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Juvenile Penaeid Shrimp Density, Spatial Distribution and Size Composition in four adjacent habitats within a Mangrove-Fringed Bay on Inhaca Island, Mozambique

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Abstract—The effects of habitat characteristics (mangrove creek, sandflat, mudflat and seagrass meadow) water salinity, temperature, and depth on the density, spatial distribution and size distribution of juveniles of five commercially important penaied shrimp species (*Metapenaus monoceros, M. stebbingi, Fenneropenaeus indicus, Penaeus japonicus* and *P. semisulcatus*) were investigated during a high shrimp recruitment peak lasting from January to June 2002, in four contiguous habitats within a non-estuarine mangrove bay at Saco da Inhaca, Inhaca Island, Southern Mozambique. A total of 14,976 specimens representing the five species were collected by means of a 1m beam-trawl fitted with a 2 mm mesh net with a cod-end. Every two weeks corresponding with spring tides on three consecutive nights, three trawls of 50 meters each were carried out each night in each habitat at 1.40–2.15 a.m. after the daily spring tide high water peak. Species distributions among the four habitats during the six months sampled showed significant differences in habitat preference ($p>0.001$). *Fenneropenaeus indicus, M. stebbingi* and *P. japonicus* dominated the catches in sand flats with densities of 27 ± 0.94, 18 ± 0.98 and 7 ± 0.76 shrimp /50 m^2, respectively. *Metapenaeus monoceros* dominated catches in mudflats at a density of 21 ± 0.78 /50 m^2 followed by *M. stebbingi* with 13 ± 1.2 /50 m^2. *Penaeus semisulcatus* was almost exclusively captured in seagrass meadows at densities of 8 ± 0.57 /50 m^2. Only the *Metapeneaus* species showed a wide range of habitat utilization. The differences in habitat preference emphasises spatial partitioning between shrimps, reducing competition. Multiple linear regressions of juvenile shrimp densities for each species with water depth, salinity and temperature showed some significant effects. *Fenneropenaeus indicus* density showed a significant negative relationship with salinity and water depth and a positive relationship with temperature and turbidity. *Metapenaeus stebbingi* numbers showed a significant positive correlation with increasing salinity and temperature, but a negative one with depth. *Penaeus japonicus* numbers were significantly related to decreasing salinity and depth. *Penaeus semisulcatus* abundance was significantly related to decreasing temperature, and increasing turbidity and depth. More than 50% of the total shrimps captured had carapace length of ≤ 3 mm, substantiating the nursery function of the different habitats sampled in the study.

INTRODUCTION

All penaeid shrimps that comprise the bulk of the fisheries are believed to have a similar life cycle with the following developmental sequences: planktonic larvae, with several naupliar, protozoeal, mysid and postlarval stages, followed by benthic juvenile and adult stages (Dall et al., 1990). The greatest differences between the larval, juvenile and adult stages are attributed to habitat

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preferences, either demersal or pelagic and predominantly estuarine, inshore or offshore (Dall et al., 1990). Because the various life stages of penaeids often occupy different habitats, migration is a necessary component of their life cycles.

Studies on penaeid shrimp populations have demonstrated different migration patterns. Larvae and postlarvae migrate from the spawning grounds to the nursery grounds, juveniles migrate out of the nursery areas, and adults migrate to deeper water; spawning migrations are therefore common in some species(Garcia & Le Reste, 1981; Dall et al., 1990).

Habitat requirements for juveniles have been described by different authors for different species and may include associations with macro-vegetation, or sediment type. The habitats preferred by penaeid species are diverse and include mangroves, seagrasses and macroalgae, as well as estuaries, mudflats and sand flats (Hughes, 1966; Macnae, 1974; Staples, 1979; Staples et al., 1985; de Freitas, 1986; Robertson & Duke, 1987; Primavera & Lebata, 1995). Habitat choice by juvenile shrimp has been reported to be species-dependent, varying from a specific nursery habitat to more than one habitat type (Coles et al., 1987; Dall et al., 1990).

