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Diet and feeding behaviour of juvenile and adult banana prawns *Penaeus merguiensis* in the Gulf of Carpentaria, Australia

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ABSTRACT: The diet of *Penaeus merguiensis* de Man was studied by examining the contents of the foreguts of 432 juveniles collected from estuarine and 467 adults from offshore habitats in the Gulf of Carpentaria between February 1985 and November 1989. The juveniles in the estuary had fed mainly at night and on rising or near-high tides; the largest amount of food was found in prawns collected 2 h after high tide. Crustaceans, bivalves, gastropods and polychaetes were the most common food items in the guts of both juveniles and adults. Copepods and other crustaceans were significantly more common in the diet of juvenile prawns caught at night. Foraminiferans, nematodes and algae were found less frequently as the size of the prawns increased. Comparative analysis of foregut contents showed no difference between schooling and non-schooling adult *P. merguiensis*. The study shows that tidal stage, daylight, and the size of *P. merguiensis* affect the composition of the diet.

INTRODUCTION

The banana prawn *Penaeus merguiensis* de Man is the most abundant penaeid prawn caught commercially in the Gulf of Carpentaria in northern Australia. Juvenile *P. merguiensis* live in coastal wetlands along the mangrove margins of creeks and inlets and mangrove forests along the shore (Chong & Sasekumar 1981, Staples et al. 1985), probably because the mangroves provide food and shelter (Robertson 1988). During the wet season, the juveniles migrate offshore, where they grow to adulthood (Staples 1980).

The natural diet of adult *Penaeus merguiensis* from the Straits of Malacca (Hall 1962) and the Philippines (Tiews et al. 1972) has been described but sample sizes were small and were restricted to a narrow size class. Ontogenetic changes in the diet of banana prawns from day-catches in Malaysia (Chong & Sasekumar 1981) and of only juvenile banana prawns from the east coast of Australia (Robertson 1988) have also been described. Nonetheless, we still do not have a clear picture of how such factors as day-night cycles and tides affect either the diet and feeding patterns of juveniles or the change in diet from juveniles in estuaries to adults offshore.

Juvenile *Penaeus merguiensis* enter the mangroves during the flooding tide and concentrate along the water's edge as the tide recedes (Staples & Vance 1979, Robertson 1988). This tidal behaviour may affect their feeding behaviour as it does that of *P. monodon* (Marte 1980) and *P. duorarum* (Sastrakusumah 1971). Staples & Vance (1979) found that juvenile *P. merguiensis* of less than 12 mm carapace length (CL) appeared to feed on the early flooding tide; their foreguts were almost all empty 14 h later when they emerged from the mangroves as the tide ebbed. However, these authors sampled over a single 24 h period and did not sample during the night. We therefore extended our study to include diel and tidal effects on the amount of food in the foregut. Such effects are easily identified in animals that clear their guts relatively rapidly. Other species of penaeids do so (Marte 1980, Hill & Wassenberg 1987) but it was not known whether *P. merguiensis* does. We therefore measured the rate at which food is cleared from the foregut of juvenile *P. merguiensis*.

Adult *Penaeus merguiensis* live offshore where they periodically form aggregations or 'schools' that may contain up to 400 t of prawns (Munro 1973). Why they school is not known; Munro (1973) suggested that they

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may be feeding on preferred food on the seabed. We investigated this possibility by comparing the foregut contents of adult banana prawns collected from schools with those that were not in schools.

MATERIALS AND METHODS

Laboratory study of foregut clearance rates. The rate of clearance of the foregut of *Penaeus merguiensis* was measured by Hill's (1976) method. The prawns, held in water at about 24.5 °C and starved for 24 h, were allowed to feed for 10 min on peeled and weighed abdomens of *Metapenaeus bennettae*. The uneaten food was removed, blotted dry and weighed. Batches of 10 prawns were killed by immersion in an ice slurry 0, 30, 60 or 90 min after they had fed. The foregut was then removed and the contents dried to constant weight at 70 °C. Ten pieces of abdomen of *M. bennettae* were oven dried at 70 °C to constant weight to obtain factors for converting wet weight of the food to dry weight.

Diel and tidal effects on feeding of juveniles. Catches of juvenile *Penaeus merguiensis* are often restricted to short periods of the day or night and the type of tide, because the stage of tide and the day-night cycle all influence catches (Vance & Staples 1992). The numbers of juveniles caught also tend to drop off sharply after low tide and for a given tide height, catches are greater on the ebb tide than on the flood tide. There is also a seasonal effect. The size range of *P. merguiensis* we wanted (>8.0 mm CL) is only available from November to about April each year. To build up a reasonable sample size and to examine the main effects of day-night and tide stage on the amount of food in the foregut and the type of prey eaten, we collected juveniles over several years and selected stages of the tide.

