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**N. Ahmad Adnan · N.R. Loneragan · R.M. Connolly**

# Variability of, and the influence of environmental factors on, the recruitment of postlarval and juvenile *Penaeus merguiensis* in the Matang mangroves of Malaysia

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**Abstract** Postlarval and small juvenile *Penaeus merguiensis* were sampled fortnightly by beam trawls on the ebb tides over 4 years in the Matang mangroves on the west coast of peninsular Malaysia. Larger juveniles were sampled by bag nets on both the ebb and flood tides every fortnight over 5 years. Rainfall is consistently high throughout the year (>100 mm in each month) and the annual rainfall ranges from about 1,800 to 2,600 mm. Water temperatures ranged from 27°C to 36°C and salinity from 14‰ to 32‰ during this study. Fortnightly catches by beam trawls and bag nets were highly variable but showed a single broad period of postlarval and juvenile recruitment extending from December to May and an extended broad period of juvenile emigration from February to July. Beam trawl catches of postlarvae and juvenile prawns were consistently low between June and August. Higher catches of postlarvae and juveniles were recorded at two sites in close proximity to small adjoining creeks than one with no adjacent creek. Catches of juveniles in bag nets were higher during the day than the night and were correlated with the strength of the water flow. Environmental variables generally accounted for only a small proportion of the variation in catches, even for rainfall. The small proportion of variation explained by environmental variables is probably because of their relatively small seasonal variation in the Matang region. The lack of environmental influence on the catches of *P. merguiensis* implies that managing the mangrove nursery habitats and fishing pressure may be the main considerations for sustaining their stocks in the Matang region.

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N. Ahmad Adnan
Fisheries Research Institute, Department of Fisheries, Malaysia, 11960 Batu Maung, Penang, Malaysia

N. Ahmad Adnan · R.M. Connolly
School of Environmental and Applied Sciences, Griffith University, PMB 50, Gold Coast MC, Qld 9726, Australia

N.R. Loneragan (✉)
CSIRO Division of Marine Research, PO Box 120, Cleveland, Qld, 4163, Australia

E-mail: neil.loneragan@csiro.au
Tel.: +61-7-38267255
Fax: +61-7-38267222

## Introduction

The white banana prawn, *Penaeus merguiensis*, is widely distributed and is one of the most important species in commercial fisheries from the Red Sea in the west, to the south and central Pacific islands in the east, and tropical Australia to the south (Grey et al. 1983; Dall et al. 1990). *P. merguiensis* was renamed *Fenneropenaeus merguiensis* by Pérez Farfante and Kensley (1997). However, because there is some controversy over the revised nomenclature (W. Dall, CSIRO Marine Research, personal commication), we are using the older name. Adult *P. merguiensis* spawn in offshore waters and the eggs, after hatching, develop through a series of larval stages before becoming postlarvae (Dall et al. 1990). The larvae are advected towards the shore by prevailing currents and settle as postlarvae along mangrove-lined mud banks in estuaries (Staples et al. 1985; Vance et al. 1990). The juveniles remain in the inshore nursery areas for about 3 months before migrating to coastal waters where they mature at about 6 months of age (Rothlisberg et al. 1985).

The life-cycle dynamics of this species can vary between different localities depending on the prevailing environmental conditions (Dall et al. 1990). In some cases, the annual production of penaeid prawns is strongly correlated with environmental factors such as rainfall, temperature and river flow (e.g. Dall et al. 1990; Loneragan and Bunn 1999). One of the strongest correlations with rainfall is for commercial catches of *P. merguiensis* in the southeast Gulf of Carpentaria where rainfall is highly seasonal and accounts for about 75% of the variation in commercial catches (Vance et al. 1985, 1998).

Few long-term studies (i.e. longer than 2 years) have investigated the timing of recruitment and emigration of juvenile *P. merguiensis* from their estuarine, mangrove nursery grounds. All published studies exceeding 2 years in duration were completed in the Gulf of Carpentaria, Australia, where 80% of rain falls in the summer months from December to April (Staples and Vance 1985; Vance et al. 1998). These studies have demonstrated a difference in the timing of the life cycle between the north-eastern and south-eastern regions of the Gulf (Vance et al. 1998). In the southeast, prawns spawned from August to November settled and survived more successfully than those spawned at other times of the year (Rothlisberg et al. 1985). In the north-eastern Gulf, however, postlarvae and juveniles spawned from February to May survived and settled more successfully than those from August to November. These results highlight the need for long-term data sets to clearly identify the timing of the life cycle and the influence of environmental variation on the populations.

In this study we examine the seasonal and annual variation (over 4–5 years) in the recruitment patterns of postlarval and juvenile *P. merguiensis* in the mangrove forest of Kuala Sepetang, Perak, western peninsular Malaysia. We also attempt to establish the environmental factors that influence the recruitment of postlarval and juvenile *P. merguiensis* and the emigration of larger juveniles from the estuary. These results are compared with those from other areas, particularly the Gulf of Carpentaria (e.g. Staples and Vance 1986; Vance et al. 1998), where rainfall is highly seasonal.

## Materials and methods

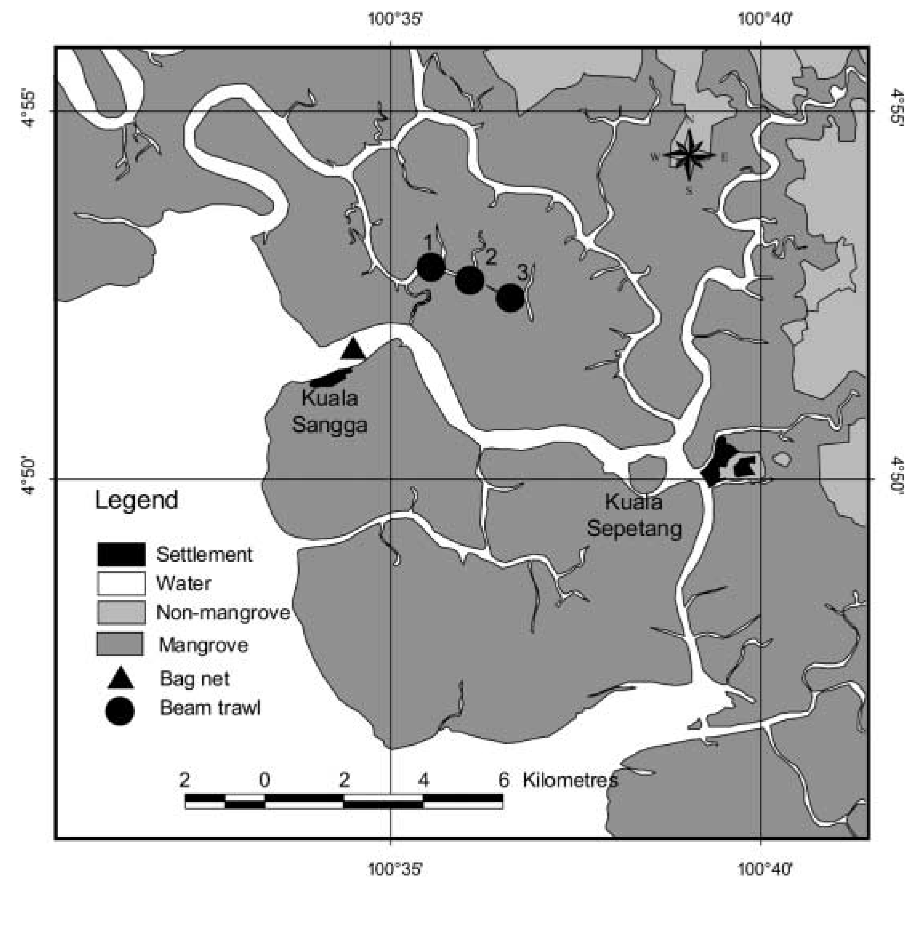
This study was carried out in the Matang mangroves (latitude 4°15′–5°1′N and longitude 100°2′–100°45′E) in the state of Perak, on the west coast of peninsular Malaysia (Fig. 1). This is the largest single mangrove forest (40,150 ha) in peninsular Malaysia and reputed to be the best managed (Gan 1995). The main fishing methods in this area are trawls, trammel, push and bag nets, with the two latter methods used in the rivers and very nearshore waters.

