Vol. 228: 165–177, 2002 | MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser | Published March 6

Distribution of juvenile penaeid prawns in mangrove forests in a tropical Australian estuary, with particular reference to *Penaeus merguiensis*

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ABSTRACT: Several species of prawns, including juveniles of *Penaeus merguiensis*, will move into mangrove forests when the forests are inundated by flood tides. However, we do not know how extensively the prawns use the forests or whether some parts of the forests are more valuable to the prawns than others. We assessed the distribution of juvenile prawns in 3 different mangrove communities in intertidal forests adjacent to a small creek and a river in northern Australia between December 1993 and February 1995. The 3 mangrove communities were dominated, respectively, by the structurally complex *Rhizophora stylosa*, and the more open *Ceriops tagal* and *Avicennia marina*. We used stake nets (100 m long, 2 mm mesh) to sample discrete areas of the mangrove forests, and fyke nets (2 mm mesh) to sample prawns moving through the forests. The area of each stake net site ranged from 430 to 650 m^2 and the distance of the midpoint of each site inland from the creek or river mangrove fringe ranged from 13 to 225 m. A large size range of juvenile *P. merguiensis* (2 to 21 mm carapace length, CL) was caught in the mangroves and prawns were caught as far as 200 m into the forests. In the creek forest, there was no clear relationship between mangrove community type and prawn catches. The highest densities of *P. merguiensis* were recorded in the creek and were 28.1 and 27.6 prawns 100 m^{-2} in *Rhizophora* sp. and *Ceriops* sp. forest respectively. The highest mean catches were taken 59 m from the creek mangrove fringe. In contrast to the creek, in the river mangrove forest, there was a clear pattern of catches: the number of *P. merguiensis* caught decreased with distance into the mangroves and at shallower water depths. We have hypothesised that the distribution of juvenile *P. merguiensis* inside the mangroves depends largely on the local topography and pattern of water currents within each forest. Large numbers of unidentified *Metapenaeus* spp. and smaller numbers of *M. ensis* and *P. monodon* were also recorded from the samples inside the mangrove forests.

KEY WORDS: Penaeid · Juvenile · Mangroves · Stake net · Distribution · Intertidal

INTRODUCTION

The banana prawn, *Penaeus merguiensis*, is one of several species of commercially important penaeid prawns throughout the world whose life-cycle is closely tied to mangrove ecosystems. It has long been known that the juvenile stage of *P. merguiensis* is associated with mangroves in estuaries in many countries of the Indo-West Pacific (e.g. Australia: Robertson & Duke 1987, Staples & Vance 1979, Staples et al. 1985; Malaysia, Chong et al. 1990; India: Mohan et al. 1995; Philippines: Primavera 1998). Several studies have correlated commercial catches of penaeid prawns with the distribution of mangroves (see review by Baran & Hambrey 1998) but a causal link has not been clearly demonstrated (Robertson & Blaber 1992).

Sampling at the edges of mangrove forests with set nets (Robertson 1988) and with beam trawls (Vance & Staples 1992) has shown that juvenile *Penaeus merguiensis* move into the mangroves when the forests are inundated around high tide. The prawns leave the

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forests as the water recedes towards low tide. By sampling inside mangrove forests with stake nets, Vance et al. (1996) in Australia and Rönnbäck et al. (1999) in the Philippines showed that juvenile *P. merguiensis* moved substantial distances into the mangroves on flood tides. In Australia, juvenile prawns were caught at least 43 m into the mangroves and in the Philippines, they were caught at least 55 m into the mangroves and in 3 different mangrove communities. However, despite this species' importance to commercial and artisanal fisheries, and the continuing threats to mangrove forests from development, very little is known about how juvenile *P. merguiensis* and other mobile marine animals use the mangrove forests. We do not know why they enter the forests — whether for food or protection from predation — and we do not know how much of the forest they occupy and what determines their distribution within the forests.

It is becoming increasingly critical to understand the use of mangrove forests by prawns and other marine species. Large areas of mangrove forest have been destroyed in the past and the loss of mangroves in some parts of the world is continuing. However, many countries are now attempting to preserve at least some mangrove habitat and even to re-establish mangrove forests where they have been degraded in the past. When deciding on how much mangrove forest to preserve or which areas to re-vegetate with mangroves, it is vital to know more about the relationships between mangrove forests and the animals that use them. In particular, are some areas of mangrove or mangrove community more important for the survival of commercially important prawns, and for the integrity of the whole ecosystem, than others?

This paper expands on previous research in the Embley River, northern Australia, by Vance et al. (1996). By sampling from a small tributary creek and 2 of the 3 main mangrove communities in this region, they found that juvenile banana prawns moved into the mangroves at high tide and moved further in with increased tide height. There was no apparent preference for a particular mangrove type. In this paper, we compare the distribution patterns of juvenile prawns in mangroves lining the same small creek with mangroves lining the main river, and also compare the patterns of distribution in the creek mangroves over 2 yr. We have also assessed the influence of water depth, distance into the mangrove forests, and hydrology, on the distribution of the prawns within the mangrove forests.

There are 3 main mangrove communities in the Weipa area, including the Embley River (Long et al. 1992), characterised by their dominant species: *Rhizophora stylosa*, *Ceriops tagal* var. *australia* and *Avicennia marina* var. *eucalyptifolia*. Several other minor species also occur in each community. We used stake nets and fyke nets to compare the distribution of prawns in these 3 mangrove communities in the main river and in a small creek, and have focused on the most abundant commercially important penaeid prawn in this region, *Penaeus merguiensis*[1]. As several other species of penaeid prawns are also closely associated with mangrove forests for at least part of their lifecycle (see review by Robertson & Blaber 1992), we have also presented some results for 3 other penaeid species groups — *P. monodon*, *Metapenaeus ensis* and *Metapenaeus* spp. (i.e. *Metapenaeus* that could not be identified to species level).

MATERIALS AND METHODS

Sampling was carried out in the Embley River and in a small side creek, about 14 and 17 km upstream from the mouth of the river respectively (Fig. 1). From 1986 to 1992 this river and creek were sampled regularly by small beam trawls in order to study the population dynamics of juvenile *Penaeus merguiensis* (Vance et al. 1998). It was important to sample both the creek and the river, because previous sampling with beam trawls outside the mangroves had shown that catches were much higher in the creek, and that the size range was quite different in the 2 locations (Vance et al. 1998). The particular sites were chosen because all 3 mangrove communities occurred reasonably close together at these sites.

Stake nets. We used stake nets to completely enclose areas of mangroves, as described by Vance et al. (1996). One stake net, 100 m long × 2 m high, was used to enclose the sites at the creek and river mangrove fringes. The other net, 100 m long × 1 m high, was used to enclose the sites at the *Ceriops* sp. and *Avicennia* sp. sites. The mesh was small enough (2 mm) to catch most *Penaeus merguiensis* from the time they arrive in the estuary as postlarvae (1 to 2 mm carapace length, CL). Galvanised chain (8 mm diameter) was inserted in a hem along the base of each net. A 2 m long mesh pocket with mouth opening of 1.0 × 0.5 m was fitted to one section of each net to concentrate trapped animals; the mesh size of the body and the codend were 2 mm and 1 mm respectively.