Juvenile *Penaeus merguiensis* were collected from the Embley estuary at Weipa, Queensland (Fig. 1) with a 1.0 m × 0.5 m beam trawl, fitted with an 8 mm stretched mesh net. All the samples were collected from a 200 m section of the mangrove lined mudbank 14 km upstream from the mouth of the Embley Estuary (Fig. 1). Trawl hauls were made parallel to the shore on a steeply sloping mudbank in water less than 0.5 m deep. When the water was in the mangroves, the trawl hauls were made at the edge of the mangroves. Tidal amplitude in this estuary varies from 0.7 m on the smallest neap tide to 2.4 m on the largest spring tide. On each occasion, 1 to 3 hauls were made at times corresponding to various stages of the tide during the day and night (Table 1). Each haul lasted about 5 min and the turnaround time between successive hauls was about 3 min. A total of 70 samples was collected. The captured prawns were placed into labelled bags, immediately put on ice and, within 3 h, taken ashore and frozen.

In the laboratory, up to 10 *Penaeus merguiensis* from each sample were thawed, their carapace lengths (CL) were measured with vernier calipers, and their foreguts were removed. The content of each foregut was weighed (wet weight) and then examined under a microscope. Because no taxonomic studies have been made of the benthic fauna of the region, food items were recorded in broad categories. The number of food items in each foregut was recorded and used to calculate the percentage occurrence.

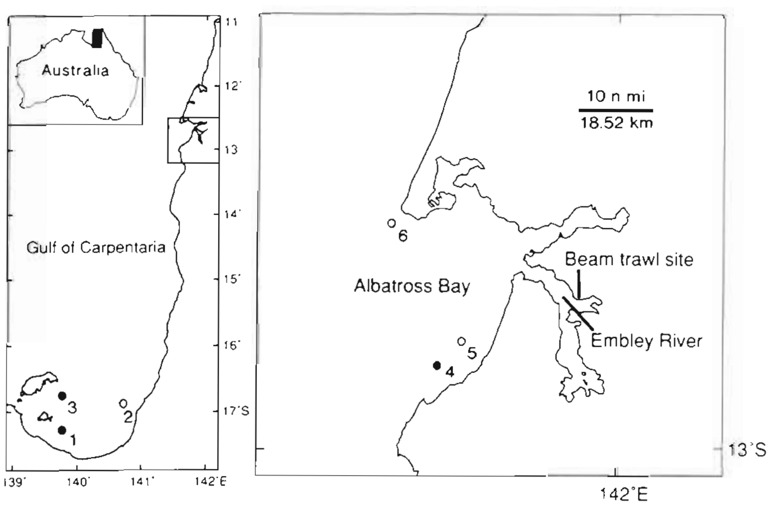

Fig. 1 Study area in the Gulf of Carpentaria, Australia, showing sampling sites for adult prawns [(•) Sites where schooling prawns were collected; (o) sites where non-schooling prawns were collected] and for juvenile prawns in the Embley estuary

Foregut weight was log-transformed to remove heterogeneity of variance. An analysis of covariance, with log-size (CL) as covariate, was used to test the hypothesis that foregut content weight did not vary over a tidal cycle or between day and night. The data were comprised of 5 samples each collected over a 24 h (approximately) period for which 8 tidal stages were defined – 4 during the day and 4 during the night – (Table 1). As not all tidal stages were represented in each sample, there were only 8 degrees of freedom for the sample × tide-stage interaction (Table 2). Tide stage was adjusted for sample differences and the interaction was adjusted for both sample and tide stage. To investigate further the effect of variation in tide, the 7 degrees of freedom

Table 1. *Penaeus merguiensis*. Sampling dates, times, tidal levels and number of hauls taken to collect juveniles from a single site in the Embley estuary for analysis of foregut weight and content. Dawn = 06:30 to 07:30 h, day = 07:30 to 18:00 h, dusk = 18:00 to 19:00 h, night = 19:00 to 0630 h. (H = high tide ± 2 h, L = low tide ± 1 h)