Food availability (plankton productivity and benthic algae, detritus) is believed to be one of the reasons postlarvae and juveniles select particular nursery areas. The presence of protective physical and structurally heterogeneous habitats (soft bottoms, mangrove roots, submerged macrophytes, etc.) is another (Williams, 1958; Zimmerman & Zamora, 1984; Staples et al., 1985; de Freitas, 1986; Coles et al., 1987; Robertson and Blaber, 1992; Stoner, 1995; Laegdsgaard & Johnson, 1995; Vance et al., 1996; Primavera, 1996; 1997; Rönnbäck, 1999; Rönnbäck et al., 2002). Lateral trapping of newly migrated postlarvae, due to the hydrodynamic retention capacity of some habitats such as mangroves, has also been accepted by ecologists to explain penaeid shrimp settlement (Chong 1995; Chong et al., 1996).

A considerable amount of information concerning the temporal and spatial abundance of penaeid juvenile shrimps is available in the literature (see Staples et al., 1985; Dall et al., 1990; Subramaniam, 1990; Haywood et al., 1995; Primavera, 1998; Vance et al., 1998). However, only a few studies have been undertaken on the small-scale, short-term variation within different habitat types to simultaneously assess the relative abundance of juveniles as well as shrimps size and abundance (Vance et al. 1996, Kangas & Jackson, 1998; Rönnbäck et al., 1999; 2002)..

Knowledge of the early development of penaeid shrimps in the eastern Africa region is relatively scarce and this limits geographical comparisons. Shrimp fisheries are important in the region and this lack of information also impedes the development of effective shrimp fishery management protocols.

In Mozambique, only four studies have attempted to assess juvenile penaeid shrimp distribution patterns and seasonality in the marginal areas of Maputo Bay (de Freitas, 1986) and Inhaca Island (Hughes, 1966; Abdurremane, 1998; Rönnbäck et al. 2002; Macia, unpublished data). Generally these studies were performed in different periods of the day and tidal height. Hughes (1966) and de Freitas (1986) sampled penaeid shrimps during low tide while Abdurremane (1998) sampled during the peak of high tide. Despite the differences in the sampling periods, their results were quite similar in terms of the species of shrimps they found, with a slight differences in the presence of certain species in the catches. Rönnbäck et al. (2002) assessed the habitat preferences for juvenile penaied shrimps in mangroves based on sampling habitats during high tide periods, when shrimps can actively choose between the different habitat types. These authors found distinct habitat preferences between *F. indicus* and *M. monoceros*; *F. indicus* preferred mangrove habitats over adjacent sand flats whereas *M. monoceros* exhibited preference for sand flats rather than mangrove intertidal forest. However, species like *P. japonicus, P. semisulcatus* and *M. stebbingi* were not well represented in their catches, but were reported by Macia (unpublished data) to occur in relatively high numbers in the adjacent intertidal sand flat.

The study reported here expands this work to other habitats such as the mudflats, the creeks, and seagrasses in order to assess how and in what proportions and sizes, postlarvae and juveniles of all the species occurring in the area may utilize these habitats, as well as which environmental factors (such as temperature, salinity, turbidity and depth) influence their abundance. The study was carried out during the on-going ebb tide because shrimp catches were sufficiently high for population studies near the mangrove area at Saco da Inhaca. The study of penaeid shrimps in the mangrove-adjacent areas is important for coastal resources management planning.

MATERIALS AND METHODS

Study Area

Saco da Inhaca is a small mangrove-fringed bay located at southern Inhaca Island (26°07S, 32°56E´) (Fig. 1). Detailed descriptions of its general ecology, fauna and flora of the Island can be found in the literature (Hughes, 1966; Macnae & Kalk, 1969; de Boer and Longamane, 1996; Guerreiro et al., 1996; de Boer 2000; Rönnbäck et al., 2002). The climate of Inhaca is characterized by two seasons, hot and rainy (September–March) and warm and dry (April-August) (Macnae & Kalk, 1969). The tides of Inhaca Island are semi-diurnal with a mean spring and neap tidal range of 2.2 m and 0.7 m respectively (de Boer et al., 2000). The whole western coast of Inhaca Island is shallow, sheltered and gently sloping, showing large extensions of sand and mud flats, seagrass beds, coral reefs and mangrove forests in the northern and southern part (Saco da Inhaca).