### Environmental variables

Daily rainfall data were obtained from a small meteorological station operated by Forest Research Institute of Malaysia (FRIM), on the outskirts of the village of Kuala Sepetang (4°51′N, 100°38′E) from January 1987 to November 1995 (no data were available after this time). The daily rainfall data and also the number of days when rain fell were summed for each month. The monthly means for rainfall and the number of days when rain fell were then calculated for each month for all years from 1987 to 1995.

An index of water current strength during one tidal cycle was measured as the difference between the highest and lowest water levels (i.e. the tidal amplitude) during that cycle. The index was determined for each bag net haul and each beam trawl sampling day, since all beam trawls were completed within one tidal cycle.

**Fig. 1.** Beam trawl and bag net sampling sites in the Kuala Sepetang region of Perak, western peninsular Malaysia



Salinity and surface water temperature data were also recorded at the time of sampling. They were measured before the first tow at each of the beam trawl sampling sites, and before each bag net sample was collected. The mean salinity and mean surface water temperature over all three beam trawl sites and all four bag net samples for each sampling were then calculated.

## Sampling

*P. merguiensis* were sampled using beam trawls and bag nets every fortnight on the spring tide. Sampling by bag net was started in January 1991 and by beam trawls in February 1992 and continued until October 1995 for both methods.

### *Beam trawl*

The beam trawl used to sample postlarval and juvenile *P. merguiensis* measured 1×0.5 m at the mouth, with 2 mm mesh in the body and 1 mm mesh in the cod-end. Trawling was carried out at three sites along one of the tributaries of the Sungei Sangga Besar that joins the main river about 2 km from the river mouth (Fig. 1). Three or four 10 m trawls were pulled perpendicular from the riverbank into the channel at each site during the last third of the first ebb tide of the day, i.e. just before or just after sunrise, when the catchability of small banana prawns is highest (Vance and Staples 1992). These perpendicular trawls provide good estimates of the full size range in the population when prawns are abundant (Vance et al. 1998). Sampling was completed within one day and sites were sampled in the same sequence each day; i.e. site 1, 2, and then 3. All *P. merguiensis* were preserved in alcohol and measured in 1-mm size-classes (carapace length) under a stereomicroscope in the laboratory.

### *Bag net*

The bag net used for sampling juvenile *P. merguiensis* was made from polyethylene and had a mouth opening of 10 m. The lower ends of both wings were fixed to the riverbed while the upper ends were tied to rings and the head rope attached to floats, thus allowing the net to fish the whole water column, which ranged from 2.5 to 4.4 m deep. The stretch mesh size of the main components of this net were: 50 mm in the wings, 30 mm in the belly, and 25 mm with a 3-mm mesh net cover in the cod-end. Samples were collected at a fixed location close to the mouth of Sungei Sangga Besar, about 3 km downstream from the beam trawl site 1 (Fig. 1). Four samples were collected within a 24-h period based on tidal and diurnal phases; i.e. night-ebb tide, day-flood tide, day-ebb tide and night-flood tide. Prawns were collected from the cod-end 2 h before the highest water level for the flood tide sampling, and 2 h before the lowest water level for the ebb tide.

The carapace lengths (CLs) of postlarval and small juvenile ( $<10$ mm CL) *P. merguiensis* were measured as described for the prawns caught in beam trawls, while larger prawns ( $>10$ mm CL) were measured using vernier callipers.

## Analysis of data

### *Testing sources of variation in catches*

The variation in beam trawl catches between months, years and sites was tested by an analysis of variance (ANOVA). Data for the period between July 1992 and June 1995 were analysed, with the year taken from July of one year until June of the following year. Separate analyses were run for postlarvae ( $<3$ mm CL) and three size categories of juveniles: 3–9.9 mm CL, ≥10 mm CL and all juveniles (≥3 mm CL). The variation in bag net catches between months, years, and diurnal phase (day and night) was also tested using ANOVA for ebb and flood tides between July 1991 and June 1995. Three size categories of juveniles were analysed separately: small = 12 mm CL, medium = 12–16.9 mm CL, and large≥ 17 mm CL. Each variable was checked for homogeneity of variances and transformed $[\log_{10}(n+1)]$ prior to ANOVA where appropriate. When significant differences were found, the Ryan-Einot-Gabriel-Welsch multiple stepdown procedure based on *F*-test (REGWF) was used to detect those means that differed significantly.

The seasonal variation in beam trawl and bag net was examined by calculating the mean catches for each month of postlarval (1–2.9 mm CL, trawl only) and juvenile prawns (≥3 mm CL). A monthly mean was then calculated over all years of the study, for years when data were available for a complete biological cycle, i.e. between July and June.

### *Length frequency distributions*

The CL frequency distribution of prawns in the beam trawl area was determined for each site and for all sites combined, pooled over the entire sampling period (i.e. February 1992 until October 1995). The size distribution of the bag net catches was calculated for the ebb and flood tide from January 1991 until October 1995.

### *Relationship between catches and environmental variables*

The effects of environmental variables on the variation in catches were examined using correlation and multiple regression analyses. For each analysis, the presence of autocorrelation in the data was investigated using the Durbin-Watson test (Draper and Smith 1981). When significant auto-correlation was found, the analyses were repeated using subsets of the data that excluded times of consistently low catches.