At each stake net site a pathway up to 1.5 m wide was cut through the mangroves to allow the net to be set from a small dinghy. Prop-roots and small seedlings were cut off at ground level so that the bottom of the stake net would sit closely on the substrate. Each site

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[1] *Penaeus merguiensis* has recently been renamed *Fenneropenaeus merguiensis* by Pérez Farfante & Kensley (1997). We do not agree with this nomenclature and have retained the old name for this paper

was made as close as possible to a square with sides 25 m, but in order to avoid damaging large trees, the pathways cut were sometimes irregular. Wooden stakes were driven into the substrate along the perimeter of each site about 5 m apart, so that at least 3 m of each stake remained above the ground level.

For all samples, the stake net was set as close as possible to high tide, using a small dinghy (see Vance et al. 1996). The net was first fixed to one of the wooden stakes near the lowest point of the site and then deployed as the dinghy was poled along the perimeter of the site. The floatline was supported by hooks on each wooden stake to keep the top of the net above the water level. The site was completely enclosed by the net and the 2 ends were joined with velcro tape. Once the water had completely drained from the site (i.e. after 3 to 4 h), all animals trapped by the net were collected from the codend and from the net or substrate along the edge of the net. Very rarely was an animal seen lying on the mud in the middle or near the inner edges of the site.

Fyke nets. Some samples were also taken in the mangrove forests with a fyke net — a trap net modified from a design by Crowe (1950). The net was 1 m high and had a leader 7 m long (Fig. 2). Two wings, each 1.5 m long, were connected to the mouth (1.0 × 1.0 m) of the net. From the mouth, a funnel with an end diameter of 100 mm led to the trap section of the net. A detachable codend was fitted to the rear end of the trap section to enable the catch to be removed easily. The leader, wings and body of the net were all made from 2 mm mesh net. This net catches animals that are either actively moving or drifting with currents, giving an indication of the density of animals that would have passed through the site since the net was set. In contrast, stake nets indicate the abundance of animals in the area enclosed by the net at the time it is set.

Stake net sites. Eight stake-net sites were set up in a section of the creek where the 3 main mangrove community types were present in almost monospecific stands (Fig. 1). Four sites were marked out in *Rhizophora* sp. forest and 2 each in *Ceriops* sp. and *Avicennia* sp. forests. In the main river, 6 sites were set up — 2 in each of the main mangrove communities (Fig. 1). In the creek, 3 sites were set up at the creek fringe in the *Rhizophora* sp. mangrove forest such that one side of each site was just outside the mangroves at the creek mangrove border (*Rhizophora* A, *Rhizophora* B and *Rhizophora* C) (Fig. 1). One site (*Rhizophora* D) was set up in *Rhizophora* just near the *Rhizophora*-*Ceriops* border and about halfway across the mangrove forest. Two sites were set up in the *Ceriops* forest (*Ceriops* A and *Ceriops* B), inland from *Rhizophora* A and *Rhizophora* C respectively, and 2 sites were set up in the middle of the *Avicennia* forest (*Avicennia* A and *Avicennia* B). The approximate midpoint of each site inland from the creek mangrove fringe ranged from 13 to 110 m and the area of the sites ranged from 430 to 650 m^2 (Table 1). The *Avicennia* sites were the highest: from 1.40 to 1.55 m above the substrate height at the creek mangrove fringe. The largest height variation was at the *Rhizophora* sites at the creek mangrove fringe, for example from 0 to 1.22 m above the fringe substrate level at *Rhizophora* C (Table 1).

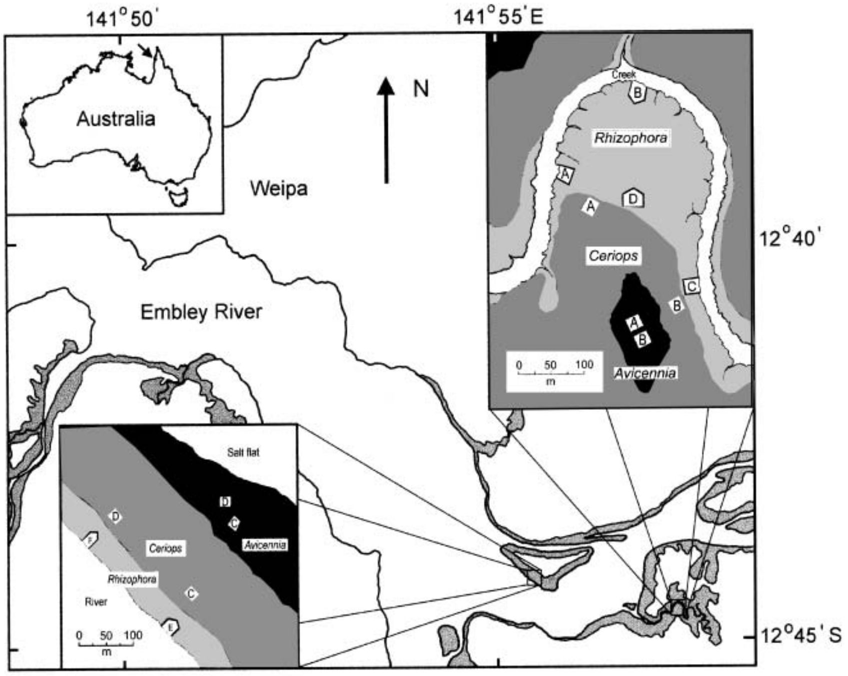

Fig. 1. Stake net sampling sites (approx. to scale) and mangrove communities in Embley River and small side creek, Gulf of Carpentaria, Australia. Sites identified by letters as in section 'Stake net sites'

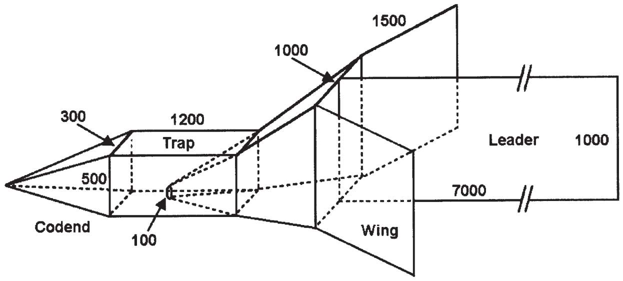

Fig. 2. Diagram of fyke net used to sample prawns in creek mangrove forests of the Embley River. Measurements in mm

Table 1. Area, distance from creek or river mangrove fringe and substrate heights relative to the substrate level at the mangrove fringe, for each stake-net site

