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Do Penaeid Shrimps have a Preference for Mangrove Habitats? Distribution Pattern Analysis on Inhaca Island, Mozambique

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Scientific information on how penaeid shrimps are distributed within mangrove ecosystems is scarce, which presents an obstacle for fisheries as well as mangrove management. This study investigated the prime nursery microhabitats for the two major commercial species in Mozambique—*Penaeus indicus* and *Metapenaeus monoceros*. Stake net enclosures were used to sample shrimps living among unvegetated shallows and mangroves at Inhaca Island, Mozambique, during three consecutive spring tide periods. Four microhabitats were sampled: (1) sand flat; (2) fringe *Avicennia marina* on sandy substrate; (3) fringe *A. marina* on muddy substrate; and (4) interior *A. marina* adjacent to the supratidal terrestrial margin.

P. indicus had a significant preference for fringe mangroves over the adjacent sand flat ($P<0.001$ and $P=0.05$). Postlarval shrimps only occupied the sand flat, whereas the mangrove was utilized by postlarval, juvenile and sub-adult life stages. Within the fringe mangrove, there was no correlation between shrimp abundance and organic content of sediment ($5.7–11.6$ shrimps m^{-2}). Shrimps utilized the most interior margin of the mangroves (0.35 shrimps m^{-2}), although catch rates were significantly lower than in the mangrove fringe ($P<0.001$). *M. monoceros* was significantly ($P<0.01$), more abundant in the sand flat ($0.44–2.1$ shrimps m^{-2}) than in the mangrove fringe ($0.04–0.61$ shrimps m^{-2}), although this habitat preference was not evident for juvenile and sub-adult life stages.

The results demonstrate the extensive use of mangrove habitats by penaeid shrimps. The confinement to mangroves for *P. indicus*, but not for *M. monoceros*, is discussed in the context of habitat characteristics and predation avoidance behaviour. Methodological considerations of the stake net technique are also outlined.

Keywords: penaeid; shrimps; mangrove; *Avicennia marina*; intertidal microhabitat preference; stake nets; Mozambique

Introduction

Penaeid shrimps are, in terms of volume of catch and value per unit catch, one of the most important fishery resources world-wide (Rönnbäck, 1999). These shrimps constitute a major part of global shrimp fisheries catch, which ranged from 2·1 to 2·5 million t annually in 1993–1997 (FAO, 1999). In Mozambique, penaeid shrimp landings ranged from 7600 to 9900 t yr^{-1} (1992–1997), representing 23–32% of the country's total recorded fisheries landings by weight and considerably more by value (FAO, 1999). The more commercial penaeid shrimps, i.e. the large-sized genera *Penaeus* and *Metapenaeus*, have a life cycle where they spawn at sea and after a few weeks the postlarval shrimps settle in inshore and estuarine waters (Dall *et al.*, 1990), which they use as nurseries during their critical early life stages. After a few months in their nursery grounds, the sub-adult shrimps start their emigration offshore to complete their life cycle.

The structure and function of these nursery grounds are usually characterized and influenced by the presence of vegetation like mangrove forests and seagrass beds. Penaeid shrimp species reported to have a preference for mangroves as nursery habitat in the Indo-Pacific include *Penaeus indicus* (de Freitas, 1986; Chong *et al.*, 1990), *P. merguiensis* (Staples *et al.*, 1985; Robertson & Duke, 1987; Vance *et al.*, 1990), *P. monodon* (de Freitas, 1986), and *P. penicillatus* (Chong *et al.*, 1990). Other penaeid shrimp species are, however, not confined to mangrove habitats as nursery grounds. For instance, *P. duorarum*

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(Sheridan, 1992), *P. esculentus* and *P. semisulcatus* (Staples *et al.*, 1985; de Freitas, 1986; Robertson & Duke, 1987) seem to have a preference for submerged macrophytes like seagrass and algal beds. *Metapenaeus monoceros* (de Freitas, 1986) and *M. ensis* (Staples *et al.*, 1985; Robertson & Duke, 1987) are more widespread, occurring on seagrasses, mud flats, mangrove channels, etc.

It must be emphasized that most studies of penaeid shrimp distribution in their nursery grounds have not sampled the dominant feature of the mangrove eco-system, i.e. the intertidal forest, which is a serious shortcoming if the objective is to discuss habitat preference for these shrimps (Rönnbäck *et al.*, 1999). Instead, mangrove waterways, mud flats, sand flats and seagrass beds have been sampled during spring low tide, when the intertidal forest is usually completely drained of water. Fauna that enter the intertidal mangrove forest at high tide, would subsequently be passively transported by the outgoing ebb tide and concentrated in other adjacent habitats on spring low tides. Any assessment of the habitat preferences for aquatic fauna in mangrove environments should therefore be based on sampling during high tide periods, which is when vagile fauna like shrimps can actively choose between habitat types. Furthermore, penaeid shrimps are most active at night and near the times of high tide (Vance, 1992), which supports the idea of an active habitat choice at high tide. Another shortcoming among previous studies is the use of qualitative gear such as gill nets, barrier nets, seines or trawls with low or variable catch efficiencies. In order to facilitate spatial and temporal comparisons with other studies, quantitative gear such as enclosure nets, drop traps or visual census techniques with a known sampling area should be used.