Date	Time (h)	Tidal stage	Number of hauls
03 Mar 87	16:30	H-2	1
	21:01	H+2	1
04 Mar 87	06:00	H-2	1
	12:30	H+2	1
01 Dec 87	02:30	H+2	3
	05:30	L-1	3
	08:30	L+1	1
	13:00	H-2	1
	17:00	H+2	1
02 Dec 87	17:30	H+1	2
	19:00	H+2	3
	21:30	L-1	3
	24:00	L+1	3
03 Dec 87	03:00	H-2	3
	05:00	H+2	3
	07:00	L-1	3
14 Apr 88	21:00	L-1	3
15 Apr 88	01:00	L+1	3
	03:00	H-2	1
	07:00	H+2	1
	09:00	L-1	1
	12:00	L+1	1
	15:00	H-2	1
	19:00	H+2	3
7 Nov 89	15:53	H-2	2
	19:14	H+2	3
8 Nov 89	05:36	L-1	3
	07:43	L+1	3
	18:07	H-2	3
9 Nov 89	06:30	L-1	2
	08:30	L+1	3
	13:44	H-2	2
	17:48	H+2	2

for tide stage were subdivided into single degrees of freedom for comparisons of: night × day; falling tide × rising tide; high tide × low tide and their interactions (Table 2). The sample × tide stage interaction was used as the error term because the variation due to this term was greater than the variation between prawns caught in the same sample at the same tide stage.

Not all prey occurred in every foregut examined. Because of the large number of zeros recorded for each prey category, we used non-parametric tests in our analysis of the number of prey eaten during the day or night or during different tide stages. In this instance a Mann-Whitney *U*-test was used to test the hypothesis that there were no diel differences with day/night as the independent variable. A Kruskal-Wallis test was used to test the hypothesis that there were no nocturnal tidal differences in the diet of *Penaeus merguiensis*. The test was repeated for each prey category with the tidal stages as the independent variable.

Table 2. *Penaeus merguiensis*. Details of the analysis of covariance for the log of gut content weight of juveniles collected from a 200 m section of a mangrove lined bank in the Embley estuary. *$p < 0.05$; ***$p < 0.001$; $\Phi = 0.05 < p < 0.10$

Source of variation	df	Mean square
(a) Covariate		
Size	1	5.73***
Factors		
Samples	4	0.69 Φ
Tide stage	7	0.54 Φ
Sample × tide stage	8	0.203***
Residual	411	0.057
(b) Analysis of tide phase components		
Night vs day	1	1.42*
Falling vs rising tide	1	0.02
Night-day × fall-rise	1	0.17
Low vs high tide	1	1.16*
Night-day × low-high tide	1	0.04
Fall-rise × low-high tide	1	0.53
Night-day × fall-rise × low-high tide	1	0.46
Residual (Sample × tide stage)	8	0.203

Ontogenetic changes in diet. To examine ontogenetic changes in diet, we collected juvenile *Penaeus merguiensis* from the Embley estuary and adults from offshore in Albatross Bay. As errors in estimates of dietary importance due to different digestion rates of tissues may be minimised by sampling during or close to the peak period of feeding (Hyslop 1980), we made a preliminary analysis of diel and tidal effects on feeding. The foreguts of the juveniles were fullest at night and those of the adult prawns did not show a diel effect, so only samples collected at night were used. All the samples for this comparison were collected over 2 nights during December 1987 to minimise possible changes in prey availability over time or any other temporal effects. On the first night, the juveniles were collected from a single haul along the edge of the mangrove-lined mudbank of the estuary and the following night the adults were collected from a single haul in about 15 m deep waters offshore.

After capture, the juveniles (n = 113) were stored in an ice slurry and then frozen while the adults (n = 100) were immediately frozen on board the trawler. In the laboratory, the carapace length of each prawn was measured and the contents of the foregut were removed and examined. The number of items in each food category was recorded. A Kruskal-Wallis analysis of variance was used to test the null hypothesis that there was no difference in the number of each prey eaten by the different size-classes of *Penaeus merguiensis*. This test was repeated for each prey item across the size classes.

Diet of schooling and non-schooling adult prawns. Adult schooling and non-schooling *Penaeus merguiensis* were collected from chartered commercial and research prawn trawlers from 6 sites in the Gulf of Carpentaria (Fig. 1) during the 5 mo period when commercial fishing was not permitted. The prawns were frozen immediately and the foregut contents analysed as described above. The number of items in each food category was recorded and the frequency of occurrence and the numerical composition for each food category were calculated.

It was suggested that the schooling behaviour of *Penaeus merguiensis* may be a response to the presence or absence of a particular food item (Munro 1973). In order to examine for differences in diet between sexes in each of the samples and between schooling and non-schooling prawns (samples combined) we used the Mann-Whitney *U*-test on individual prey types and repeated the test for each prey category.