Site	Area (m^2)	Midpoint (min. – max.)			
		Distance from mangrove fringe (m)		Substrate height above mangrove fringe (m)	
Creek					
Rhizophora A	640	13	(0–26)	0.43	(0.0–0.85)
Rhizophora B	640	17	(0–34)	0.41	(0.0–0.82)
Rhizophora C	525	15	(0–30)	0.61	(0.0–1.22)
Rhizophora D	650	110	(93–127)	1.04	(0.95–1.12)
Ceriops A	580	59	(43–75)	0.96	(0.91–1.01)
Ceriops B	625	38	(26–50)	1.28	(1.22–1.34)
Avicennia A	430	102	(89–115)	1.43	(1.40–1.45)
Avicennia B	515	102	(90–114)	1.48	(1.40–1.55)
River					
Rhizophora E	525	14	(0–28)	0.40	(0.0–0.80)
Rhizophora F	484	15	(0–30)	0.36	(0.0–0.71)
Ceriops C	572	91	(79–102)	0.90	(0.85–0.95)
Ceriops D	545	77	(65–88)	0.80	(0.75–0.85)
Avicennia C	441	204	(192–215)	1.02	(0.98–1.05)
Avicennia D	457	225	(208–242)	0.93	(0.90–0.95)

In the river, 2 sites (*Rhizophora* E and *Rhizophora* F) were set up in *Rhizophora* at the river mangrove fringe in a similar configuration to those at the creek mangrove fringe (Fig. 1). In the *Ceriops* sp. forest, 2 sites (*Ceriops* C and *Ceriops* D) were set up inland from *Rhizophora* E and *Rhizophora* F respectively, and 2 sites were set up in the middle of the *Avicennia* forest (*Avicennia* C and *Avicennia* D) inland from *Ceriops* C. The midpoint of each site inland from the river mangrove fringe ranged from 14 to 225 m and the area of each site ranged from 441 to 572 m^2 (Table 1). The *Avicennia* sp. sites were again the highest, from 0.90 to 1.05 m above the substrate height at the river mangrove fringe.

The *Rhizophora* sp. forest, with its dense prop roots, was much more structurally complex than the more open *Ceriops* sp. or *Avicennia* sp. forests. The mangrove surface area up to 1 m above the substrate in the *Rhizophora* community was about 250 times the surface area of mangrove in the *Ceriops* community and about 550 times that in the *Avicennia* community (Conacher et al. 1996).

Stake nets were set on 4 spring tides at times of the year when juvenile *Penaeus merguiensis* are usually abundant in the estuary (Vance et al. 1998). At these times, mean sea levels and mangrove forest inundation are at their highest for the year. In the creek, samples were taken at 6 sites in December 1993 (all creek sites except *Rhizophora* C and *Rhizophora* D) and at all 8 sites in 2 separate periods between December 1994 and February 1995. In January 1994, samples were taken at 6 sites in the main river. For every sampling period, each site was sampled twice with 1 sample taken each day from each of 2 sites. No site was sampled on consecutive days, in order to minimise any possible effect of site disturbance on subsequent catches at each site, and so that each site was sampled on a range of maximum tide heights, as the tidal amplitude varied during the tidal cycle. Stake nets were always set at high tide during daylight hours, but the nets were sometimes cleared at night.

Fyke net sites. *Comparison of Ceriops* sp. *sites:* When early results from the stake nets showed large variations in catch between the 2 *Ceriops* sp. sites in the creek, we decided to test these differences by using fyke nets to estimate the relative numbers of prawns moving through the 2 sites. On 4 occasions we set fyke nets at *Ceriops* A and *Ceriops* B (Fig. 1), orientated so that prawns would be caught in the nets throughout the flood tides. The nets were set before the water level reached each site and were collected at high tide.

Prawn entry into mangroves: To estimate where prawns first entered the mangrove forest, we set fyke nets without leaders at 3 locations at the creek mangrove fringe. One net was set at the edge of the broad *Rhizophora* sp. forest near the edge of *Rhizophora* A, while the other 2 nets were set further downstream at the edge of the broad *Ceriops* sp. forest (see Fig. 5). There is a very narrow fringe (~1 tree width) of *Rhizophora* between the creek and the *Ceriops* forest in this area. The substrate was about 0.5 m higher at the *Ceriops* sites than the *Rhizophora* site. The nets were set with their mouths facing directly towards the creek edge. As they were set without leaders, they would only catch prawns that were moving into the forest directly from the creek. The nets were set before the water level reached each site and were collected at high tide.

Extent of mangrove use: We set fyke nets with leaders along part of a landward transect through the creek mangrove forest (see Fig. 5) in order to gather more data on how far the juvenile prawns actually moved into the mangroves. Sites were established at 200, 300, 400, 500 and 600 m along the transect from the creek edge in *Ceriops* sp. and *Avicennia* sp. forest. We could not set nets between 0 and 200 m in the *Rhizophora* forest because the prop roots were too dense. Four flood tides were sampled at the 200 and 400 m sites; 2 flood tides were sampled at the 300, 500 and 600 m sites; 2 ebb tides were sampled at the 200, 300, 400 and 500 m sites, but not at the 600 m site because of a logistical problem.

Biological and physical measurements. Prawns were identified to genus level, and those of the genus *Penaeus* to species level. They were measured to the nearest 1.0 mm CL with an ocular micrometer fitted to a binocular microscope. Water temperature and salinity were recorded near high tide when each stake net was set. Water depth was recorded just after each net was set: 4 random measurements were made with a graduated rod just inside each corner of the net enclosures and the mean water depth was calculated by averaging all 16 measurements. Hourly tide heights were recorded by an automatic tide gauge near the mouth of the Embley River. We measured water current speed and direction at several sites in the mangrove forest, on several flood tides, by visual observation. At each site, we released a small wooden float into the water, and using a hand-held compass, noted its direction of movement for 1 min. Current speed was estimated by measuring the distance the float moved in 1 min with a graduated rod. These measurements were made at least every 1/2 h at each site, from the time that water first reached the site until there was no discernible current movement at high tide.

Statistical analyses. We analysed the creek and river data separately. Stake net catches for each prawn species at each site were converted to densities, as the number of prawns per 100 m^2. We investigated differences in catches between sites with ANOVA, using the GLM procedure of the SAS statistical package, and tested for differences between individual sites with the REGWQ option (SAS Institute 1990a). REGWQ performs the Ryan-Einot-Gabriel-Welsch multiple range test on all main effect means. For the creek sites, the independent variables included in the analysis were sampling period, site and the interaction between period and site. For the river data, site was the only variable tested in the ANOVA. We also used ANOVA to compare catches between mangrove communities at the creek and river. Independent variables for the creek data were period, mangrove community and the interaction term. We also tested for significant relationships between catches, water depths and distances into the mangroves with correlation analyses (SAS Institute 1990b).

RESULTS

A total of 5257 penaeid prawns, made up of 4 species or species groups, were caught in the stake nets over the 4 sampling periods. The 2 largest groups were *Metapenaeus* spp. (2838 prawns) — probably mostly *M. moyebi*, but possibly also some very small *M. ensis* — and *Penaeus merguiensis* (2062 prawns). We also caught 315 *M. ensis* and 42 *P. monodon*. Water temperatures were high for all sampling periods, ranging from 28.8°C in January 1995 to 34.6°C in January 1994. Salinities were more variable and ranged from 23.2 in February 1995 to 38.7 in December 1993.

