts that contribute to the fishery.

From 1987 to 1990 the fishing season opened on 15 April each year. Most of the prawns in the commercial catch are between 28 and 34 mm CL, although *Penaeus merguiensis* recruits to the fishery at about 23 mm CL, (P. Crocos, CSIRO Division of Fisheries, personal communication). Forward projections of the juvenile growth rates suggest that most of the commercial catch in 1987 and 1988 consisted of prawns that settled as postlarvae in the estuary before the end of January in 1987 (Cohorts 1 to 6) and 1988 (Cohorts 13 to 18) (Fig. 9). Slower rates of growth during the pre-wet season of 1988 meant that only those postlarvae which settled before early December 1988 (Cohorts 25 to 29) would form part of the fishery in April 1989.

Cohorts that settle in the Embley River after February are unlikely to receive sufficient rainfall to stimulate emigration, and so probably remain in the river during the dry season (Rothlisberg et al. 1985). These prawns will grow relatively slowly because of lower temperatures and will suffer high estuarine predation rates for a longer period than prawns that emigrated over the preceding wet season. At the end of the dry season they will be relatively large (>20 mm CL), although their numbers will be low. They are the first prawns to emigrate during the pre-wet season.

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Literature cited

Benfield, M. C., Bosschie, J. R., Forbes, A. T. (1990).Growth and emigration of *Penaeus indicus* H. Milne-Edwards (Crustacea, Decapoda, Penaeidae) in the St. Lucia Estuary, Southern Africa. Fish. Bull. U.S. 88: 21–28

Beverton, R. J. H., Holt, S. J. (1957). On the dynamics of exploited fish populations. Fishery Invest., Lond. (Ser. 2) 19: 1–533

Bhattacharya, C. G. (1967). A simple method of resolution of a distribution into its Gaussian components. Biometrics 23: 115–135

Dall, W., Hill, B. J., Rothlisberg, P. C., Staples, D. J. (1990). The biology of the Penaeidae. In: Blaxter, J. H. S.; Southward, A. J. (eds.) Advances in marine biology. Vol. 27. Academic Press, London, p. 1–489

Doi, T. (1981). Population dynamics and management of the shrimp fishery in the Seto Inland. Kuwait Bull. mar. Sci. 2: 289–300

Edwards, R. C. C. (1977). Field experiments on growth and mortality of *Penaeus vannamei* in a Mexican lagoon complex. Estuar. cstl mar. Sci. 5: 107–121

Gayanilo, F. C. Jr., Soriano, M., Pauly, D. (1989). A draft guide to the compleat ELEFAN. ICLARM software 2. International Centre for Living Aquatic Resources Management, Manila, Philippines

Heron, M. L., Wang, H. X., Staples, D. J. (1993). Transport processes affecting banana prawn postlarvae in the estuaries of the Gulf of Carpentaria. Proceedings of the Boedan Workshop on Larval Dispersal and Recruitment. In: P. Sammarco (ed.) Coastal and estuarine studies. American Geophysical Union, Washington, D.C. (in press)

Koranteng, K. A., Pitcher, T. J. (1987). Population parameters, biannual cohorts, and assessment in the *Pagellus bellottii* (Sparidae) fishery off Ghana. J. Cons. int. Explor. Mer 43: 129–138

Laney, R. W. (1981). Population dynamics of penaeid shrimp in two North Carolina tidal creeks. Doctoral dissertation. Graduate Faculty of North Carolina State University, Raleigh

Lucas, C., Kirkwood, G., Somers, I. (1979). An assessment of the stocks of the banana prawn *Penaeus merguiensis* in the Gulf of Carpentaria. Aust. J. mar. Freshwat. Res. 30: 639–652

Macdonald, P. D. M., Green, P. E. J. (1988). User's guide to program MIX: an interactive program for fitting mixtures of distributions. Release 2.3. Icathus Data Systems, Ontario, Canada

Macdonald, P. D. M., Pitcher, T. J. (1979). Age-groups from size-frequency data: a versatile and efficient method of analyzing distribution mixtures. J. Fish. Res. Bd Can. 36: 987–1001

Maguire, G. B., Leedow, M. I. (1983). A study of the optimum stocking density and feed rate for school prawns *Metapenaeus macleayi* (Haswell) in some Australian brackishwater farming ponds. Aquaculture, Amsterdam 30: 285–297