The problematic nature of sampling among the extensive mangrove root system is probably the main reason for the limited scientific information on which fish and crustacean species utilize the intertidal forest as habitat. Consequently, the knowledge of distribution pattern within the intertidal forest is even scarcer, which makes it difficult to assess the relative importance of different ecological types of mangroves. From a fisheries management perspective, one key parameter is to identify prime nursery and feeding habitats among riverine, fringe and basin mangrove microhabitats. It could also be argued that any discussion of the functional role of mangroves as habitat, especially concerning the refuge from predation, should be built on baseline information of how fauna is distributed within the system.

Up to date only two studies have assessed the distribution pattern of penaeid shrimps within the intertidal forest. In northern Australia, Vance *et al.* (1996) used stake nets to sample *P. merguiensis* and fish from four discrete mangrove microhabitats: two at the creek mangrove fringe and two at further distance into the forest. Two mangrove communities, one dominated by the structurally complex *Rhizophora stylosa*, the other by the more open *Ceriops tagal*, were sampled. Rönnbäck *et al.* (1999) also used stake nets to sample shrimps and fish from four mangrove microhabitats in Pagbilao, the Philippines. The microhabitats differed in dominating mangrove community [*Avicennia marina*, *A. officinalis*, *R. apiculata* (replanted and natura)], structural complexity of the root system and proximity to open water habitat.

The main objective of the present study is to investigate whether penaeid shrimps exhibit a preference for mangrove intertidal forest habitat over adjacent sand flats. Another objective is to assess the distribution pattern of penaeids among three different *Avicennia marina* microhabitats: (1) fringe *A. marina* on sediments of high organic content; (2) fringe *A. marina* on sediments of low organic content; and (3) interior *A. marina*. The present study is original in a number of aspects. Sampling methodology is improved and sample area uniformed. The use of relatively small stake nets (3 × 3 m) allowed time for spatial replication, which make this the first study to assess catch variability of penaeid shrimps within and between mangrove microhabitats. Furthermore, the most inland portion of the mangrove ecosystem was sampled by selecting interior microhabitats located only a few metres from the terrestrial supratidal margin. Marine mangroves in Mozambique were chosen as the study site, whereas previous studies have worked in riverine settings in the Philippines and Australia. The study focuses on the two major commercial shrimp species in Mozambique—*Penaeus indicus* and *Metapenaeus monoceros*—which comprise 85% of the country's shrimp landings (Palha de Sousa, 1996).

Materials and methods

Study area

Inhaca is a small island (42 km^2) situated in the southern part of Mozambique, East Africa (26°S 33°E) (Figure 1). The island is positioned in a transitional region of tropical to warm subtropical conditions (Macnae & Kalk, 1969) and constitutes a barrier between Maputo Bay and the Indian Ocean. The climate of Inhaca Island is characterized by hot, wet (September–March) and warm, dry (April–September) seasons. A detailed description of the
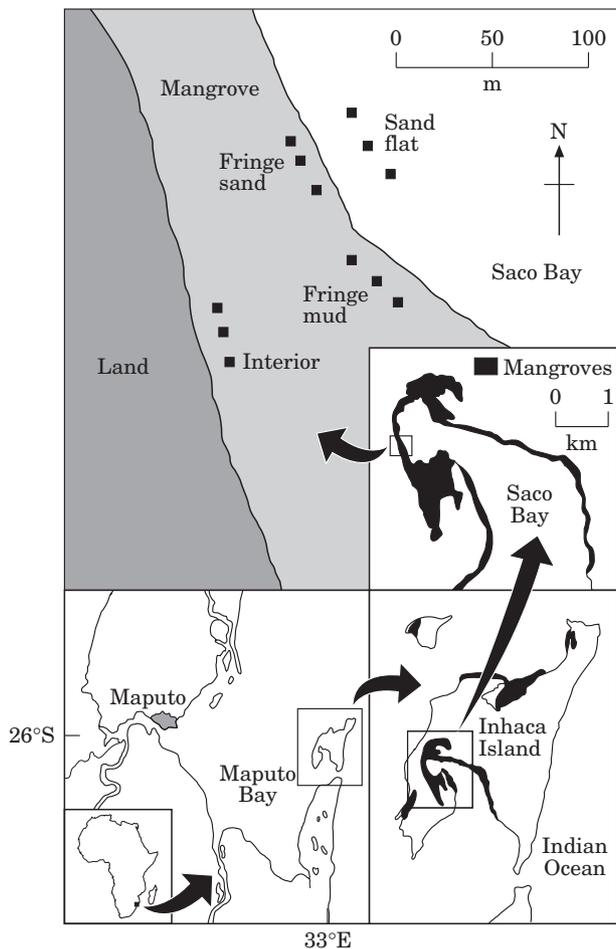
FIGURE 1. Location of stake net sampling sites at Inhaca Island, Mozambique.