For beam trawls, we examined the relationships between fortnightly beam trawl catches of postlarvae and juveniles (for each sampling site as well as pooled across for all sites) and the following variables: rainfall accumulated for 1, 3, 7, 10, 14 and 28 days before sampling, salinity and water surface temperature recorded at the time of sampling and averaged over all sites, the highest and lowest water level around the time of sampling (from tide tables), and the tidal amplitude (used as an index of current strength). The distributions of these environmental variables were first examined for normality and where necessary, were transformed $[\log(n+1)$ or $\sqrt{(n+0.375)}]$. The Durbin-Watson test showed that for the whole data set, significant autocorrelation was often present. This was reduced substantially by only analysing data from October to May.

The relationships between the fortnightly catches and the environmental variables were also explored using forward stepwise multiple regression analyses. However, only rainfalls accumulated over 3, 7 and 10 days before sampling were entered into the analyses. To minimise the autocorrelation, only data between October and May were used. Similar analyses were completed for each size category of the bag net catches for each of the flood and ebb tides. For the correlation analyses with rainfall, the catch was averaged over day and night while for the analysis with salinity, temperature and tidal amplitude, data from individual samples were used. For the multiple regression analyses, salinity, temperature and tidal amplitude were averaged over day and night samples for each tidal phase.

Pearson correlations were calculated between the average fortnightly catches of juveniles in beam trawls, pooled over all sites, and the average fortnightly bag net catches of different size categories using various time lags.

# Results

## Environmental variables

The mean annual rainfall between 1987 and 1995 was 2,109 ± 303 mm, ranging from 1,794 mm (1994) to 2,587 mm (1991). The mean monthly rainfall in Kuala

Sepetang exceeded 100 mm in each month and was less than 150 mm in only 4 months of the year (July, August, February and June) (Fig. 2). The mean monthly rainfall was higher than 200 mm from September to November, with a maximum in November of about 300 mm. The number of days when rain fell ranged from 145 days (1992) to 187 days (1988), with the months of September to November, and April having more rainy days than the other months.

The mean salinity ranged from 14‰ to 30‰ at the beam trawl sites and from 17‰ to 32‰ at the bag net sites (Fig. 3a, b). The mean surface water temperature ranged from 27°C to 31°C at the beam trawl sites and from 28°C to 34°C at the bag net site.

## CL frequency distribution

### *Beam trawl*

The CL of *P. merguiensis* caught in beam trawls ranged from 1 mm to 21 mm. Postlarvae (1–2.9 mm CL) made up 38% of the total catch for all sites combined and the modal size group was 2–2.9 mm CL, which contributed 32% to the total catch (Fig. 4a). The size groups larger than 10 mm CL each contributed less than 1% to the total catch. In contrast to the pooled CL frequency distributions and those for sites 1 and 2, postlarvae comprised only 10% of the catch at site 3 and the dominant size groups were the juveniles of 3–3.9 mm CL (25%) and 4–4.9 mm CL (21%).

### *Bag net*

The CLs of *P. merguiensis* caught in bag nets ranged from 5.5 to 35.0 mm CL (Fig. 4b). The dominant size classes were from 12 to 15 mm CL that made up 39% of the total catch. The size group between 12 and 17 mm CL contributed 62% of the total catch. The modal size of prawns was 1 mm larger on the ebb (14 mm CL) than the flood (13 mm CL) tide.

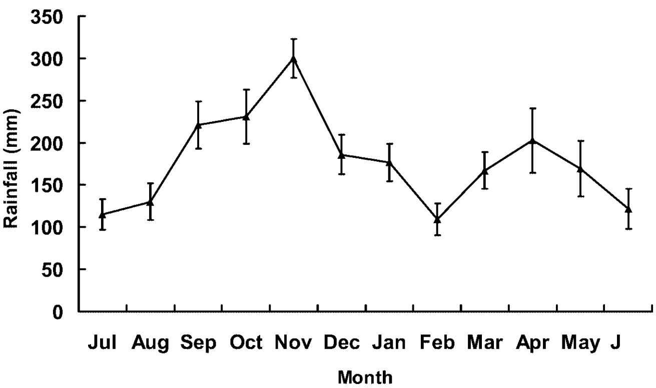



**Fig. 2.** The mean monthly rainfall (±1 SE) from the Kuala Sepetang meteorological station in Perak, western peninsular Malaysia for the years between 1987 and 1995. Data were provided by the Forestry Research Institute of Malaysia

## Temporal variation in catches

### *Beam trawl*

Catches of both postlarvae and juveniles in the study area showed a clear pattern of seasonal variation (Fig. 5). Catches of postlarvae were higher from December to April and were lowest in July and August. They were significantly higher between February and April (range of means 4.1 $m^{-2}$–4.9 $m^{-2}$) than in all other months, except January (Table 1, Fig. 5). The mean monthly catches of juveniles followed a similar seasonal pattern to those of postlarvae, and were significantly higher between November and May (range of means 3.7 $m^{-2}$–14.9 $m^{-2}$) than in all other months. The very high mean catch of juveniles (>20 $m^{-2}$) recorded in January was due to exceptionally large catches of juveniles at site 1 in January 1993.

Beam trawl catches of postlarvae and juvenile prawns sometimes varied markedly between consecutive sampling times (Fig. 6). For example, very low numbers of postlarvae and juveniles were occasionally caught even during the high catch periods of December–April and November–May, respectively.

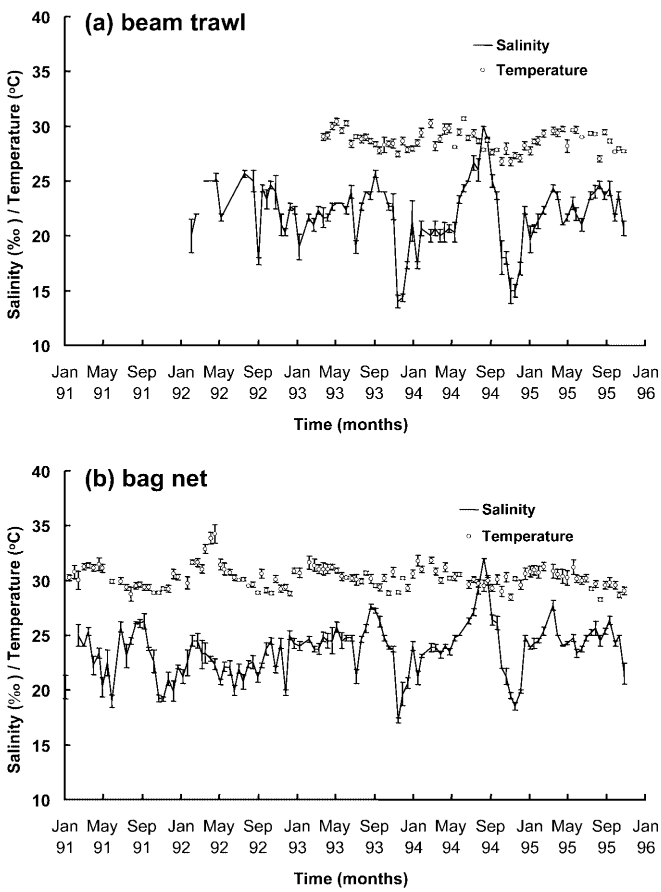



**Fig. 3.** The mean salinity (±1 SE) and mean water surface temperature (±1 SE) of **a** the beam trawl sampling sites and **b** the bag net sampling site