RESULTS

Foregut clearance rate

In the laboratory, juvenile *Penaeus merguiensis* (17.3 to 24.6 mm CL) ate up to 20 mg of tissue (wet weight) in 10 min of feeding. Nearly 20 % of that amount was lost by the prawn shredding its food; only about 80 % was found in the foregut of prawns killed immediately after feeding (time 0 min). Soft tissue was quickly digested: only 60 % of ingested material remained in the foregut after 30 min and less than 18 % after 90 min (Fig. 2). The rate of clearance may be described by the exponential decay function:

$$\text{Foregut content weight (mg)} = 15.2\ e^{-0.02145\ \text{Time(min)}}.$$

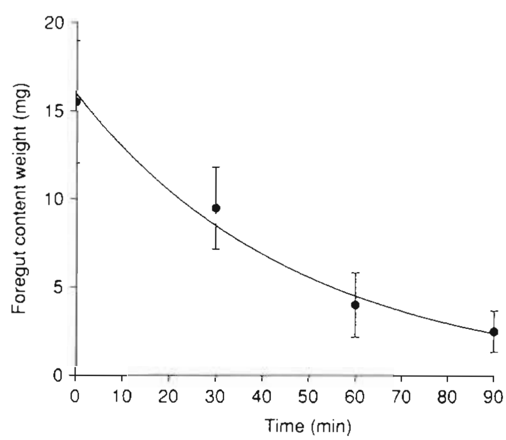

Fig. 2. *Penaeus merguiensis*. Mean dry weight (± 2 SE), of soft tissue in the foregut of juveniles at intervals after feeding was stopped. n = 10 at each point. The curved line is an exponential function: $y = 15.2\ e^{-0.02145x}$

Diel and tidal effects on feeding in juveniles

The foregut contents of 432 juvenile *Penaeus merguiensis* (8.0 to 21.1 mm CL) collected over 5 (each approximately 24 h) sampling periods in the Embley estuary were weighed. Of the prawns caught in the estuary during daytime (06:30 h to 18:30 h), 10 % had empty foreguts. Only 1.6 % of those caught at night (18:30 h to 06:30 h) had empty foreguts.

In the analysis of covariance, the coefficient for the covariate (log-size) was 1.53 (SE = 0.17, $t = 9.02$). The interaction of sample × tide stage was highly significant ($p < 0.001$) and the systematic sample and tide stage effects were nearly significant ($0.05 < p < 0.10$) when compared with the interaction (Table 2). In further analysis of the components of tide stage, only night vs day and low vs high tide were significant ($p < 0.05$) (Table 2).

Juvenile *Penaeus merguiensis* had significantly ($p < 0.05$) more food in their foregut at night (adjusted mean log weight = 0.288 g, SE = 0.029) than during the day (adjusted mean log weight = 0.169 g, SE = 0.045; Fig. 3). The quantity of food in the foregut showed that most feeding took place just after dusk, between 18 and 20 h (Fig. 4).

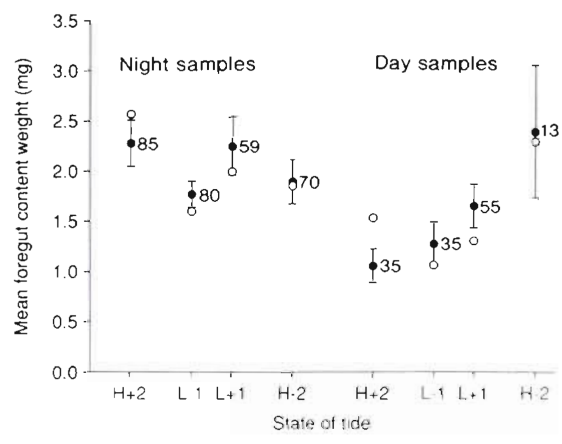

Fig. 3. *Penaeus merguiensis*. Mean foregut content weights (±2 SE) of juvenile prawns collected at each tidal stage during the day and night over 10 diel periods. (o) Same data adjusted for the size of the prawns. Sample size is shown next to each point. (H ± 2 indicates high tide ± 2 h; L ± 1 indicates low tide ± 1 h). The tidal stages are spaced on a time scale of 6 h between low and high tide