island's general ecology, fauna and flora is given in Macnae and Kalk (1969).

This study was performed in the southern bay of Inhaca Island, the Saco da Inhaca (Figure 1). The bay covers an area of $15 \cdot 4$ km^2 and is surrounded by mangrove communities comprised of five species, which cover a further area of $1 \cdot 4$ km^2 (de Boer, 2000). *Avicennia marina* is the most common species and fringes the bay, while *Rhizophora mucronata* lines the mangrove channels and creeks. The interior areas can have extensive mangrove thickets made up of *Ceriops tagal* and *Bruguiera gymnorrhiza* (de Boer, 2000). The fifth species—*Lumnitzera racemosa*—is less common.

Sampling was conducted at the western part of the Saco da Inhaca in four different microhabitats: (1) sand flat; (2) fringe *Avicennia marina* on sandy substrate; (3) fringe *A. marina* on muddy substrate; and (4) interior *A. marina* on sandy substrate (Table 1, Figure 1). Three replicate sites were randomly

selected within each microhabitat type. The sand flat replicates were positioned 38–75 m from the mangrove fringe. The fringe mangrove microhabitats were all located within 5–10 m from the sand flat habitat in the bay. The three replicates of the interior mangrove habitat were only 10–20 m from the supratidal terrestrial margin, and their proximity to the bay mangrove fringe was 76–88 m. The individual replicates were separated by at least 10 m, which minimized the risk of disturbing animals in adjacent replicates during the setting of nets.

All three replicates in each microhabitat were measured for elevation, water depth, organic content in sediment and structural complexity. The relative elevation of each replicate was established by synchronous measurement of water depth in all replicates and at a reference point. During all sampling events, water depth was recorded at this reference point. For organic content analysis, the top 5 cm from five different sediment cores were pooled for each replicate site. Structural complexity was defined as ratio of root surface to sediment area. The mangrove roots (pneumatophores) were considered to be true cylinders. For each replicate, the numbers of roots m^{-2} and the average surface area per root was established. The mangrove microhabitats did not encompass any mangrove trees, only roots and some seedlings.

Sampling schedule and procedure

The sampling schedule and statistical analysis were developed in accordance with the life history dynamics of penaeid shrimps. The study was carried out during three consecutive spring tides in April and May 1999. This period was chosen since it coincides with the peak recruitment of penaeid shrimps into their nursery grounds in the area. Furthermore, these shrimps are known to both immigrate to and emigrate from coastal areas in large numbers during spring tides (Dall *et al.*, 1990). Consequently, the availability of shrimps within the nursery ground can change markedly over short time periods. On the basis of the above, microhabitats to be compared were always sampled simultaneously. Two microhabitat types were sampled each night, i.e. a total of six nets (three in each microhabitat) were set each night. The investigated microhabitats were always sampled on two consecutive nights during each spring tide period, which gave a total of six replicates.

Stake nets with a mesh size of 1 mm were used to catch the newly immigrated penaeid shrimp post-larvae. In the present study, a stake net can be likened

Table 1. Relative substrate elevation, range of water depth at high tide, structural complexity (ratio of mangrove root surface to sediment area) and organic content of sand flat and Avicennia marina mangrove microhabitats sampled at Inhaca Island, Mozambique (April–May, 1999) (mean ± SE) (n=3)

	Elevation (m)	Water depth (m)	Structural complexity	Organic content (%)
Sand flat	0–0·16	1·23–1·63		0·90 ± 0·04
Mangrove				
Fringe mud	0·55–0·66	0·73–1·08	0·30 ± 0·04	11·8 ± 0·6
Fringe sand	0·64–0·74	0·68–1·17	0·15 ± 0·02	3·0 ± 0·2
Interior	1·33–1·37	0·34–0·48	0·011 ± 0·004	3·1 ± 0·6