Penaeus merguiensis

Creek

Stake net. The pattern of catch variation of *Penaeus merguiensis* across creek sites was quite consistent over the 3 sampling periods, with no significant differences in catches between the sampling periods. However, catches differed significantly between sites when all sampling periods were combined (ANOVA, $F_{7,22} = 9.11$, $p = 0.0001$) (Fig. 3). There was no significant interaction between site and period. Mean catches at *Ceriops* A were highest in all sampling periods although not significantly higher than at *Rhizophora* B. Catches at *Ceriops* B and the 2 *Avicennia* sp. sites were usually lower than the other sites. Catches differed significantly between some mangrove communities ($F_{2,35} = 4.55$, $p = 0.02$). Mean catches were significantly lower in the *Avicennia* sp. community than in the other communities, but did not differ significantly between the *Rhizophora* sp. and *Ceriops* sp. mangroves. Catches at sites in the same mangrove community varied widely. Catches at *Ceriops* A were always significantly higher than *Ceriops* B, although *Ceriops* B was closer to the creek mangrove fringe (Figs. 3 & 4). Mean catches at *Rhizophora* B were always highest of the sites at the creek mangrove fringe, but were not significantly higher than those at the other creek fringe sites (*Rhizophora* A and *Rhizophora* C). Catches tended to decline with distance into the mangroves from the creek mangrove fringe, but there was no significant relationship ($r = -0.33$, $p = 0.07$, $n = 32$). In general, catches were lower further into the mangrove forest, but the highest catches were taken over 50 m into the mangrove forest (*Ceriops* A) as well as at the creek mangrove fringe (*Rhizophora* B). There was also large variation in catches taken at only short distances into the mangroves (e.g. *Rhizophora* A and *Rhizophora* B). Catches were not significantly correlated with water depth at the time that the stake nets were set ($r = -0.06$, $p = 0.76$, $n = 32$). There was no consistent relationship between the size of stake net catches and the maximum tide height for samples taken at each site.

Fyke nets at Ceriops A and Ceriops B. Fyke nets were set at *Ceriops* A and *Ceriops* B sites on flood tides on 4 consecutive days in January 1995. On all occasions the catch of *Penaeus merguiensis* at *Ceriops* A was substantially higher than at *Ceriops* B. Overall,

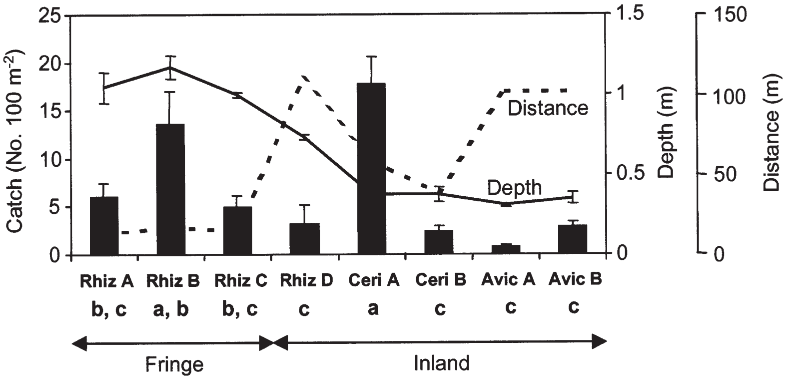

Fig. 3. *Penaeus merguiensis*. Mean stake net catches (+1 SE) at each creek mangrove site over 3 sampling periods. Each histogram is a mean of 6 samples, except Rhiz C and Rhiz D, means of 4 samples. (——), mean water depth when nets set; (- - -) approx. mid-point of each site from nearest creek mangrove fringe. Catches at sites with same lower case letter below site identifiers are not significantly different from each other. Rhiz = *Rhizophora*; Ceri = *Ceriops*; Avic = *Avicennia*

the mean catch per flood tide (±1 SE) at *Ceriops* A (41 prawns per flood tide ± 6.4) was 3 times higher than the catch at *Ceriops* B (14 prawns per flood tide ± 2.5) ($F_{1,6}$ = 15.62, p = 0.01).

Prawn entry into mangroves. When we set fyke nets without leaders at the creek mangrove fringe we found substantial differences between nets set simultaneously at different locations. Prawn catches were much higher in the net set at the edge of the *Rhizophora* sp. forest (16 prawns per flood tide) than in either of the nets set at the edge of the *Ceriops* sp. forest (1 prawn per flood tide) (Fig. 5). The substrate at the edge of the *Rhizophora* sp. forest was much lower than the *Ceriops* sp. forest so water entered the *Rhizophora* sp. forest about 3 h earlier than it entered the *Ceriops* sp. forest on flood tides during this sampling.

Catches along a transect. When fyke nets were set simultaneously along the transect bisecting the mangrove forest, we caught some *Penaeus merguiensis* in all but 1 of the samples (Fig. 5). The largest catches were in the *Ceriops* sp. forest, near the border between *Rhizophora* and *Ceriops* mangroves, about 200 m along the transect from the creek mangrove fringe. However, we did not sample closer to the mangrove fringe, as the dense prop roots in the *Rhizophora* sp. forest along the transect did not allow us to set nets there. Catches further inland along the transect were always less than at the 200 m site, on both flood and ebb tides, and were zero at the inland fringe of the mangroves on the flood tide. Maximum water depth at the inland fringe site was less than 20 cm. No sample was taken on the ebb tide at this site. Where samples were taken on both flood and ebb tides, catches were always higher on the corresponding ebb tides. The furthest into the mangrove forest that we caught prawns, measuring in a direct line from the nearest creek mangrove fringe, was ~200 m, at the 500 m transect site.

Main river

The pattern of catch variation in stake nets set at the 6 sites in the main river differed from that seen at the creek sites. The highest mean catches were at the 2 *Rhizophora* sites at the river mangrove fringe. Fewer prawns were caught in the landward *Ceriops* sp. forest while only 1 prawn was caught in 4 stake nets at the *Avicennia* sites (Fig. 6). These differences between sites were not significant ($F_{5,6}$ = 2.26, p = 0.17). However, when sites were combined over mangrove communities (i.e.