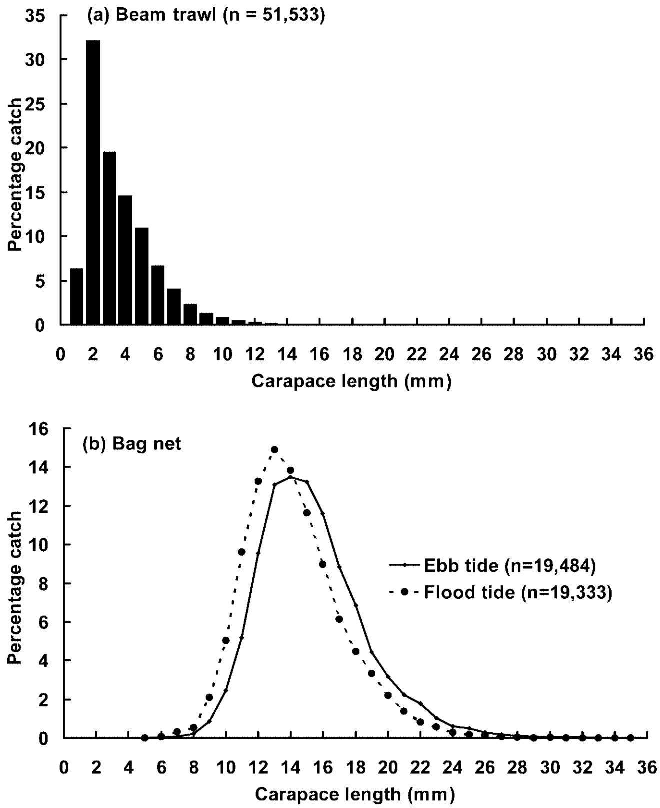



**Fig. 4.** Carapace length frequency distribution of *Penaeus merguiensis* for **a** beam trawls from all sampling sites (February 1992–October 1995) and **b** bag net on the ebb and flood tides (January 1991–October 1995)

*Bag net*

The average monthly bag net catches, irrespective of size or tide stage, were higher between January and July than between September and December (Fig. 7a, Table 2). Both the small (< 12 mm CL) and medium (12–16.9 mm CL) size classes had similar seasonal

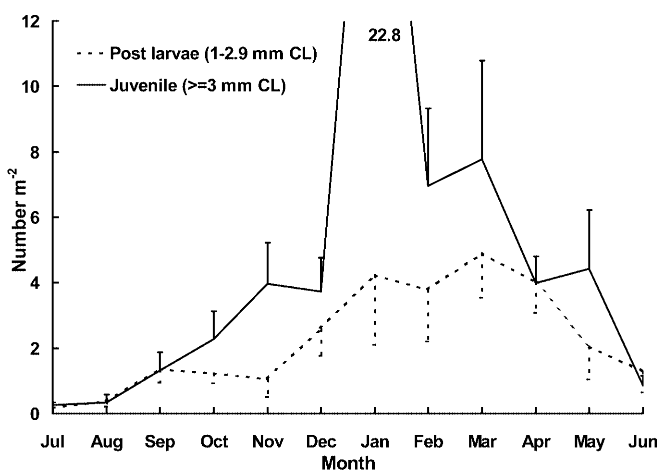



**Fig. 5.** Mean monthly beam trawl catches of *P. merguiensis* postlarvae (–1 SE) and juveniles (+1 SE) from July 1992 to June 1995

**Table 1.** Mean squares and levels of significance for catches [log(n + 1) transformed] of *Penaeus merguiensis* postlarvae and juveniles in beam trawls between July 1992 and June 1995. *df* Degrees of freedom

| Source of variation | *df* | Mean square | |
|---|---|---|---|
| | | Postlarvae | Juveniles |
| Site | 2 | 10.88*** | 14.31*** |
| Month | 11 | 8.72*** | 14.24*** |
| Year | 2 | 3.20*** | 1.78*** |
| Site × Month | 22 | 0.24 | 0.57*** |
| Site × Year | 4 | 0.73*** | 0.34 |
| Month × Year | 22 | 0.39 | 1.83*** |
| Site × Month × Year | 44 | 1.12*** | 0.42*** |
| Error | 715 | 0.30 | 0.16 |

*** $P \leq 0.001$

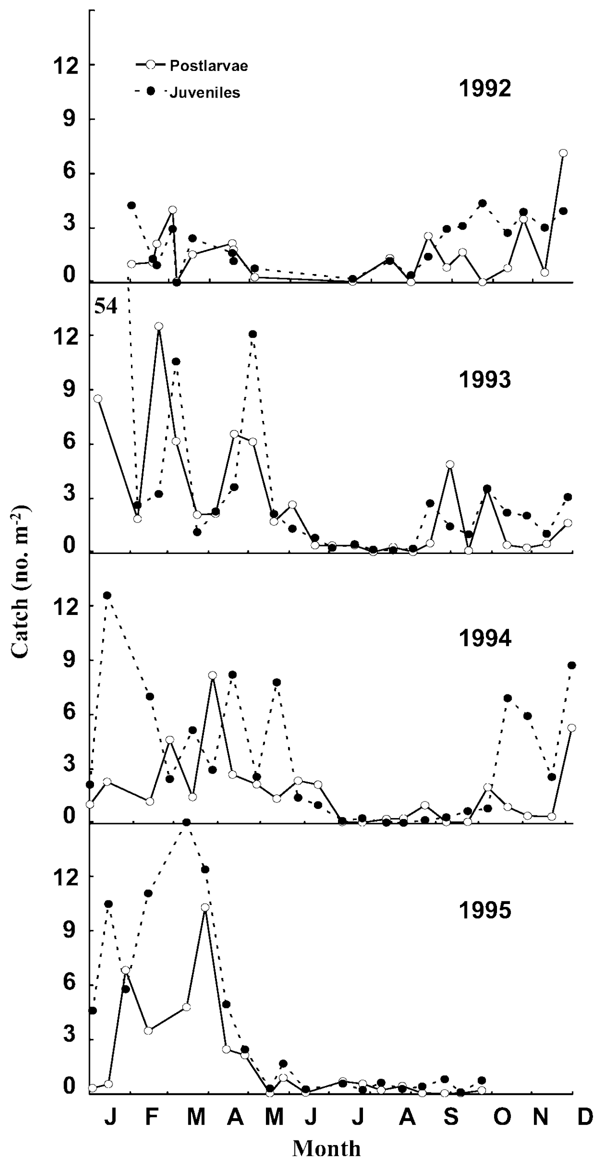



**Fig. 6.** Mean fortnightly catches of *P. merguiensis* postlarvae and juveniles by beam trawls from February 1992 to October 1995