to a square-shaped net pen (3 × 3 m) with a bamboo pole in each corner. At low tide, the bottom of the net was anchored 5–10 cm into the sediment with tent sticks, after which the remaining net was rolled down and buried into the sediment. A rope was tied to each of the four buried upper corners of the net. At the other end, these ropes were tied to a pole or branch that could be located during high tide. On the peak of the major daily high tide (occurring at 04:00–05:30 during the study), four persons would raise the net, each approaching a corner while lifting his rope. The four ropes were then tied to their respective bamboo pole so that the net reached 0·5–1·0 m above the water surface, enabling the stake net to enclose an area of 9 m². In the subsequent morning ebb tide, water drained from the sampling sites and the shrimps were aggregated around the corner of lowest elevation. Prior to the next high tide, penaeid shrimps were collected by hand and preserved in 4% seawater-formaldehyde for identification in the laboratory. *Penaeus indicus* and *Metapenaeus monoceros* were identified and separated from other shrimps following Joubert (1965) and Kensley (1972). All shrimps were measured for carapace length and grouped into size classes in the 0·5 mm interval.

Statistical analysis

The individual spring tide periods served as the temporal unit for the statistical analysis with habitat and day as variables. All data was transformed (natural logarithm), and the homogeneity of variances was tested using Cochran's test. Two-way Anova was used to analyse difference in shrimp abundance between microhabitats sampled simultaneously. All statistical calculations were performed with the STATISTICA software.

Results

Habitat characteristics

The sand flat habitat had the lowest elevation and was thus characterized by deeper water at high tide (Table 1). In contrast, the interior *Avicennia marina* habitat was only inundated by very high spring tides, when the water depth reached 0·3–0·5 m. The tidal amplitude differed up to 20 cm between some consecutive nights of sampling, and there was 42 cm difference between the minimum (14 April) and maximum (17 April) tidal amplitude observed during the sampling period.

There was a distinct difference in the organic content of sediments between the sandy and muddy fringe *A. marina* microhabitats, 3·0% and 11·8%, respectively (Table 1). The interior mangrove habitat was equivalent to the sandier of the fringe habitats, whereas the sand flat had the lowest organic content (0·9%) of all habitats.

The structural complexity of mangrove roots was one order of magnitude higher in the fringe habitats compared to the interior *A. marina* habitat (Table 1).

Shrimp distribution

A total of 2179 shrimps (1979 *Penaeus indicus* and 200 *Metapenaeus monoceros*) were caught over the three spring tide periods. For both species, the life stages caught ranged from newly immigrated shrimp postlarvae, with carapace length <1·5 mm, to sub-adult specimens (carapace length 11–12 mm). The fringe *Avicennia marina* microhabitat with high organic content in the sediment was sampled on all three spring tides. For *P. indicus*, shrimp postlarvae and early juveniles in the size range 2·0–3·5 mm carapace length
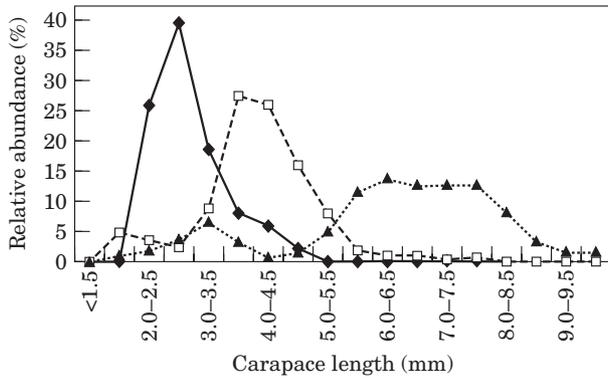
FIGURE 2. Relative abundance of *Penaeus indicus* in fringe *Avicennia marina* mangroves over three consecutive spring tides at Inhaca Island, Mozambique [3–4 April (n=517), 14–15 April (n=348), 3–4 May (n=352)]. ◆ 3–4 April; □ 14–15 April; ▲ 3–4 May.

dominated the catch on the first spring tide (Figure 2). This cohort, which had a growth rate around 1 mm in carapace length per week, comprised a major portion of the shrimp catch on the second and third spring tide period.

Consecutive sampling within each spring tide did not affect shrimp catch rates (Tables 2, 3). The interaction (time × site) was insignificant for all data sets for both species. Furthermore, there was no

consistent trend of shrimp catches being affected by differences in tidal amplitude.

(1) Mangrove vs. sand flat. Fringe *Avicennia marina* and sand flat microhabitats were sampled simultaneously on two spring tides. Almost 90% of all *Penaeus indicus* (870 out of 977 shrimps) were caught in the mangrove habitat, with an abundance of 6–12 shrimps m^{-2} (Table 4). The abundance on the sand flat habitat was significantly lower for this species (Table 2, Figure 3).

The opposite distribution pattern was observed for *Metapenaeus monoceros*, which was significantly more abundant on the sand flat habitat ($P<0.01$) (Table 3, Figure 3). The maximum recorded abundance of *M. monoceros* (2·1 shrimps m^{-2}) in the sand flat was about three times as high as the simultaneous catch in the mangrove habitat (Table 5).