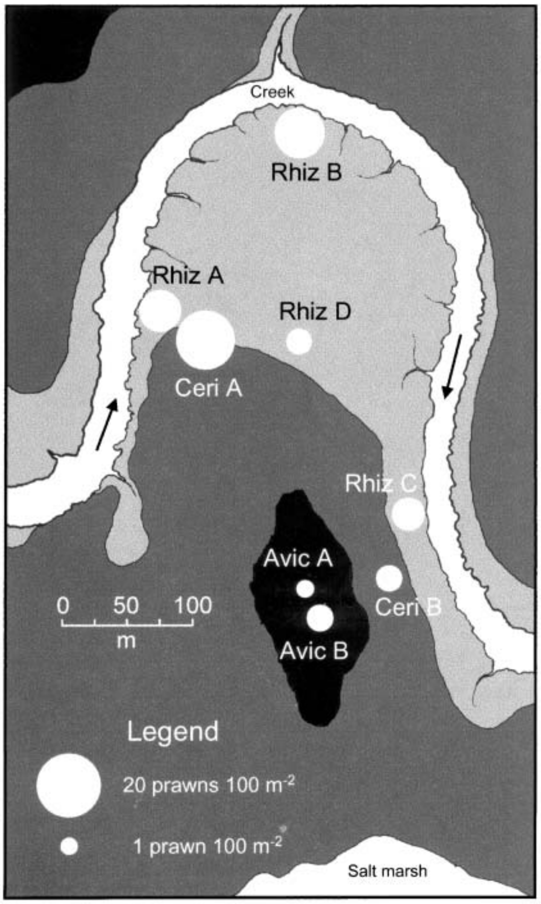

Fig. 4. *Penaeus merguiensis*. Mean stake net catches at each creek mangrove site for 2 sampling sessions combined (December/January 1994/95 and January/February 1995). Each bubble mean of 4 samples. Rhiz = *Rhizophora*; Ceri = *Ceriops*; Avic = *Avicennia*

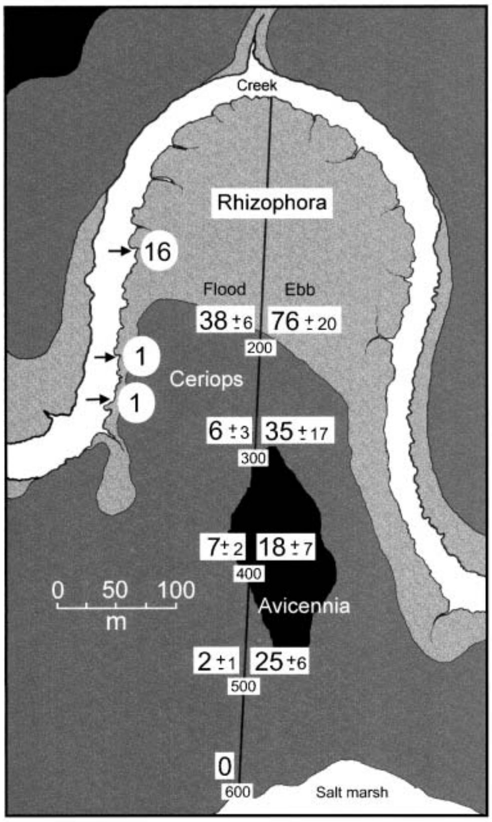

Fig. 5. *Penaeus merguiensis*. Fyke net catches: numbers inside circles, total catches at 3 creek mangrove fringe sites for 1 flood tide— arrows indicate point of entry of prawns into mangroves; numbers inside rectangles, mean catches per flood tide (±1SE) at sites along transect through creek mangrove forest. Numbers to left of transect line, catches taken on flood tides; numbers on right, catches on ebb tides. Number below each pair of catches, distance (m) along transect line from creek mangrove fringe

sites were used as replicates for mangrove communities), catches differed significantly between mangrove communities ($F_{2,9}$ = 4.97, p = 0.04). They were significantly higher in the *Rhizophora* sp. community than in the *Avicennia* sp. community, but catches in the *Ceriops* sp. community did not differ significantly from those in the other 2 communities. Catches of *Penaeus merguiensis* decreased significantly as distance into the mangrove forest increased (r = –0.69, p = 0.01, n = 12) and increased significantly with water depth (r = 0.61, p = 0.03, n = 12).

Size

We caught a large size range of juvenile *Penaeus merguiensis* at both river and creek stake-net sites; however, the overall length-frequency distributions at the river and creek were quite different (Fig. 7). The modal length-frequency was much lower (5 mm CL) at the creek *Rhizophora* and *Ceriops* sites than at the river sites (17 mm CL). There were more very small prawns (2 to 3 mm CL) caught at the creek *Rhizophora* sites than at the creek *Ceriops* or *Avicennia* sites.

***Metapenaeus* spp.**

Most of the *Metapenaeus* species group were caught in *Rhizophora* sites at the creek or river mangrove fringe (Fig. 8). The mean density at these sites over all samples was 12.4 prawns 100 m^{-2}, which was about 23 times the mean density at all sites inland from the mangrove fringe. In contrast to *Penaeus merguiensis*, catches of *Metapenaeus* spp. at *Ceriops* A were very low (0.8 prawns 100 m^{-2}). Catches were also very variable between some apparently similar sites, e.g. *Rhizophora* E and F (Fig. 8). The size of prawns caught ranged from 2 to 11 mm CL and, as for *P. merguiensis*, more smaller prawns were caught at the creek sites than the river sites.

Metapenaeus ensis

Although catches of *Metapenaeus ensis* were relatively low, the pattern of catches was distinctly different to the patterns for the other species groups (Fig. 9). The mean densities of prawns at the inland (0.44 prawns 100 m^{-2}) and mangrove fringe sites (0.41 prawns 100 m^{-2}) were virtually the same when all creek and river samples were combined. However, in the river, catches of *M. ensis* in the *Avicennia* forest, over 200 m into the mangroves, were much higher than in the *Rhizophora* forest at the river fringe

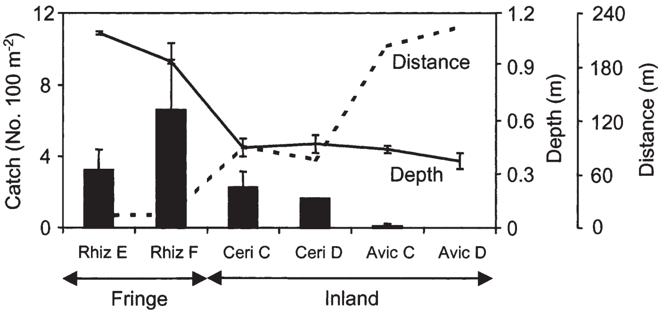

Fig. 6. *Penaeus merguiensis*. Mean stake net catches (+1 SE) at each river mangrove site for 1 sampling period (January 1994). Each histogram, mean of 2 samples. (——), mean water depth when nets set; (- - -), mean distance of each site from nearest river mangrove fringe. Rhiz = *Rhizophora*; Ceri = *Ceriops*; Avic = *Avicennia*