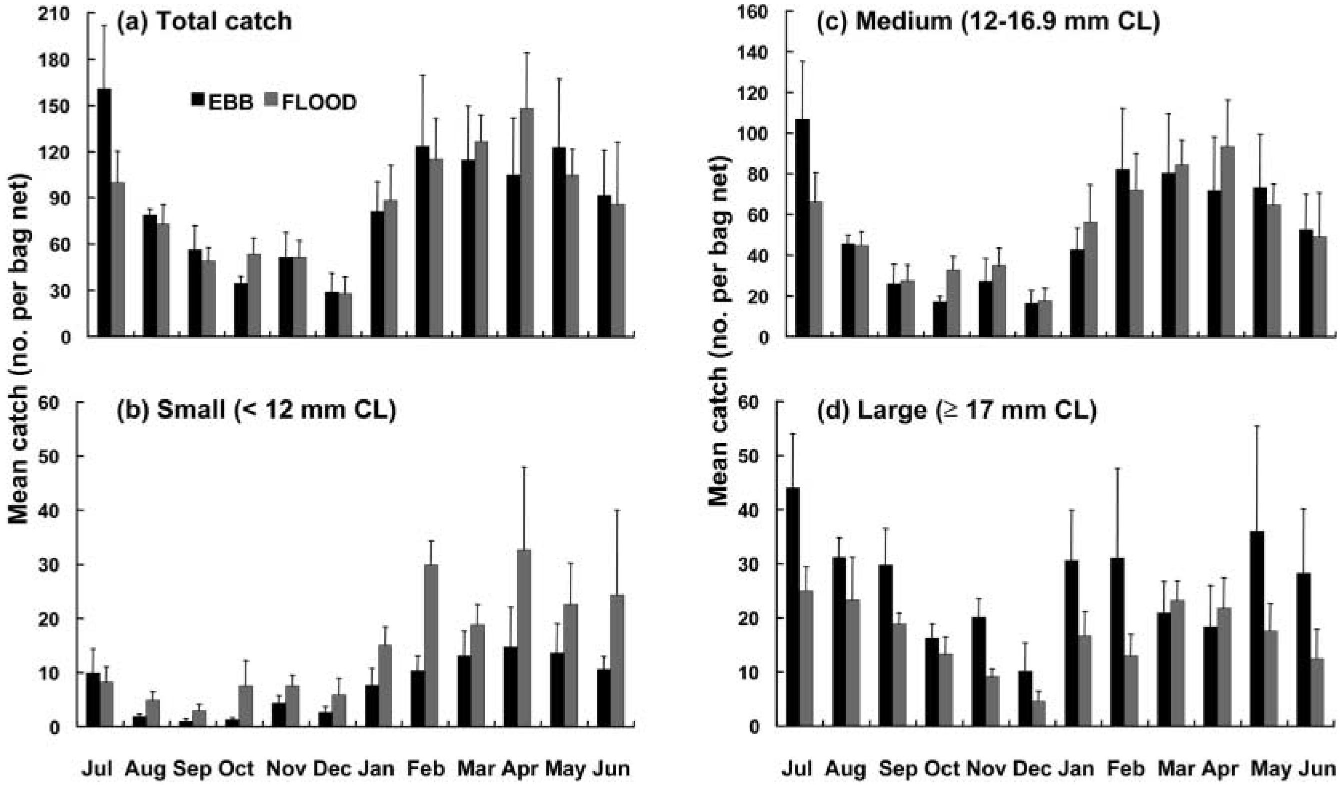



**Fig. 7.** Mean monthly average catch of *P. merguiensis* **a** total catch, **b** small (< 12 mm CL), **c** medium (12–16.9 mm CL) and **d** large (≥17 mm CL) juveniles (+1SE) in bag nets on ebb and flood tides from July 1991 to June 1995

patterns of variation to that for the overall catch (Fig. 7b, c). The mean catches of the largest size group (≥17 mm CL) fluctuated throughout the year, particularly on the ebb tide (Fig. 7d). The highest ebb tide catches were recorded in July. However, the large error bars during the months of high ebb tide catches, reflect large variation in catches between years.

For the smallest size class in bag nets, average catches were generally much higher on the flood than the ebb tide (Fig. 7b). Average catches of the medium size prawns were generally similar on the ebb and flood tides (Fig. 7c). In contrast, catches of the largest group were generally higher on the ebb than the flood tide (Fig. 7d).

## Testing sources of variation in catches

### *Beam trawl*

Catches of postlarvae and all juveniles (≥3 mm CL) differed significantly between sites, months and years (Table 1). The site × month and month × year interactions were also significant. However the mean squares for site and month were far higher than those for the other terms in the analysis. Only the main effects of site and year and the site × month interaction are discussed below (differences between months are discussed in the earlier Results section on temporal variation in catches, Figs. 5, 6).

**Table 2.** Mean squares and levels of significance for catches of juvenile *P. merguiensis* in bag nets in the Kuala Sepetang area, peninsular Malaysia between July 1991 and June 1995. *df* Degrees of freedom. *Small* = < 12 mm CL; *medium* = 12–16.9 mm CL; *large* = ≥17 mm CL

| Source of variation | Ebb tide | | | | Flood tide | | | |
|---|---|---|---|---|---|---|---|---|
| | *df* | Small | Medium | Large | *df* | Small | Medium | Large |
| Year | 3 | 1.80*** | 2.70*** | 1.41*** | 3 | 1.14** | 0.10 | 0.17 |
| Month | 11 | 1.24*** | 0.85*** | 0.63*** | 11 | 1.64*** | 1.02*** | 0.56 |
| Diurnal | 1 | 2.71*** | 5.13*** | 2.99*** | 1 | 0.19 | 0.57 | 0.08 |
| Year × Month | 33 | 0.16 | 0.31 | 0.27* | 33 | 0.32 | 0.31 | 0.21 |
| Year × Diurnal | 3 | 0.22 | 0.07 | 0.02 | 3 | 0.05 | 0.01 | 0.05 |
| Month × Diurnal | 11 | 0.14 | 0.22 | 0.69*** | 11 | 0.31 | 0.23 | 0.13 |
| Year × Month × Diurnal | 33 | 0.19 | 0.16 | 0.11 | 33 | 0.09 | 0.11 | 0.10 |
| Error | 92 | 0.19 | 0.22 | 0.17 | 90 | 0.27 | 0.28 | 0.39 |

* $0.01 < P \leq 0.05$; ** $0.001 < P \leq 0.01$; *** $P \leq 0.001$

The REGWF multiple range test showed that the mean catch of postlarvae at site 2 (3.6 $m^{-2}$) was significantly higher than at site 1 (1.8 $m^{-2}$), which was significantly higher than that at site 3 (1.2 $m^{-2}$). In contrast, the mean catch of juveniles at site 3 (4.7 $m^{-2}$) was significantly higher than at site 2 (4.1 $m^{-2}$), which was significantly higher than at site 1 (3.8 $m^{-2}$).