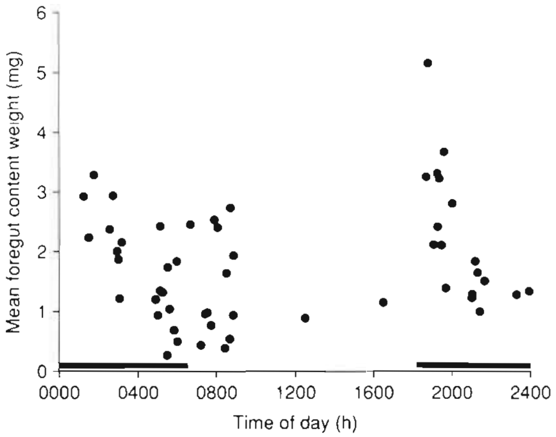

Fig. 4. *Penaeus merguiensis*. Mean weight of foregut content at various times of collection over 10 diel periods in the Embley estuary. n = 6 to 10 at each point. Dark bar indicates night

The weight of food in the foregut at night was greater in juvenile *Penaeus merguiensis* caught on the flooding tide (L+1) and 2 h after high tide (H+2) than in those caught 1 h before low tide (L−1) (Fig. 3). The difference was significant ($p < 0.05$). The average weight of all the foregut contents, for all samples combined, was greatest 2 h after high tide (H+2) at night and was lowest at 1 h before low tide (L−1) during the day (Fig. 3).

As the mean size of *Penaeus merguiensis* collected was not significantly different between night and day it was possible to test for differences in the frequency of prey in the diet between night and day. Vascular plant material, harpacticoid copepods and crustaceans were significantly more frequent in the diet during the night than during the day (Table 3). Similarly, the mean size of *P. merguiensis* caught at different nocturnal tidal stages was not significantly different, allowing us to test for differences in diet at 4 tide stages. Compared to the other samples, 8 prey items were significantly different with 7 being more frequent in the diet of samples collected 1 h after low tide (L+1) (Table 2), while crustaceans were more frequent in the diet 2 h before high tide (H−2).

Ontogenetic changes in diet

Ontogenetic differences were found for many prey items in the diet of *Penaeus merguiensis* from the Embley estuary and Albatross Bay. With increasing prawn size, foraminiferans, algae and nematodes decreased in frequency (Fig. 5) and were rarely found in adult prawns offshore. In contrast, bivalves, gastropods and polychaetes rose significantly ($p < 0.05$) (Fig. 6). The occurrence of crustaceans was high in the diet of both juvenile and adult prawns. Small amounts of fishbones

Table 3. *Penaeus merguiensis*. Diel and nocturnal tidal differences in the frequency of occurrence of prey in the diet of juveniles in the Embley Estuary. *$p < 0.05$, ***$p < 0.001$. H = high tide ±2 h, L = low tide ±1 h

Prey items	% Frequency of occurrence for: Day	Night	Tidal stage (night) H+2	L−1	L+1	H−2
Teleostei	3.6	3.1	3.5	0.0	6.8	2.9
Mollusca						
Bivalvia	3.6	5.1	9.4	2.5	10.2	0.0*
Gastropoda	34.8	32.0	25.9	27.5	54.2	25.7***
Scaphopoda	2.2	2.0	1.2	1.3	6.8	0.0***
Crustacea						
Decapoda	8.0	6.5	9.4	1.2	13.6	2.9***
Copepoda	15.6	21.4***	28.2	12.5	22.0	22.9
Other	40.6	57.8***	65.0	46.2	35.6	80.0***
Annelida						
Polychaeta	12.3	8.1	7.1	3.7	11.9	11.4
Protozoa						
Foraminifera	33.3	26.5	27.1	17.5	42.4	22.9***
Plant material (vascular)	4.3	11.2*	14.1	1.2	25.4	7.1***
Algae	18.1	12.6	14.1	10.0	11.9	14.3
Unidentified	29.7	24.8	17.6	30.0	40.7	14.3***
Sand	0.7	2.7	2.4	1.2	1.7	5.7
Mean prawn size	13.09	12.9	12.98	12.7	13.6	12.7
2 SE	0.40	0.29	0.64	0.52	0.58	0.5
(n)	(138)	(294)	(85)	(80)	(59)	(70)

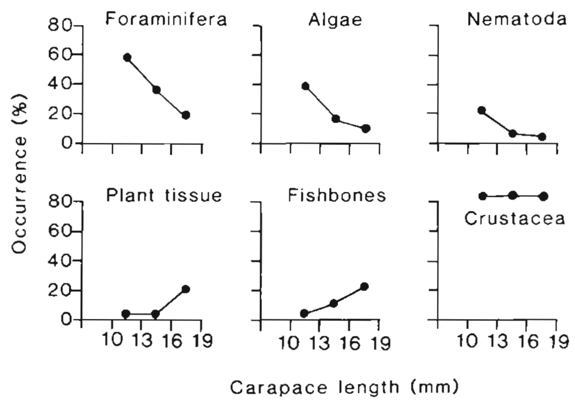

Fig. 5. *Penaeus merguiensis*. Frequency of occurrence of 6 food items in the foregut of 3 mm size classes of juvenile prawns collected at night in the Embley estuary. Sample sizes for successive sizes are 29, 35 and 49

(Fig. 5) were found in the foreguts of juvenile prawns from the estuary, while fish scales (>2.0 mm diam.), but no fish bones, were found in the foreguts of adult prawns offshore (Fig. 6).