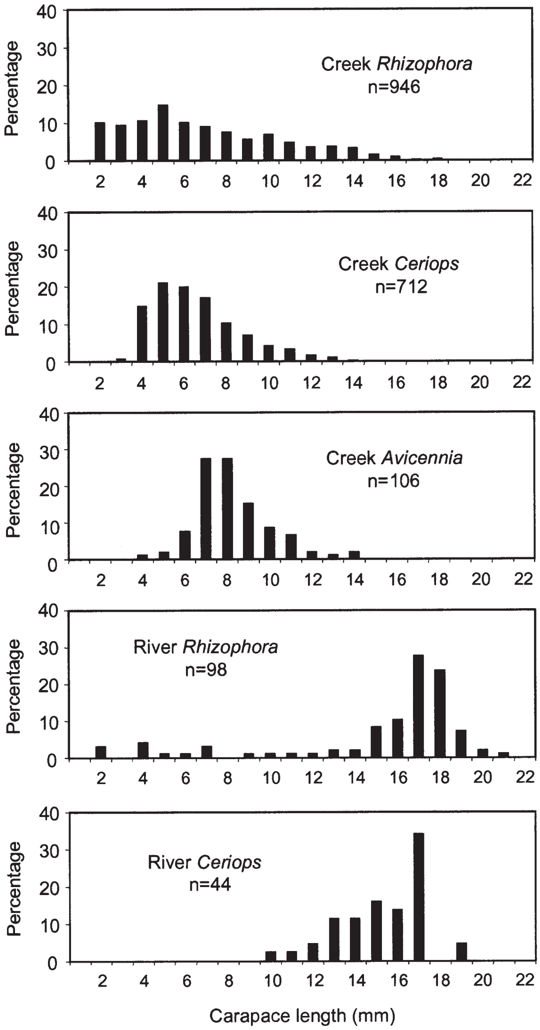

Fig. 7. *Penaeus merguiensis.* Length-frequency distributions of all prawns caught in stake nets at river and creek mangrove communities

(Fig. 9). Catches were also higher at the river sites than at the creek sites. The prawns ranged in size from 2 to 15 mm CL; the larger ones were caught at the river sites. As for *Penaeus merguiensis*, more smaller prawns were caught at the creek fringe than at the inland sites.

Penaeus monodon

This species was mostly caught at the creek and river fringe sites (Fig. 10). Of a total of 42 prawns, only 4 were caught away from the *Rhizophora* fringe. As for the *Metapenaeus* spp. group, catches were quite variable between similar sites. The size of prawns caught ranged from 5 to 24 mm CL.

Water currents

There were marked differences in the patterns of water movement through the mangroves at the river and creek sites. At all river sites the pattern of water flow was almost identical and consistent throughout the flood tide: water entered all sites almost perpendicularly to the direction of the river edge and maintained that direction, or a very slight upstream direction, throughout the flood tide. However, in the creek mangrove forest, the pattern of water flow was neither as simple nor as consistent between sites or throughout the flood tide (Fig. 11). At some sites, a mostly constant direction was maintained throughout the flood tide, but at several sites flow direction changed by at least 90° during the tide. Water current speeds observed in the river and creek mangroves were quite variable throughout the flood tide and between different locations. They ranged from 0 to 6 m min^{-1}.

DISCUSSION

Despite the importance of mangrove forests to many commercial marine species, little is known about how, or to what extent they are used by mobile marine species such as prawns and fish. The distribution of penaeid prawns within mangrove habitat, based on sampling different sites inland from the fringing mangroves, had previously been studied only by Rönnbäck et al. (1999) and Vance et al. (1996).

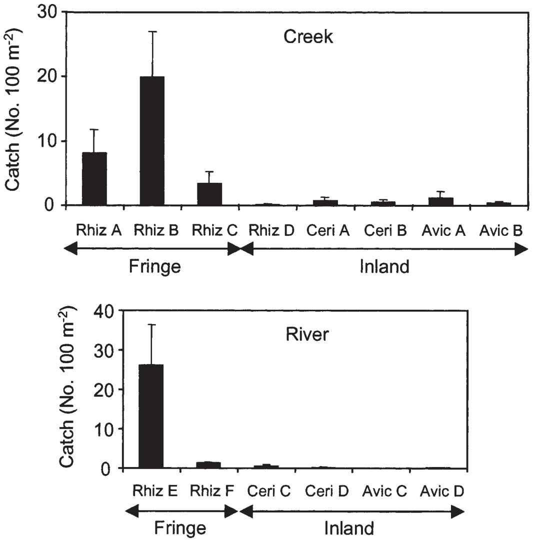

Fig. 8. *Metapenaeus* spp. Mean (+1 SE) stake net catches at each creek and river site. Creek sites: each histogram mean of 6 samples, except for Rhiz C and Rhiz D, means of 4 samples. River sites: each histogram mean of 2 samples. Note changes in scale. Rhiz = *Rhizophora*; Ceri = *Ceriops*; Avic = *Avicennia*

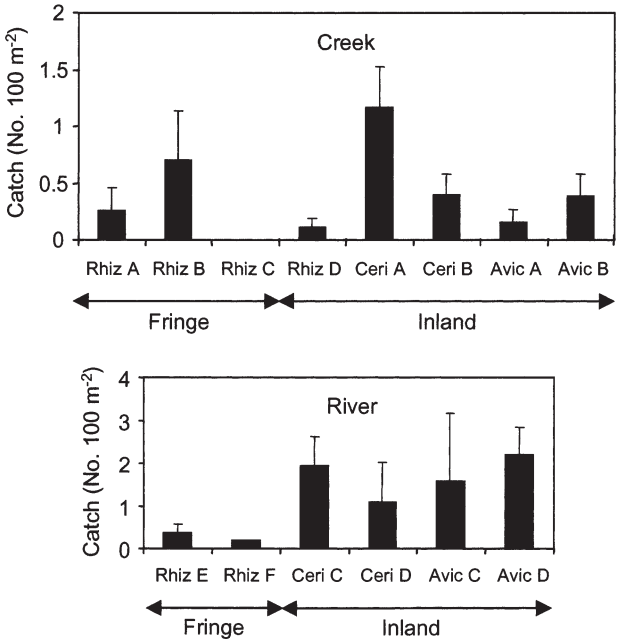

Fig. 9. *Metapenaeus ensis*. Mean (+1 SE) stake net catches at each creek and river site. Creek sites: each histogram mean of 6 samples, except for Rhiz C and Rhiz D, means of 4 samples. River sites: each histogram mean of 2 samples. Note changes in scale. Rhiz = *Rhizophora*; Ceri = *Ceriops*; Avic = *Avicennia*

Penaeus merguiensis

River-creek distribution

In our study we found clear differences between the stake net catches of *Penaeus merguiensis* from river and creek sites. Overall, catches from the creek were higher than from the river, but the prawns from the creek were smaller. This agrees with previous findings using beam trawls at low tide (Vance et al. 1998), that *P. merguiensis* in the waters of the creeks were smaller than those in the rivers. It was suggested that this difference was due to the larger prawns gradually migrating from the creek to the main river.

The pattern of distribution of stake-net catches between creek and river sites was also quite different. In the river, the highest catches were taken in the *Rhizophora* sp. forest at the river mangrove fringe, and catches decreased with increased distance into the forest and with decreased water depth. In contrast, the highest catches in the creek were taken in both *Rhizophora* sp. and *Ceriops* sp. forest, at the creek mangrove fringe and further inland. There was no strong relationship between stake-net catches in the creek and distance from the mangrove fringe or water depth.