The mean monthly catches for postlarvae and juveniles were similar for all sites from July to December. For most of the other months, the catches of postlarvae at site 2 were much higher than those at the other sites. The catches of juveniles between January and May varied between sites and were consistently lower at site 1 than the other sites, except in January 1993.

The mean annual catch of postlarvae in 1992–1993 (3.1 $m^{-2}$) was significantly higher than those in 1993–1994 and 1994–1995 (both 1.8 $m^{-2}$). Like the postlarvae, the mean annual catch of juveniles in 1992–1993 (5.5 $m^{-2}$) was also significantly higher than those in 1993–1994 (3.0 $m^{-2}$) and 1994–1995 (4.1 $m^{-2}$).

*Bag net*

The catches of the small, medium and large prawns in bag nets on the ebb tide differed significantly between diurnal phase, years, and months (Table 2). None of the interaction terms were significant except for the large prawns, where the month × diurnal phase and the year × month interaction were significant. The largest mean squares were those due to day/night, followed by year and month.

For each size class, the mean ebb tide catch was significantly greater in the day than the night, particularly for the smallest size class (0.70 for day, 0.44 for night). The monthly mean catches during the day were much higher than those at night during the period of high catches, i.e. between February and July for the small and medium size classes and between February and August for the large size class. However, the catches of the large size class were always slightly higher during the night from October to January.

The mean ebb tide catch of the small prawns was significantly higher in 1994–1995 (16.9) than in the other years (range 4.0–6.5). The mean catches of the medium prawns during ebb tides were significantly higher in 1993–1994 and 1994–1995 (62.0 and 82.5, respectively) than in 1991–1992 (24.4). For the large prawns, the mean catches during ebb tides were significantly higher in 1992–1993 and 1993–1994 (35.3 and 35.9, respectively) than in 1991–1992 (15.5).

Few significant differences were found in the ANOVA of bag net catches on the flood tide (Table 2). Catches differed significantly between months only for the small and medium size classes (Fig. 7b, c) and not between diurnal phases. The catches of the smaller juveniles also differed significantly between years, with significantly larger catches in 1994–1995 (31.2) than the other years (range 7.4–11.3). For the large size class, none of the terms in the ANOVA were significant.

## Relationships between catches and environmental variables

*Beam trawl catches*

In general, the patterns of correlation between catches and environmental variables for the individual sites were similar to those for the combined data. The highest correlations between the mean fortnightly catches of postlarvae and environmental variables were found with the height of the highest water level before sampling (–ve) and surface water temperature (+ve) (Table 3). Catches of postlarvae were negatively correlated with the accumulated amount of rainfall for 3 and 7 days prior to sampling. The mean fortnightly catches of juvenile prawns (≥3 mm CL) were positively correlated with water temperature and negatively correlated with the height of the highest water level before sampling (Table 3).

The height of the highest water level before sampling was the only significant variable fitted to the multiple regressions for both postlarval and juvenile fortnightly catches. This variable explained 39% of the variation in postlarval catches ($n = 54$, $P \leq 0.001$) and 14% of the variation in juvenile catches ($n = 54$, $0.001 < P \leq 0.01$). The Durbin-Watson test did not detect any significant autocorrelation in these multiple regressions.

*Bag net*

In most cases the correlations between environmental variables and bag net catches explained less than 10% of the total variation in catches. It should also be noted that significant autocorrelation was found in some of the analyses. The whole data set was used since limiting the data set to specific periods did not eliminate all the significant autocorrelations.

**Table 3.** Pearson correlations between catches [log($n$+1) transformed] of *P. merguiensis* postlarvae and juveniles in beam trawls and environmental variables for all sites combined. Only variables with at least one significant relationship are listed. *CL* carapace length

| Variable | *n* | Postlarvae (1–2.9 mm CL) | Juveniles (≥3.0 mm CL) |
|---|---|---|---|
| Rainfall | | | |
| 3 days before | 57 | –0.32* | n.s. |
| 7 days before | 57 | –0.28* | n.s. |
| Water temperature | 38 | 0.51*** | 0.35* |
| Highest water level | 57 | 0.58*** | 0.29* |
| Tidal amplitude | 57 | 0.33* | n.s. |

n.s. $0.05 < P$; * $0.01 < P \leq 0.05$; *** $P \leq 0.001$

Catches of the smallest size class of *P. merguiensis* (< 12 mm CL) were significantly correlated with surface water temperature on both the ebb and flood tides (Tables 4, 5). On the flood tide, the catches were also significantly correlated with tidal amplitude. Water temperature was the first variable fitted in the multiple regression analyses for both the ebb and flood tide. Tidal amplitude was also fitted to the equation for the flood tide (Table 5).

The medium size class of *P. merguiensis* (12–16.9 mm CL) was strongly correlated with tidal amplitude on both the ebb and flood tide (Tables 4, 5). Only catches during the ebb tide were significantly correlated with rainfall (–ve), i.e. accumulated over 10, 14 and 28 days. Rainfall (accumulated over the preceding 28 days) was the only variable fitted to the regression for catches on the ebb tide (Table 4). In contrast, tidal amplitude was the only variable fitted to the regression for catches on flood tides, and rainfall was not fitted to this equation (Table 5).

Catches of the largest size group of *P. merguiensis* in bag nets (≥17 mm CL) were significantly correlated with tidal amplitude on both the ebb and flood tides (Tables 4, 5). Catches on the ebb tides (but not the flood) were significantly correlated with 28-day rainfall (–ve). Catches of this size group were also correlated with salinity (+ve) for both the ebb and flood tides. Tidal amplitude, 28-day rainfall and water temperature were fitted to the multiple regression for catches of large juveniles on the ebb tide (Table 4). Tidal amplitude and salinity were fitted to the equation for catches of large juveniles on the flood tide, though salinity only accounted for an additional 1.9% of the variation (Table 5). In general, the sub-sets of data covering periods of higher catches were not autocorrelated. In such cases, water temperature was generally the most significant variable entered into the regression model, followed by 28-day rainfall and tidal amplitude. The various models for the relationship between catches, temperature, rainfall and tidal amplitude explained between 35% and 42% of the total variation in catches, with water temperature accounting for about 18% of this variation.