There were distinct differences in the size range of shrimps caught in the two habitat types. In the sand flat habitat, 98% of all *P. indicus* individuals (105 out of 107 shrimps) had a carapace length below 3·0 mm, and no shrimps with carapace length over 4·0 mm were caught. In the simultaneous sampling of the fringe mangrove habitat, a wide range of size classes were caught and only 43% of *P. indicus* were smaller than 3·0 mm in carapace length (Figure 2). Consequently, the mangrove preference was statistically

TABLE 2. ANOVA test summary of *Penaeus indicus* abundance with microhabitats and time as variables. Type III sums of square

Source of variation	df	SS	MS	F	P
Mangrove *vs.* sand flat[a]					
Time × Site	1	0·133	0·133	0·149	0·711
Time	1	0·279	0·279	0·312	0·594
Site	1	4·990	4·990	5·567	0·050
Error term	7	6·275	0·896		
Mangrove *vs.* sand flat[b]					
Time × Site	1	0·429	0·429	0·895	0·372
Time	1	<0·001	<0·001	0·001	0·977
Site	1	32·010	32·010	66·770	<0·001
Error term	8	3·835	0·479		
Fringe *vs.* interior mangrove					
Time × Site	1	0·189	0·189	0·276	0·614
Time	1	1·244	1·244	1·814	0·215
Site	1	22·294	22·294	32·498	<0·001
Error term	8	5·488	0·686		
Sandy *vs.* muddy mangrove sediment					
Time × Site	1	0·292	0·292	0·697	0·428
Time	1	0·573	0·573	1·367	0·276
Site	1	0·267	0·267	0·638	0·448
Error term	8	3·352	0·419		

[a]3–4 April; [b]14–15 April.

TABLE 3. ANOVA test summary of *Metapenaeus monoceros* abundance with microhabitats and time as variables. Type III sums of square

Source of variation	df	SS	MS	F	P
Mangrove *vs.* sand flat[a]					
Time × Site	1	0·159	0·159	0·543	0·485
Time	1	0·044	0·044	0·151	0·709
Site	1	3·765	3·765	12·832	0·009
Error term	7	2·054	0·293		
Mangrove *vs.* sand flat[b]					
Time × Site	1	0·160	0·160	0·327	0·583
Time	1	1·671	1·671	3·423	0·101
Site	1	5·675	5·675	11·625	0·009
Error term	8	3·905	0·488		

[a]3–4 April; [b]14–15 April.

TABLE 4. *Penaeus indicus* abundance (shrimps m^{-2}) among sand flat and *Avicennia marina* mangrove microhabitats at Inhaca Island, Mozambique (mean ± SE) (n=6)

	Sand flat	Mangrove fringe, mud	Mangrove fringe, sand	Mangrove interior
3–4 April	1·8 ± 0·35	11·6 ± 5·2[a]		
14–15 April	0·15 ± 0·08	6·4 ± 1·6		
17–18 April			6·0 ± 2·3	0·35 ± 0·18
3–4 May		6·5 ± 1·4	5·7 ± 2·0	

[a]n=5.

TABLE 5. *Metapenaeus monoceros* abundance (shrimps m^{-2}) among sand flat and *Avicennia marina* mangrove microhabitats at Inhaca Island, Mozambique (mean ± SE) (n=6)

	Sand flat	Mangrove fringe, mud	Mangrove fringe, sand	Mangrove interior
3–4 April	0·44 ± 0·12	0·04 ± 0·03[a]		
14–15 April	2·1 ± 0·40	0·61 ± 0·23		
17–18 April			0·24 ± 0·10	0·07 ± 0·04
3–4 May		0·06 ± 0·03	0·09 ± 0·05	

[a]n=5.

stronger on the second spring tide ($P<0·001$) compared to the first spring tide ($P=0·05$), when newly immigrated postlarvae dominated the catch (Table 2). Postlarval *M. monoceros* comprised around 70% of total catch in both habitat types. The relative abundance of larger shrimps was, however, higher in the mangrove habitat. *M. monoceros* with carapace length over 6·0 mm contributed to 17% of the shrimp catch in the mangrove and only 6% in the sand flat. For this size class, there was only a marginal difference in abundance between the two habitat types.