Factors determining distribution in mangroves

Mangrove type. Although we found some significant differences between catches in different mangrove communities, these results were not consistent between the river and creek sites. Moreover, the results are confounded by corresponding differences in substrate elevation and distance of the mangrove communities from the mangrove fringe. Our results suggest that the type of mangrove community or mangrove structure is unlikely to have determined the distribution of *Penaeus merguiensis* at the creek mangrove sites. For example, catches at *Ceriops* A did not differ significantly from those at *Rhizophora* B over each sampling period. Far larger differences in catches were seen between sites within the same mangrove community. Catches at *Rhizophora* B were consistently higher than at *Rhizophora* A or C, although all these sites were at the mangrove fringe. The highest catches were consistently made at one of the sites in the *Ceriops* sp. community (*Ceriops* A), which was of intermediate structural complexity compared to the other communities and located 59 m from the mangrove fringe. Previous sampling at 3 of these sites (*Rhizophora* A, *Rhizophora* B and *Ceriops* A) by Vance et al. (1996) also suggested that neither mangrove community type nor mangrove structure determined the distribution of juvenile *Penaeus merguiensis*. (Note that *Rhizophora* B in this paper is the site referred to as *Rhizophora* C in Vance et al. 1996). In contrast, in the Philippines, higher

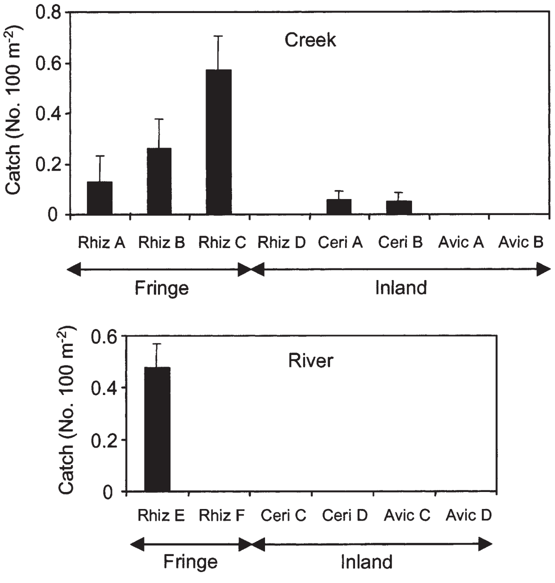

Fig. 10. *Penaeus monodon*. Mean (+1 SE) stake net catches at each creek and river site. Creek sites: each histogram mean of 6 samples, except for Rhiz C and Rhiz D, means of 4 samples. River sites: each histogram mean of 2 samples. Note changes in scale. Rhiz = *Rhizophora*; Ceri = *Ceriops*; Avic = *Avicennia*

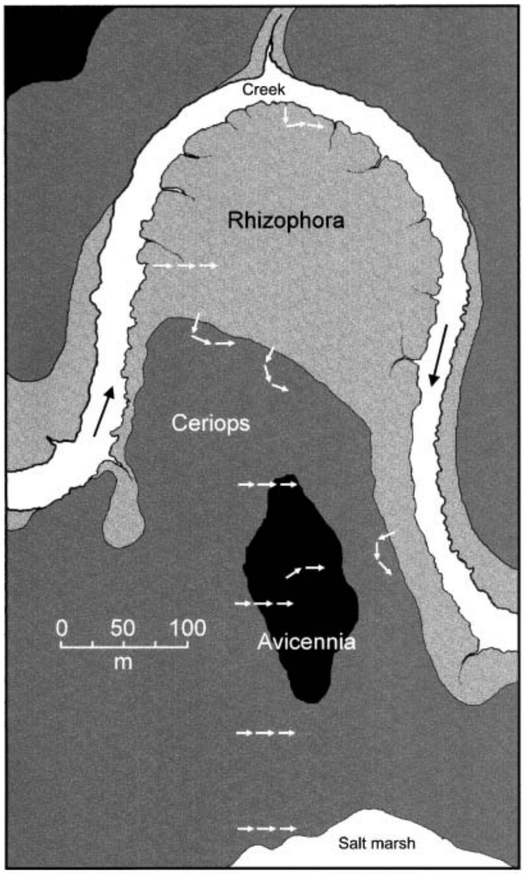

Fig. 11. Direction of water currents in creek mangrove forest during flood tide. Each arrow indicates approximate direction of current for ~1/3 of the flood tide at each location, measured over 2 flood tides

mean densities of *P. merguiensis* were found at a structurally more complex *Rhizophora* site than at less complex *Avicennia* and *Rhizophora* sites, although it is not clear that the differences were statistically significant (Rönnbäck et al. 1999). Laboratory experiments by Primavera & Lebata (1995) suggested that juvenile *Penaeus merguiensis* are not strongly attracted to submerged structures. However, we have occasionally seen small *P. merguiensis* clinging to mangroves in the inundated mangrove forests. Their behavioural response to structure needs to be further tested, particularly any interactions with tidal cycles. The apparent differences in distribution of prawns in the Philippines and Australia also highlight the need for further research in a range of locations.

Water depth/distance from mangrove fringe. Catches at the river sites were significantly correlated with distance from the mangrove fringe and with water depth. Highest catches were closest to the mangrove fringe and at greatest water depths. However, this pattern was not as clearly repeated at the creek sites. It is likely that neither depth nor distance are solely responsible for the distribution of *Penaeus merguiensis* in the mangroves.

Topography/water currents. Water currents in the river mangroves followed a consistent pattern throughout the flood tide and at each site in the mangroves. This uniform pattern of water currents within the mangroves probably contributed to the reasonably clear distribution pattern of *Penaeus merguiensis* in the river mangroves; catches decreased with increased distance into the forest. However, water currents in the creek mangroves were more variable throughout the flood tide and in their direction at different sites, presumably because of the topography of that section of the creek. This may have led to the quite different pattern of catches seen in the creek mangrove communities.

Local topography seems to affect the entry of prawns into the mangrove forest. On one occasion we saw that most of the *Penaeus merguiensis* entered the creek mangroves through the fringing *Rhizophora* sp. rather than through the fringing *Ceriops* sp. forest (Fig. 5). This is presumably because the *Rhizophora* sp. forest is at a much lower elevation than the *Ceriops* sp. forest, and is inundated much earlier. It is possible that the distribution of *Penaeus merguiensis* in the creek mangroves is determined to a large extent by a combination of the local topography or substrate elevation, the local water currents in the forests, and the activity patterns of the prawns themselves. Our sampling strategy was not designed to test this hypothesis, nor were our measurements of currents in the mangroves rigorous enough to give more than a general picture of current movements. Further sampling is clearly needed to more accurately determine the factors affecting prawn distribution in mangroves, including all the possible factors mentioned above.