## Relationships between catches of different size classes

The correlations between the juveniles in beam trawls and the small size class in bag nets were highest at a lag time of 2–8 weeks (Fig. 8). For the medium and large size classes, the highest correlations were obtained with longer lags (8–16 weeks) and the strength of the correlations declined after a lag of 16 weeks.

**Table 4.** Pearson correlation coefficients ($r$) between fortnightly ebb tide catches [log ($n+1$) transformed] of three size classes of *P. merguiensis* juveniles and environmental variables. Only variables with at least one significant relationship are listed. Percentages of catch variation explained by each significant variable in forward stepwise multiple regression analyses. $n=111$; *CL* carapace length; + = log ($n+1$) transformed; + + = v($n+0.375$) transformed

| Variable | $n$ | Small (< 12 mm CL) | Medium (12–16.9 mm CL) | Large (≥17 mm CL) |
|---|---|---|---|---|
| Pearson correlations ($r$) | | | | |
| Rainfall | | | | |
| 10 days before + + | 115 | n.s. | –0.20* | n.s. |
| 14 days before + + | 115 | n.s. | –0.21* | n.s. |
| 28 days before + + | 115 | n.s. | –0.31*** | –0.28** |
| Salinity + | 223 | n.s. | 0.19** | 0.21** |
| Water temperature + | 221 | 0.31*** | 0.19** | n.s. |
| Tidal amplitude + | 228 | n.s. | 0.20** | 0.56*** |
| Multiple regressions ($R^2$, %) | 111 | | | |
| Tidal amplitude + | | n.s. | n.s. | (+)13.5*** |
| Water temperature + | | (+) 10.2** | n.s. | (–) 5.8** |
| 28-day rainfall | | n.s. | (–) 8.4** | (–) 6.8** |
| Total $R^2$ | | 10.2 | 8.4 | 26.1 |

n.s. $0.05 < P$; * $0.01 < P \leq 0.05$; ** $0.001 < P \leq 0.01$; *** $P \leq 0.001$

**Table 5.** Pearson correlation coefficients ($r$) between fortnightly flood tide catches [log ($n+1$) transformed] of three size classes of *P. merguiensis* juveniles and environmental variables. Only variables with at least one significant relationship are listed. Percentages of catch variation explained by each significant variable in forward stepwise multiple regression analyses. $n=110$; + = data log($n+1$) transformed

| Variable | $n$ | Small (< 12 mm CL) | Medium (12–16.9 mm CL) | Large (≥17 mm CL) |
|---|---|---|---|---|
| Pearson correlations ($r$) | | | | |
| Salinity + | 219 | n.s. | n.s. | 0.14* |
| Water temperature + | 217 | 0.26*** | n.s. | n.s. |
| Tidal amplitude + | 224 | 0.34*** | 0.54*** | 0.60*** |
| Multiple regressions ($R^2$, %) | 110 | | | |
| Tidal amplitude + | | (+) 9.0** | (+) 31.1*** | (+) 46.9*** |
| Water temperature + | | (+) 9.6** | n.s. | n.s. |
| Salinity + | | n.s. | n.s. | (+) 1.9* |
| Total $R^2$ | | 18.6 | 31.1 | 48.8 |

n.s. $0.05 < P$; * $0.01 < P \leq 0.05$; ** $0.001 < P \leq 0.01$; *** $P \leq 0.001$

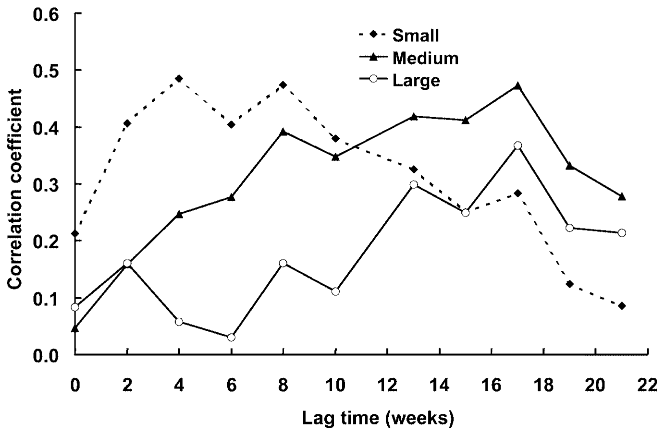



**Fig. 8.** Pearson correlation coefficients between juvenile catches of *P. merguiensis* in beam trawls and different size classes in bag nets with different time lags (0–21 weeks)

## Discussion

### Seasonal changes in catches

Mean monthly catches of postlarval and juvenile *P. merguiensis* in beam trawls showed a single, extended period of abundance, between December and April and between November and May, respectively. A single peak in abundance of postlarval *P. merguiensis* was also found in the Angsa-Klang Straits, about 250 km south of this study site (November and December, Chong 1980) and for *P. merguiensis* juveniles at Jepara, Indonesia (November–June, Noor-hamid 1976). Other studies in different regions have shown two peaks in abundance during the year, e.g. the east coast of Australia (Dredge 1985), the Kali Estuary on the west coast of India (April and October–November, Gunaga et al. 1989) and in Tamil Nadu (August and October, Mohan et al. 1995). The timing of the major peak in recruitment in Tamil Nadu varied between years, as in the present study and the comprehensive 6-year study of postlarval and juvenile *P. merguiensis* recruitment in the north-eastern Gulf of Carpentaria, Australia (Vance et al. 1998). In this latter study, peaks in abundance of the postlarvae and juveniles were found at anytime between October and May but the timing of these peaks varied between years. However, when the 6 years' data were averaged, a bimodal distribution of catches was observed, with peaks in November–December and April.

The catches of postlarval *P. merguiensis* in an estuary are influenced by the time of spawning and the hydrodynamics in the region (Rothlisberg et al. 1983, 1996). The times of peak catches of postlarvae recorded in our study suggest an extended main period of spawning (at least from November to March) for *P. merguiensis* in this region of western peninsular Malaysia. However, low catches of postlarvae at other times of year may be caused by adverse hydrodynamic conditions and not an absence of spawning activity. For example, in the south-eastern Gulf of Carpentaria, reproductive activity has a major peak in autumn (March) and a minor one in spring (September–October) in offshore waters (Crocos and Kerr 1983). However, due to the prevailing tidal currents, larvae from the major autumn peak are advected away from the inshore nursery grounds (Rothlisberg et al. 1983). The interaction of spawning activity, larval behaviour and currents resulted in one consistent peak of postlarvae in spring and a second, less consistent peak, in autumn (Rothlisberg et al. 1983; Staples and Vance 1985).