According to de Boer & Longomane (1996), Saco da Inhaca (a small circular cove) occupies a total area of 66 ha and comprises several closely related habitats adjacent to the mangrove fringe and is described in relation to sediment type and degree of exposure. Saco da Inhaca is connected to Maputo Bay and the Indian Ocean at high tide but at low tide 94% of its intertidal area is exposed (de Boer, 2000) thus preventing circulation with Maputo Bay, the major shrimp trawling area, and the Indian Ocean. During low tide most of the swimming fauna are expected to follow the water withdrawal and juvenile shrimps concentrate in the creeks, channels and water flanks (Hughes, 1966; personal observ.).

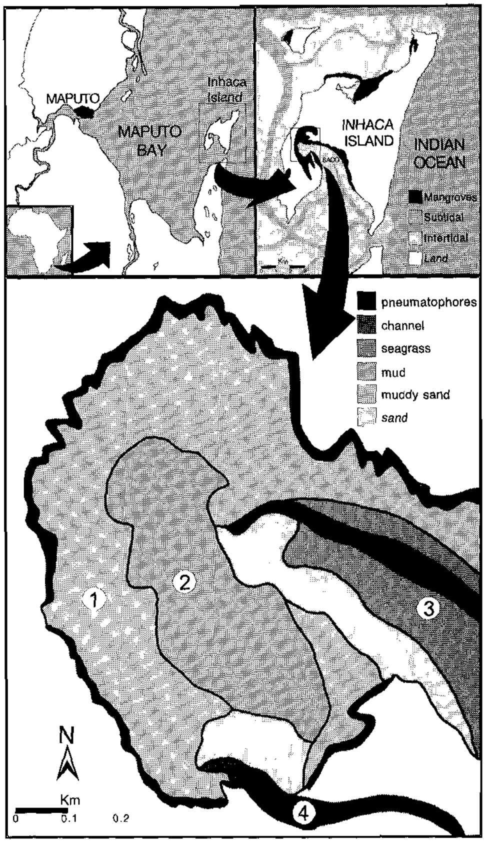

Fig 1. Map of Saco da Inhaca showing the sampling locations

The study was conducted in four different habitats adjacent to the fringing mangrove forest (Fig.1). The sandflat and the creek habitats were closer to the mangrove fringe while the mudflat habitat was located in the central part of the cove and the seagrass further away in the channel in a subtidal area. The creek habitat is lined by *Rhizophora mucronata* and patches of *Avicennia marina* and exhibits bottom sediment of coarse sand. The sand flat habitat lies adjacent to the *A. marina* fringe and is characterized by sediment of coarse sand and mangrove debris. The mudflat habitat occurs in the central part of the bay and is characterized by a relatively high percentage of very fine sediment. The seagrass meadows occur along the subtidal channel at the entrance of the bay and are characterised by the occurrence of *Cymodocea serrulata,* patches of *Thalassodendron ciliatum,* and *Halodule wrightii.* Additional characteristics of the sampled area are described by de Boer (2000) and are supplied together with the results on the environmental parameters measured in the area (Table 1).

Table 1. Mean values of temperature, salinity, turbidity and depth in January–June 2003 in the main sampling habitats at Saco da Inhaca

Habitat	Temperature (°C)	Salinity (‰)	Turbidity (g/l)	Depth (m)	Characteristics	Sediment
Sand flat	26.42 ± 0.60	34.89 ± 0.82	0.12 ± 0.03	0.82 ± 0.18	Gently sloping intertidal sand flat	Coarse/fine
Mud flat	25.83 ± 0.57	34.82 ± 0.82	0.12 ± 0.03	0.94 ± 0.13	Gently sloping intertidal mudflat	Very fine
M-Creek	26.25 ± 0.60	34.67 ± 0.82	0.16 ± 0.10	0.91 ± 0.15	Mid mangrove channel (intertidal)	Coarse
Seagrass	25.38 ± 0.56	34.59 ± 0.83	0.12 ± 0.03	1.08 ± 0.19	Channel bank vegetated (subtidal)	Fine