(2) Fringe vs. *interior mangroves.* The shrimp abundance in fringe (5–10 m from open water in bay) and interior (76–88 m from bay) mangroves was investigated during one spring tide. The shrimp catch was mainly comprised of *Penaeus indicus* individuals (341
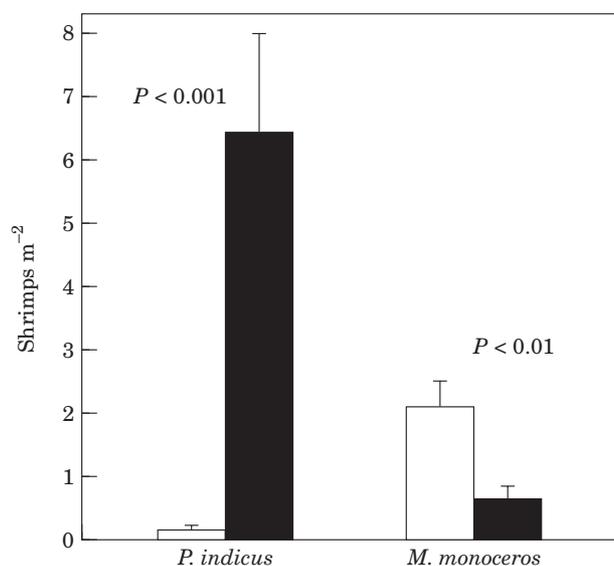
FIGURE 3. Abundance (mean ± SE) of *Penaeus indicus* and *Metapenaeus monoceros* in sand flat and fringe *Avicennia marina* mangrove microhabitats at Inhaca Island, Mozambique, 14–15 April 1999 (n=6). □ Sand flat; ■ Mangrove.

FIGURE 4. Abundance (mean ± SE) of *Penaeus indicus* in *Avicennia marina* mangrove microhabitats at Inhaca Island, Mozambique (n=6). (a) Interior and fringe mangrove (17–18 April), (b) sandy and muddy fringe mangrove (3–4 May). □ Interior mangrove; □ Fringe, sandy mangrove; ■ Fringe, muddy mangrove.

out of 358 shrimps). This species was significantly ($P<0.001$) more abundant in the fringe mangrove microhabitat than in the interior habitat [Table 2, Figure 4(a)]. *Metapenaeus monoceros* was also more abundant in the fringe habitat (Table 5), although this was not tested statistically due to the low shrimp abundance in both mcirohabitats.

(3) Low vs. *high organic content in mangrove sediment.* Fringe *Avicennia marina* microhabitats with low and high organic content in sediment (3·0% and 11·8%, respectively) were sampled during one spring tide. *Penaeus indicus* was again the dominant (99%) shrimp species in the mangrove habitat. There was no statistically significant difference between *P. indicus* abundance in the sandy (5·7 shrimps m^{-2}) and muddy (6·5 shrimps m^{-2}) mangrove microhabitats [Table 4, Figure 4(b)].

Discussion

Sand flat vs. *mangrove*

The shrimp population caught in this study was dominated by postlarval and juvenile life stages, which confirms the role of mangrove-dominated environments as nursery habitat for penaeid shrimps. *Penaeus indicus* exhibited a clear preference for mangrove habitats over adjacent sand flats, with an overall
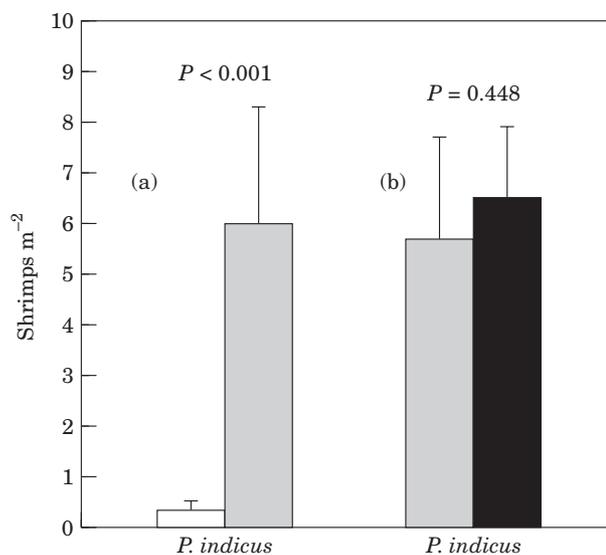
abundance ratio of 9:1 on simultaneous sampling events. Apparently this species express an active choice of entering the vegetated mangrove habitat with incoming high tide. The mangrove preference for *P. indicus* became even more pronounced as individuals grew. *P. indicus* with carapace length over 4 mm, which corresponds to individuals having spent 2–3 weeks in their nursery ground (based on a growth rate of 1 mm carapace length per week), was never found in the sand flat habitat. Apart from indicating an active and absolute choice of mangrove habitat for juvenile and sub-adult shrimps, this pattern could also be explained by higher mortality rates for individuals not entering the mangrove forest. Other studies having worked with *P. indicus*, or the closely related morphospecies *P. merguiensis*, have also reported a strong preference for mangrove habitats over adjacent habitats such as seagrass and algal beds, as well as unvegetated mud and sand flats (Staples *et al.*, 1985; de Freitas, 1986; Robertson & Duke, 1987; Chong *et al.*, 1990; Vance *et al.*, 1990).