The catch from bag nets consisted of much larger juveniles than those caught in beam trawls. Although the catchability of prawns in the different nets would partly explain these differences in size distribution (e.g. larger prawns are better able to avoid small beam trawls than small prawns), it is unlikely to account for the lack of small prawns in the bag nets. The peak abundance of smaller sizes ($<12$ mm) in the bag net catch was between February and July, about 3 months later than the peak for beam trawls. However, the pattern of abundance was influenced by the direction of the tide and the size of the juveniles. A higher proportion of larger juveniles was caught on ebb tides, whereas more smaller juveniles were caught on flood tides, and approximately equal numbers of medium sized juveniles were caught on both tides. This suggests that as prawns increase in size there is a net emigration from the river to the open sea on the ebb tides (see also Haywood and Staples 1993; Vance et al. 1998). Possibly, some of the medium size group in the Matang region are temporary residents at the river mouth, which would account for the lack of difference in catches between flood and ebb tides.

The extended period of high catches of emigrating *P. merguiensis* in the Matang area contrasts with the situation in the Gulf of Carpentaria, where rainfall and emigration are highly seasonal. Catches of emigrating *P. merguiensis* are highest for a short period in the summer, wet season: December–March in the southeast (Staples and Vance 1985) and December–February in the northeast Gulf (Vance et al. 1998). In the southeast Gulf, catches of juveniles during flood tides are small and much lower than those caught on the ebb tides (Staples 1980). The overall pattern of juvenile emigration to the sea is much less clearly defined in the Matang area than in the Gulf of Carpentaria.

### Other sources of variation in catches

The analysis of variance of the beam trawl catch data for postlarval and juvenile *P. merguiensis* showed that site was the largest source of variation in catches, followed by month and year. The catches of postlarvae and juveniles at the two downstream sites (1 and 2), both located near the mouths of small creeks, were higher during times of high recruitment (between January and May–June) than at the upstream site (3), which did not have a small creek in close proximity. This suggests that postlarval *P. merguiensis* tend to settle in higher densities in small creeks than larger water bodies. Similar findings have been reported for postlarval *P. merguiensis* in other regions, where catches were higher in creeks than the main rivers and water bodies (Vance et al. 1990, 1998; Mohan et al. 1995). In our study, the *P. merguiensis* caught at creek sites were generally less than 10 mm CL. This supports the hypothesis that postlarvae settle in higher densities in small narrow creeks, and as the juveniles increase in size they migrate downstream into larger water bodies (see Vance et al. 1990, 1998).

Diurnal phase was the most important source of variation in the monthly ebb tide catches from bag nets with higher catches during the day than the night. These differences were particularly marked during periods of high abundance, which suggests that during periods of high emigration, the prawns in this region have a tendency to move out from the estuary during the day.

The second largest source of variation in catches for all three size classes of juveniles caught in bag nets during the ebb tide was year. Annual variation in juvenile abundance was also seen during the long-term studies of emigrating *P. merguiensis* in the Gulf of Carpentaria (Staples and Vance 1986; Vance et al. 1998). In these studies, it was suggested that environmental variables affected catches. The peak year for the postlarvae and juveniles caught in beam trawls differed from the small size group caught in bag nets, although the size range of these juveniles were very similar. Possibly, the small prawns caught in bag nets came from a number of tributaries and creeks, where the success of postlarval settlement may have differed from those at the beam trawl sampling sites. In Goa, India (Goswami and George 1978) and the north-eastern Gulf of Carpentaria (Vance et al. 1998), the time of peak postlarval and juvenile abundance differed between adjacent, nearby estuaries.

In marked contrast to the bag net catches on ebb tides, there were few significant sources of variations for flood tide catches. Possibly, those prawns caught on the flood tides were temporary residents in the area and their catches may have been influenced more by environmental factors, such as current flow, and random movements, rather than reflecting an upstream migration into the river.

## Relationships between environmental variables and prawn catches

Although several environmental variables were correlated with prawn catches, the amount of variation explained was low. The height of highest water level was the most important factor affecting postlarval and juvenile catches in beam trawls, with fewer prawns caught as the maximum tidal height increased. This contrasts with results from the Gulf of Carpentaria where postlarval catches were higher with greater water heights (Vance et al. 1998). It was suggested that higher tidal flows increase the number of postlarvae being advected into rivers from the open sea.

Current strength, measured as tidal amplitude, was the most influential factor affecting the catches of juvenile prawns from bag nets further down the estuary. Prawn catches generally increased as tidal amplitude increased, but with interesting differences among size classes. Whereas catches of all size classes of juveniles increased with increased tidal amplitude on the flood tide, only the catches of larger juveniles were related to tidal amplitude on the ebb tide. This suggests a behavioural difference between the size classes. On flood tides, high rates of flow result in all size classes being caught in higher numbers, whereas on ebb tides, fewer numbers of smaller juveniles were caught than would be expected on flow rates alone. This relationship between tidal flows and catches of larger juveniles has also been shown in Gulf of Carpentaria, where higher numbers of juveniles emigrate at times with increased tidal flow (Staples and Vance 1986; Vance et al. 1998).

Both short (3 and 7 days) and medium term rainfall (10–28 days) were negatively correlated with catches of postlarval *P. merguiensis* in beam trawls and medium-sized *P. merguiensis* in bag nets on the ebb tides, respectively. However, these correlations explained less than 10% of the variation in catches. Although heavy rain may create a freshwater barrier to postlarval immigration into rivers (Staples and Vance 1985), it appears to increase the number of juveniles emigrating from these systems and the subsequent size of the commercial catches (Staples and Vance 1986; Vance et al. 1998).

The difference in the importance of rainfall for emigrating *P. merguiensis* between the Matang mangroves and the Gulf of Carpentaria may be due to the very different rainfall regimes in these areas. Rainfall is highly seasonal in the north-eastern (Vance et al. 1998) and south-eastern Gulf (Staples and Vance 1985), where about 80% of the annual rainfall occurs within 4–5 months of the year. This contrasts with the Matang mangroves where rainfall is high throughout the year. The mean annual rainfall was also much higher in the Matang mangroves (2,109 mm) than in the south-eastern Gulf (1,114 mm, Staples and Vance 1986). The pattern of rainfall in the Matang area may lead to a relatively constant emigration of larger juvenile prawns, which contrasts with the highly seasonal emigration of prawns in the Gulf of Carpentaria.

## The estuarine phase of juvenile prawns

The pattern of correlations between catches of juvenile *P. merguiensis* in beam trawls and those in bag nets suggests that most of the juveniles at the beam trawl sites move to the river mouth after 4–6 weeks in the creeks and remain at the mouth for a further 8–12 weeks before emigrating from the river. The juveniles appear to start emigrating from the estuary at a size of 12–17 mm CL.

If we assume that it takes about 1 month from spawning to postlarval settlement in the estuary and an average growth rate of 1 mm CL per week (Haywood and Staples 1993), juvenile *P. merguiensis* start to emigrate at an age of about 4 months.

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