Diet of schooling and non-schooling prawns

The foregut contents of 232 schooling and 235 non-schooling *Penaeus merguiensis* were compared. No difference between sexes was found in the diet between schooling and non-schooling prawns, except in one sample where polychaetes were significantly ($p < 0.05$) more numerous in the diet of the male prawns. Schooling prawns (samples combined) had more prey items (1868) in their foreguts than non-schooling prawns (1598). About 2% of schooling prawns and 7% of non-schooling prawns had empty foreguts. The same range of dietary items was found in the diet between schooled and non-schooled *P. merguiensis* collected from all 6 sites (Table 4).

There were quantitative differences in the numbers of prey eaten by schooling and non-schooling *Penaeus merguiensis* (samples combined). In a plot of percentage numerical composition vs percentage frequency of occurrence (Fig. 7), fish scales (Teleostei) were statistically the most numerous food item in schooled prawns ($p < 0.05$) but were eaten by relatively few prawns (20 to 25%) as can be noted by the tall narrow shape of the histogram for fish scales. Bivalves were significantly ($p < 0.05$) more numerous and were eaten by about 80% of schooling prawns, while crustaceans, gastropods, echinoderms and unidentified tissue were more numerous and were eaten by about 60 to 80% of non-schooling prawns (Fig. 7). However, these quantitative differences between schooling and non-schooling prawns do not support the hypothesis that schooling behaviour may be a response to the presence or absence of a particular food type.

DISCUSSION

Despite being fragmented, most of the prey of *Penaeus merguiensis* could be identified to broad taxo-

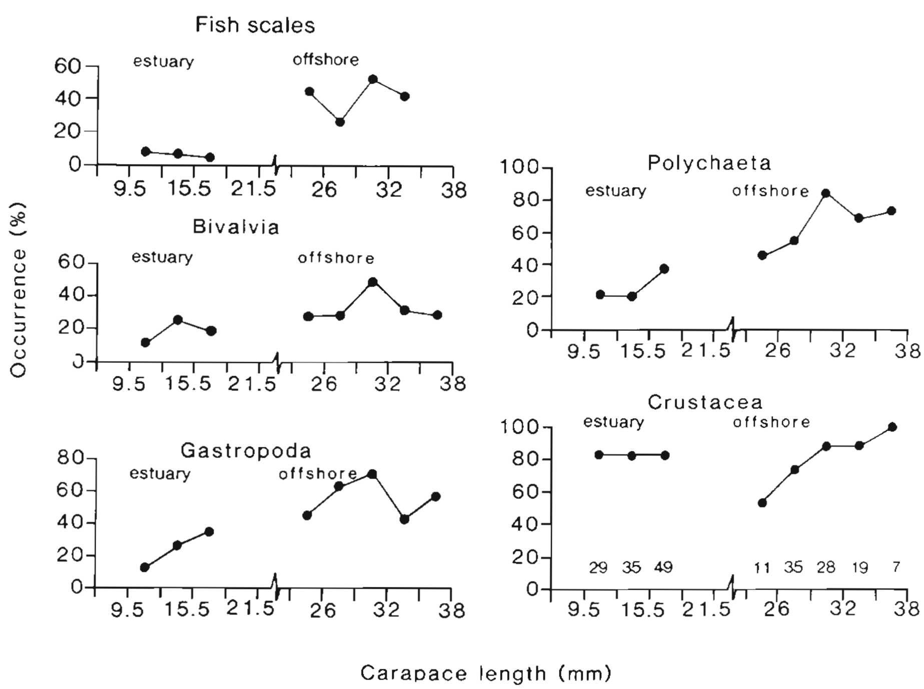

Fig. 6. *Penaeus merguiensis*. Frequency of occurrence of 5 food items in the foregut of 6 mm size classes of juvenile prawns collected at night from the Embley estuary and from 3 mm size classes of adult prawns collected from Site 6 in Albatross Bay (offshore). Sample sizes for each point are indicated in the Crustacea figure

Table 4. *Penaeus merguiensis*. Diet of prawns and statistical data for these samples collected from 6 locations in the Gulf of Carpentaria. Diets are expressed as percentage numerical composition