Prawn behaviour

Even if the distribution of prawns in the mangroves is not determined by the mangrove type, there seems to be a change in behaviour or distribution of *Penaeus merguiensis* while inside the mangroves. Outside the mangroves, prawns are mostly concentrated close to the water's edge in water less than 0.5 m deep, in a band sometimes only 5 to 10 m wide (Staples & Vance 1979, and pers. obs.). Inside the mangroves, although there are clearly some concentrations of *P. merguiensis*, the prawns are much more spread out, over a wide area and at 0.2 to 1.3 m mean water depth. If the prawns are only moving passively with the water currents in the mangroves, there would be much higher concentrations of prawns at the inner reaches of the forest. This was clearly not the case. It is not clear whether this change in behaviour is due to the presence of the mangroves themselves or whether it is related to changes in other physical parameters. For example, turbidity values are probably lower inside the mangroves, in association with the slower currents there.

Extent of mangrove use

The results from our fyke nets set along the transect (Fig. 5) showed that some juvenile *Penaeus merguiensis* moved at least 200 m into the creek mangrove forest. No prawns were caught at the inner edge of the mangrove forest, but prawns may have been present nonetheless. The water at the inner edge was less than 20 cm deep, which is too shallow for the fyke nets to fish effectively. In combination with the stake net results, it is clear that prawns occupy a large proportion of the available creek mangrove forest at some stage of the tidal inundation. Catches of *P. merguiensis* in the fyke nets set on the transect during the ebb tide were consistently much higher than flood-tide catches, which could be related to differences between water currents on the ebb tide and the flood tide. Ebb-tide currents in mangrove creeks can have twice the velocity of flood-tide currents and a different direction relative to the creek bank (Wolanski et al. 1980 and Mazda et al. 1995). These results reinforce our earlier suggestion that the movements of juvenile prawns in the mangrove forests are probably substantially influenced by local water currents.

Effect of season

The results from this sampling differ from those reported by Vance et al. (1996) for a subset of the creek sites: they found that mean stake-net catches of *Penaeus merguiensis* at *Rhizophora* A and *Ceriops* A sites were similar. Although Vance et al. (1996) took only 2 samples at each site and therefore their results are less reliable than ours, we think that the differences in distribution of the catches are probably due to differences in the patterns of inundation of the mangroves. Mean sea level in the Embley River area varies in a regular seasonal pattern — the highest sea levels and therefore the maximum inundation of the mangroves occurs in January and February each year. The samples in Vance et al. (1996) were taken in November, when mean sea levels were lower than during this study and the *Ceriops* sp. forest was inundated for a shorter time on spring high tides. Therefore, the prawns would have had less time to move into the mangroves and probably more prawns remained close to the creek mangrove fringe, resulting in the larger catches at *Rhizophora* A and lower catches at *Ceriops* A reported by Vance et al. (1996).

Other prawn species

Three other penaeid species or species groups were caught in our stake nets. These prawns are commercially important either in Australia or parts of the Indo-West Pacific (Grey et al. 1983, Dall et al. 1990). The *Metapenaeus* spp. group consisted of prawns that were too small to identify to species level, as well as many *Metapenaeus moyebi*, a commercially important species in Asian countries. Although catches of *Penaeus monodon* and *M. ensis* were lower than the other species, there was some consistency in the patterns of catch distributions between sampling periods. Nearly all the *P. monodon* and *Metapenaeus* spp. were caught in mangrove fringe sites in either the creek or river. Relatively few prawns were caught at the inland sites. In contrast, *M. ensis* moved further into the mangrove forests and catches of *M. ensis* in the creek were more similar to *P. merguiensis*; catches at *Ceriops* A were often as high or higher than catches at the creek mangrove fringe. At the river sites, 92% of *M. ensis* were caught at the 4 inland sites and the highest catches were at the 2 *Avicennia* sites, about 200 m into the forest. It is clear from these distributions that not all the prawn species encountered in our sampling use the mangrove forests in exactly the same way.

Predation in nets

Fish, as well as prawns, were always caught in the stake nets and some of the fish had penaeid prawns in their guts. Although the fish may have eaten them before being caught, the fish possibly ate some prawns when water levels inside the stake nets dropped, and the animals were concentrated at the lowest areas of each site. Our catches of prawns might, therefore, be underestimates of the real abundance of prawns at each site, but it is impossible to accurately allow for this in our estimates of prawn density. No predatory birds were seen within the stake nets.

Other intertidal habitats

In coastal habitat bordering the Gulf of Mexico in the USA, several species of penaeid prawns are known to move into intertidal salt marshes when the marshes are inundated by tidal waters. Zimmerman et al. (1984) surveyed the distribution of *Penaeus aztecus* and found higher densities of prawns in the inner (landward) zone of the salt-marsh habitat. Minello & Webb (1997) found lower densities of *P. aztecus* and *P. setiferus* in artificially created marshes than in natural marshes but suggested that the differences might be because the artificial marshes were on higher ground and therefore were inundated for a shorter time. The prawn densities were higher in the natural, more frequently inundated salt marshes. Higher densities of *P. aztecus and P. setiferus* were also found in salt marshes on lower ground by Rozas & Reed (1993), but the results were complicated by different densities of vegetation.

CONCLUSIONS

Whatever the reasons for the differences in distributions of prawns between the river and creek, the fact that there are differences is important and has implications for the management of mangrove forests in many areas. It is clearly difficult to make broad statements about the use of mangrove forests by banana prawns in all areas when we have seen these substantial differences in distributions of prawns in forests only a few kilometres apart. It is quite possible that the distribution patterns of prawns inside mangrove forests may be even more variable if more locations are sampled. Our results suggest that the distribution of prawns in mangrove forests may be determined by the topography and patterns of water currents in the forests. In a meandering creek, where there were differences in water flow between sites within the forest and during the flood tides, we saw a complex pattern of prawn distribution within the forest. However, in mangroves lining a straight section of river, the pattern of water currents was more consistent between sites and throughout the flood tide, resulting in a clearer pattern of prawn distribution in the mangroves. Our results reinforce the conclusion of Baran & Hambrey (1998) that we need to carry out more localized studies to identify areas within the mangrove habitat of particular importance to fish and prawns. Further sampling in more mangrove forests is needed to more clearly identify the factors determining the distribution of prawns inside forests.

Acknowledgements. We thank Mr Darrin Vance for braving mud, mosquitoes and midges in the middle of the night to help collect the samples. Mr Mark Tonks also suffered some discomfort in helping to clear pathways for stake net sites. Dr Rod Connolly of Griffith University, Gold Coast; Mr John Salini of CSIRO Marine Research, Cleveland; and Dr Vivienne Mawson of CSIRO Marine Research, Hobart, kindly made useful suggestions for improvements to the manuscript. We are grateful for the thoughtful and helpful comments of several anonymous reviewers. Hourly measurements of sea level were provided by, and with the cooperation of, the Beach Protection Authority, Queensland and the Queensland Department of Transport, Marine and Ports Division. This study was funded by the Fisheries Research and Development Corporation (FRDC 92/45) and by CSIRO Marine Research.

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Editorial responsibility: Otto Kinne (Editor),
Oldendorf/Luhe, Germany

Submitted: May 15, 2000; Accepted: February 1, 2001
Proofs received from author(s): February 27, 2002