In contrast, *Metapenaeus monoceros* exhibited a significant preference for sand flat habitats over mangroves. As the high tide entered the mangrove forest, this species remained on the adjacent sand flat at a ratio of almost 4:1. Another Mozambican study found *M. monoceros* to be widespread, occurring on seagrass, mangrove and mud flat habitats (de Freitas, 1986). Studies on *M. ensis*, which belongs to the same genus,

have also found this species to be widespread (Staples *et al.*, 1985; Robertson & Duke, 1987). In this study, the pattern of higher abundance of *M. monoceros* in the sand flat habitat was only present when all size classes were included in the analysis. There was no difference in absolute abundance between the sand flat and mangrove habitats for juvenile and subadult shrimps with carapace length >6·0 mm. This could be explained by higher mortality rates on the sand flat habitat for postlarval and early juvenile shrimps. It must be emphasized, however, that these indications of an ontogenetic shift in abundance ratios among nursery habitats, are only based on a small number of large-sized *M. monoceros* individuals and would thus require further study.

The confinement to mangroves for *P. merguiensis*, but not for *M. monoceros*, could be explained by behavioural differences between the two genera. Penaeid shrimp defence mainly lies in reducing visibility and using escape movements when attacked (Dall *et al.*, 1990). The importance of structural complexity in reducing predator efficiency is well established, although this shelter function is species-specific, depending on the prey behaviour and predator efficiency. For instance, in laboratory studies *Penaeus* species depend more on structural complexity as shelter compared to *Metapenaeus* species (Primavera & Lebata, 1995; Primavera, 1997). This implies that *Penaeus* species are attracted to nursery ground habitats of high heterogeneity such as the intertidal mangrove forest. The susceptibility to predation can also be reduced through an activity pattern where shrimps remain buried in the substratum during the day to emerge at night (Vance, 1992; Primavera & Lebata, 1995). Primavera and Lebata (1995) found juvenile *M. anchistrus* and *M.* sp. to burrow much more frequently (>90% during day and 33–41% at night) compared to *P. merguiensis* and *P. monodon* (>30% during day and <10% at night). *M. monoceros* also stay mostly buried during daylight, whereas *P. indicus* have been reported to bury very seldom, if ever (Hughes, 1966; Dall *et al.*, 1990). The frequent burrowing behaviour of *M. monoceros* would reduce the dependence on structural complexity as shelter from predators, and consequently this species can inhabit a wide range of habitats. This species may, however, still be dependent on mangrove ecosystems. The carbon export and the ability of mangroves to stabilize coastal water quality (Ogden & Gladfelder, 1983; Rönnbäck, 1999) indirectly support the productivity of adjacent systems like sand flats. The relative importance of this indirect support should be studied by investigating shrimp abundance on unvegetated shallows isolated from mangroves.

Mangrove microhabitats

Both shrimp species were caught in the interior *Avicennia marina* microhabitat, which was situated 76–88 m from the mangrove fringe. This microhabitat is directly adjacent to the supratidal terrestrial environment, and is only inundated by very high spring tides. It is therefore evident that penaeid shrimps utilize even the most inland portions of the mangrove forest.

Shrimp abundance was, however, significantly higher in the fringe compared to the interior microhabitat, which could be explained by differences in habitat characteristics. Low water depth and the far interior positioning mean that shrimp individuals encounter many suitable mangrove microhabitats before reaching the interior site. On the contrary, Vance *et al.* (1996) and Rönnbäck *et al.* (1999), who worked with *P. merguiensis*, did not observe any sign of declining shrimp abundance in their mangrove interior microhabitats. However, the interior mangrove sites sampled in the present study cannot be placed on a par with the interior habitat sampled in previous studies. Although Vance *et al.* (1996) and Rönnbäck *et al.* (1999) worked with interior microhabitats positioned 30–90 m from the bay/creek mangrove fringe, their habitats were still several hundreds of metres away from the supratidal terrestrial environment. In contrast, this study sampled interior mangrove microhabitats located only 10–20 m from the terrestrial environment, which certainly has a strong influence on water depth, frequency of tidal inundation as well as physiochemical properties of sediment and water. Furthermore, the structural complexity of the interior mangrove microhabitat was more than one order of magnitude lower than in the seaward *Avicennia marina* microhabitats. The shelter from predation offered by mangroves is thus severely reduced in this backwater habitat. It is, however, interesting to note that Vance *et al.* (1996) found no difference in *P. merguiensis* abundance between the structurally complex *Rhizophora* mangrove community and the inland *Ceriops* community of very low complexity. This can either be explained by passive distribution within the mangrove system for this species, or that the overall shrimp abundance in the system (0·1–0·2 shrimps m^{-2}) was insufficient for the development of any distinguished preference for the more structurally complex mangrove microhabitats.