Diet	Schooling			Non-schooling		
	Site 1	Site 3	Site 4	Site 2	Site 5	Site 6
Pisces						
Teleostei	61.0	3.6	43.4	24.4	22.4	16.6
Mollusca						
Bivalvia	8.5	33.3	36.4	15.6	12.2	7.8
Gastropoda	3.9	15.8	3.5	17.4	25.2	20.3
Scaphopoda	0.0	0.0	3.3	0.0	3.7	2.0
Crustacea	8.6	16.6	5.6	8.4	17.8	33.7
Annelida						
Polychaeta	2.9	16.8	5.6	6.1	8.4	15.5
Echinodermata						
Echinoidea	2.3	3.1	0.0	1.3	0.9	0.0
Ophiuroidea	3.0	1.0	0.7	2.2	1.9	0.6
Protozoa						
Foraminifera	5.7	8.0	1.1	3.7	0.0	0.8
Other	0.8	0.8	0.2	19.4	0.0	2.7
Unidentified	3.3	1.0	0.2	1.5	7.5	0.0
Total no. of prey items	1056	386	426	1002	107	489
Sample size	100	98	34	100	35	100
Mean size CL (mm)	30.1	28.0	32.2	30.2	34.2	29.9
Percentage with empty foregut	3.0	2.0	1.0	5.0	8.5	7.0
Sampling date	Mar 85	Feb 85	Apr 88	Feb 85	Apr 88	Dec 86

nomic groups. Much of the soft tissue was attached to or could be associated with hard parts of teleosts, molluscs, polychaetes or crustaceans. This helped reduce the bias from differential rates of tissue digestion. Furthermore, the samples were collected when the prawns were actively feeding which further reduced the bias (Hyslop 1980).

Penaeus merguiensis clears soft tissues in about 100 min. This is slightly slower than *P. esculentus*, which empties its foregut in about 60 min at the same temperatures (Hill & Wassenberg 1987) but faster than *P. monodon*, which clears about 50 % within 1 h of feeding (Marte 1980). The rate at which penaeids clear hard parts does not appear to have been studied, but their absence from the foregut of *P. esculentus* caught shortly after their emergence from the substrate in the evening indicates that they can be cleared within 12 h (Wassenberg & Hill 1987). Juvenile *P. merguiensis* collected at night, 2 h after high tide, had a large amount of food in their foregut. Juveniles collected 3 h later, 1 h before low tide, had very little soft food or hard parts in their foregut, which suggests that they may be able to clear hard parts within a few hours.

The feeding behaviour of juvenile *Penaeus merguiensis* is affected by the state of the tide and by light. Our results show that juvenile *P. merguiensis*

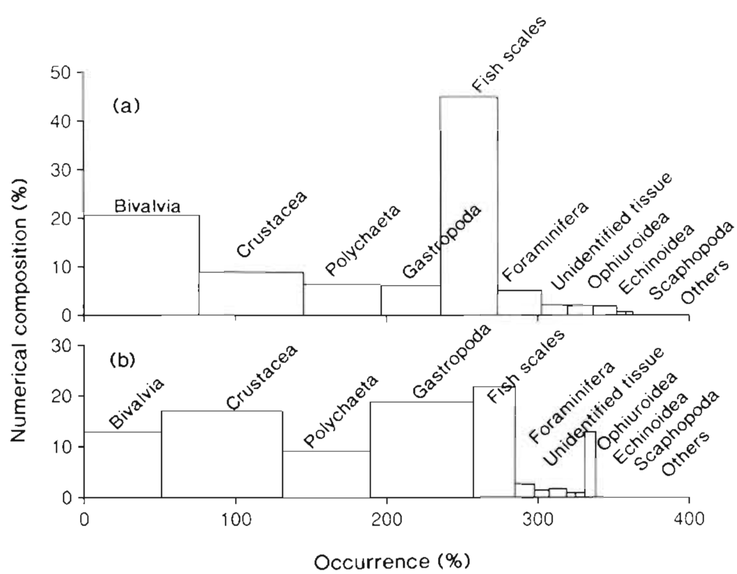

Fig. 7 *Penaeus merguiensis*. Relative importance of food items in (a) schooling (n = 98, collected from Site 3, SE Gulf of Carpentaria) and (b) non-schooling prawns (n = 100, collected from Site 2, SE Gulf of Carpentaria)

feed as the tide rises. Prawns caught at night when the tide recedes have full foreguts but their foreguts are only half full if they are caught on an ebbing tide during the day. An hour before low tide their foreguts were nearly empty, which suggests that feeding stopped around mid-ebb tide. The juvenile prawns do not appear to feed as often during the day as at night. Staples & Vance (1979) found that juvenile *P. merguiensis* feed on a flooding tide during the day as does *P. duorarum* (Sastrakusumah 1971), but their sample was from a single 24 h period and they could not catch the prawns for much of that time. We had difficulty collecting juvenile *P. merguiensis* during the day after about 08:30 h (Fig. 4). Vance & Staples (1992) found that the catchability of *P. merguiensis* decreases with increasing light; the prawns are most catchable at low tide at night.