Menz, A., Bowers, A. B. (1980). Bionomics of *Penaeus vannamei* Boone and *Penaeus stylirostris* Stimpson in a lagoon on the Pacific coast. Estuar. cstl mar. Sci. 10: 685–697

Minello, T. J., Zimmerman, R. J., Martinez, E. X. (1989). Mortality of young brown shrimp *Penaeus aztecus* in estuarine nurseries. Trans. Am. Fish. Soc. 118: 693–708

Parrack, M. L. (1979). Aspects of brown shrimp, *Penaeus aztecus,* growth in the northern Gulf of Mexico. Fish. Bull. U.S. 76: 827–836

Rothlisberg, P. C., Crocos, P. J., Staples, D. J. (1988). Recruitment dynamics of penaeid prawns in Albatross Bay, Gulf of Carpentaria. In: Proceedings of the AMSA Jubilee Conference, 14–16 December 1988. University of Sydney. Wavelength Press, Sydney, p. 37–41

Rothlisberg, P. C., Staples, D. J., Crocos, P. J. (1985). A review of the life history of the banana prawn, *Penaeus merguiensis*, in the Gulf of Carpentaria. In: Rothlisberg, P. C., Hill, B. J., Staples D. J. (eds.) Second Australian National Prawn Seminar. NPS2, Cleveland, Australia, p. 125–136

Salini, J. P., Blaber, S. J. M., Brewer, D. T. (1990). Diets of piscivorous fishes in a tropical Australian estuary, with special reference to predation on penaeid prawns. Mar. Biol. 105: 363–374

Staples, D. J. (1980). Ecology of juvenile and adolescent banana prawns, *Penaeus merguiensis*, in a mangrove estuary and adjacent offshore area of the Gulf of Carpentaria. II. Emigration, population structure and growth of juveniles. Aust. J. mar. Freshwat. Res. 31: 653–665

Staples, D. J., Heales, D. S. (1991). Temperature and salinity optima for growth and survival of juvenile banana prawns, *Penaeus merguiensis*. J. exp. mar. Biol. Ecol. 154: 251–274

Staples, D. J. Vance, D. J. (1979). Effects of changes in catchability of juvenile and adolescent banana prawns, *Penaeus merguiensis* de Man. Aust. J. mar. Freshwat. Res. 30: 511–519

Staples, D. J., Vance, D. J. (1985). Short-term and long-term influences on the immigration of postlarval banana prawns, *Penaeus merguiensis*, into a mangrove estuary of the Gulf of Carpentaria, Australia. Mar. Ecol. Prog. Ser. 23: 15–29

Staples, D. J., Vance, D. J. (1986). Emigration of juvenile banana prawns *Penaeus merguiensis* from a mangrove estuary and recruitment to offshore areas in the wet-dry tropics of the Gulf of Carpentaria, Australia. Mar. Ecol. Prog. Ser. 27: 239–252

Staples, D. J., Vance, D. J. (1987). Comparative recruitment of the banana prawn, *Penaeus merguiensis*, in five estuaries of the south-eastern Gulf of Carpentaria, Australia. Aust. J. mar. Freshwat. Res. 38: 29–45

Vance, D. J., Haywood, M. D. E., Staples, D. J. (1990). Use of a mangrove estuary as a nursery area by postlarval prawns, *Penaeus merguiensis* de Man, in northern Australia. Estuar., cstl Shelf Sci. 31: 689–701

Vance, D. J., Staples, D. J., Kerr, J. D. (1985). Factors affecting the year to year variation in the catch of banana prawns (*Penaeus merguiensis*) in the Gulf of Carpentaria, Australia. J. Cons. int. Explor. Mer 42: 83–97

Vance, D. J., Staples, D. J. (1992). Catchability and sampling of three species of juvenile penaeid prawns in the Embley River, Gulf of Carpentaria, Australia. Mar. Ecol. Prog. Ser. 87: 201–203

Zein-Eldin, Z. P., Aldrich, D. V. (1965). Growth and survival of *Penaeus aztecus* under controlled conditions of temperature and salinity. Biol. Bull. mar. biol. Lab., Woods Hole 129: 199–216

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