There was no statistical difference in shrimp abundance between fringe *Avicennia marina* microhabitats with sediments of low and high organic content. Apart from very high catch rates of *P. indicus* (11·6 shrimps m^{-2}) on the first spring tide, the

abundance ranged between 5·7 and 6·4 shrimps m^{-2}. These catch rates are very high compared to previous studies of the closely related morphospecies *P. merguiensis*: <0·45 shrimps m^{-2} (Robertson, 1988); 0·06–3·35 shrimps m^{-2} (Vance *et al.*, 1996); and 0·07–0·58 shrimps m^{-2} (Rönnbäck *et al.*, 1999). No abundance record was found for *Metapenaeus monoceros* in the literature. Rönnbäck *et al.* (1999) caught 0·01–0·05 *M. ensis* per m^2 mangrove, which is one order of magnitude lower than for the *Metapenaeus* species sampled in the present study (0·04–0·61 shrimps m^{-2} in fringe mangrove). The above clearly emphasized the relative importance of the mangroves at Inhaca Island as nursery ground. The dynamics of mangrove ecosystems as well as the well-developed seasonality of penaeid shrimp recruitment into their nursery grounds, implies, however, that catch rates cannot be transferred easily over time and between regions.

Methodological considerations

Vance *et al.* (1996) conducted the first enclosure study of discrete mangrove microhabitats. Their stake nets were deployed during high tide and fixed to the substrate by a galvanized chain. Rönnbäck *et al.* (1999) modified the method by anchoring the nets to the substrate during low tide, and raising them at high tide. This technique increases the sampling efficiency for epibenthic fauna, and minimizes the cutting of mangrove roots during site preparation. In the present study, the anchored net was completely buried into the sediment, which minimized the risk of shrimps being attracted around the net structure or deterred on the outside of the net. Another innovative aspect was that pulling a rope from a distance raised the net. This procedure probably minimized the risk of disturbing animals and thus reduced the amount of shrimps escaping.

Instead of the 480–640 m^2 microhabitats enclosed by Vance *et al.* (1996) and the 89–258 m^2 enclosed by Rönnbäck *et al.* (1999), only 9 m^2 habitats were enclosed by each stake net in the present study. This was made possible by the high shrimp abundance indicated during pilot studies. The relatively small microhabitats size, reduced the time spent on net setting and catch collection, and thus provided the opportunity for replicate samples. Consequently, this is the first study to assess catch variability within as well as between mangrove microhabitats. As noted by Vance *et al.* (1996) and Rönnbäck *et al.* (1999), stake netting is very time-consuming, especially regarding catch collection, which has to be completed prior to the return of the next high tide. In this respect, every effort to free manpower resources is critical.

Since there was no indication of shrimp catch rates being affected by tidal amplitude or consecutive sampling events, it might be possible to use each spring tide as a sample unit, whereby the number of replicates could be increased. However, Vance *et al.* (1996) found *P. merguiensis* catches to be negatively correlated with tidal amplitude, and therefore this aspect requires further investigation. It must also be emphasized, that there will be a continuous immigration of new shrimp postlarvae into the study system, which has to be accounted for if each spring tide period is to serve as the temporal unit.

Conclusion

It is evident that penaeid shrimps make extensive use of the intertidal mangrove forest. The fact that interior habitats adjacent to the supratidal terrestrial environment are utilized has to be incorporated into mangrove management plans. The conversion of all ecological types of mangroves, including the most interior zone, will affect fisheries production directly through habitat loss and indirectly through the loss of biophysical interactions. However, from a fisheries management perspective, the bay fringe mangrove habitats sampled in this study would be classified as more important than the interior habitat, based on higher shrimp abundance as well as more frequent tidal inundation.

Penaeus indicus has a distinct preference for vegetated mangrove habitat over adjacent sand flat in which only postlarvae reside. On the contrary, *Metapenaeus monoceros* has a preference for sand flat habitat, although this only applies to postlarval and early juvenile stages. This implies that in the assessment of the nursery function of different habitat types, we must look beyond total catch rates and acknowledge survival rates and potential ontogenetic shifts in habitat preference. The efficient burrowing behaviour of *Metapenaeus* species might explain their widespread distribution, whereas *Penaeus* species are more dependent on structural complexity to reduce predation, and would thus be more confined to vegetated habitats such as mangroves. Sand flats in relative isolation from mangrove ecosystems should be studied to evaluate the indirect support from mangroves to adjacent unvegetated shallows.

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