The most abundant food items found in juvenile and adult *Penaeus merguiensis* were crustaceans, molluscs and polychaetes. These groups are also the main food for many species of *Penaeus*, including *P. duorarum*, *P. setiferus* and *P. aztecus* (Williams 1955), *P. monodon* (Chaitiamvong 1980, Marte 1980), *P. semisulcatus* (Thomas 1980, Wassenberg & Hill 1987), *P. esculentus* (Moriarty & Barclay 1981, Wassenberg & Hill 1987) and *P. latisulcatus* (Moriarty & Barclay 1981). These food items were also reported in the foreguts of 31 species of penaeids, of 6 genera (*Metapenaeus*, *Metapenaeopsis*, *Penaeus*, *Parapenaeus*, *Solenocera*, *Trachypenaeus*), from the Indo-West Pacific (Hall 1962).

The diet of juvenile *Penaeus merguiensis* reported in this study is similar to that reported in other studies of this species, but there are also important differences. Our finding that *P. merguiensis* ate mainly crustaceans, molluscs and polychaetes was similar to the findings of Chaitiamvong (1980), Chong & Sasekumar (1981), Moriarty & Barclay (1981) and Robertson (1988). Foraminifera were numerous in the diet of the juvenile prawns collected during our study and from the studies by Chong & Sasekumar (1981) and Moriarty & Barclay (1981), while Robertson (1988) found that Foraminifera were only a minor dietary item of juvenile *P. merguiensis*. Insect remains were reported by Chong & Sasekumar (1981) and Robertson (1988), and detrital material by Robertson (1988), but we did not find these in the diet of juvenile *P. merguiensis* from the Embley Estuary.

Detritus has been defined by Velimirov et al. (1981) as dead material of unrecognisable origin. With care, most material in penaeid guts can be assigned to its origin, and semi-digested molluscs, crustaceans and polychaetes should not be called detritus merely because they are not intact (Dall et al. 1990).

Harpacticoid copepods and other crustaceans were significantly more numerous in the diet of prawns caught at night than during the day, probably because the availability of prey for juvenile *Penaeus merguiensis* varied with light and tidal level. Our study suggests that the juveniles are less active, or at least feed less during the daytime than at night. They certainly were less catchable during the day. Hindley (1975) found that, in the laboratory, juvenile *P. merguiensis* were more, but not exclusively, active at night. In a laboratory study that simulated tidal effects but excluded a day-night cycle, Vance (1992) found that the prawns were most active around or just after high tide and were least active near low tide. When he imposed a day-night cycle as well as a tidal cycle, the prawns were most active near high tide, at night. Reduced activity during the day may explain some of the diel differences we found in the diets of *P. merguiensis*. Alternatively, the prey may become more active and more vulnerable to predation by prawns on the flooding tide at night. In nearshore waters polychaetes, mysids, various amphipods and other crustaceans emerge from the substratum into the water column at night (Hobson & Chess 1976, 1979). The prey eaten by *P. merguiensis* during our study – harpacticoid copepods, amphipods, cumaceans, tanaids, ostracods and polychaetes – are found near the bottom during the day and move up in the water column at night (Jacoby & Greenwood 1988).

Some of the ontogenetic differences in the diet of *Penaeus merguiensis*, such as the decrease in occurrence of small prey items like foraminiferans, nematodes, copepods and algae in the larger prawns, may reflect changes in the prawns' ability to manipulate small prey. Other differences could be due to availability of food items; for example, algae were virtually absent from the diet of adult prawns collected offshore. Changes in diet with increasing body size have been found in other studies of penaeids – *P. merguiensis* (Hall 1962, Robertson 1988) and *P. esculentus* and *P. semisulcatus* (Wassenberg & Hill 1987).

It has been suggested that the schooling behaviour of *Penaeus merguiensis* may be a response to the presence or absence of a particular food item (Munro 1973). The results of our study do not support this hypothesis. Except for prawns from schools associated with fish, there were no noteworthy differences in diet between schooling and non-schooling prawns.

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