Sample Collection

Quantitative samples were collected fortnightly at the four defined habitats (Fig.1) during three consecutive nights, as the shrimps are typically more active at night (Vance 1992). Collection were by means of a 1-m (1 x 0.25 m mouth aperture) beam trawl equipped with 2-mm mesh size net at both body and cod-end. The inferior part of the net aperture had a tickler chain (Kuipers et al. 1992) to ensure effective sweeping of the bottom. A small (4 m) boat with a 25 HP outboard engine was used to pull the net. On each sampling three trawls were performed along 50-m long prefixed transects parallel to the coastline. Trawl duration was for one minute at a velocity of 3 km per hour. Samples were collected in each of the selected habitats 1:40 to 2:15 hours after the high water peak when the water depth was about 1 m. The time span of 35 minutes did not interfere with the sampling period between the habitats and was due to differences in tidal height. Preliminary samples showed that at about 1 m depth the abundance of juvenile shrimps was high and diverse near the mangrove fringe. Despite attempts to standardize depth among the habitats it was almost impossible to get all sampled transects at a similar depth due to the gently sloping topography of the habitats specifically at the seagrass meadows. The time elapsed from the first to the fourth sampled habitat was about one hour and thirty minutes. This time allowed the habitats to be sampled when water depth was more-or-less similar. The approximately similar depth in all habitats and the 4 kg of extra weight attached to the frame of the beam trawl enabled efficient sweeping of the bottom sediment. Bottom water temperature, salinity, turbidity and water depth were measured before each trawl using a salinity-conductivity-temperature meter, a turbidity meter and a hand-held portable depth sounder. Shrimps were preserved in 4% formaldehyde solution, diluted with seawater, and returned to the laboratory for examination. All shrimps were identified using Joubert (1965) and Kensley (1972) and carapace length (CL) was measured to the nearest 0.1 mm using a micrometer adjusted to the occular of a stereomicroscope for small specimens (<10 mm), and vernier scale callipers were used for larger specimens.

Data analysis

Environmental factors such as temperature, salinity, turbidity and water depth were compared statistically within and between habitats using two-way ANOVA.

Shrimp catches were expressed as total catches per habitat and as density per 50 m^2 for the whole period of the study. Catch rates (densities) of all captured species: *F. indicus, M. stebbingi, M. monoceros P. japonicus* and *P. semisulcatus* were compared statistically within and between habitats. Repeated two-way ANOVA, after logarithmic log (x+1/2) transformation of catch data, was used to compare environmental factors and shrimp catches between habitats and replicates. Cochran's C Hartley F_{max} test was used when necessary to test for homogeneity of variance before performing the ANOVA. Tukey's (HSD) multiple comparison test was used to identify differences among the mean densities and the environmental parameters (temperature, salinity, water depth and turbidity). Shrimp catches were also tested using a multiple-regression-based approach. Accordingly, in order to assess the relative importance of each environmental parameter as a factor that might influence shrimp catch, all species and each of the four environmental parameters analysed were included in a backward stepwise multiple regression.

Mean CLs were calculated for each species per habitat and sampling date. Difference in mean CL together with spatial distribution and density might help identify ontogenetic trends in habitat preferences and is an important tool in assessing growth, mortality and migration periods (Staples, 1979). Shrimps were grouped in 1-mm class intervals and numbers for each size interval expressed as a percentage of the catch in each habitat. Shrimps with 1 to ≤3mm CL were referred to as postlarvae and over 3 mm CL as juveniles. Postlarvae and juvenile shrimps were separated into groups and their numbers expressed as a percentage of the total catch in each habitat for each of the five species captured. No morphological, behavioural or physiological changes were considered to distinguish postlarvae from juveniles (Young & Carpenter, 1977; Forbes & Benfield, 1986; Haywood et al., 1995).

RESULTS

Physical conditions

The mean values of environmental parameters such as temperature, salinity, turbidity and depth are summarized in Table 1. Bottom water temperature of the four habitats sampled between January and June varied between 18 and 31 °C. The water salinity had a narrow range compared to the temperature range: 33.3 to 36.6 ppt. The water turbidity ranged from 0.09 to 0.16 g/l while water depth ranged from 0.7 to 1.4 m.

Significant differences were found in bottom water temperature, salinity and depth between the habitats (Table 2), but none between water temperature, salinity and turbidity within the habitats (Table 2). The Tukey's HSD multiple comparison test showed that no differences in bottom water temperature were detected between sand flats, mudflats and creeks ($P_1 = P_2 = P_3 > 0.05$), but differences were encountered between all three habitats (sand flat, mudflat and creek) and the seagrass meadows ($P_1 < 0.001$; $P_2 = 0.004$; $P_3 < 0.001$). No differences in water salinity between sand flat, mudflats and creek habitats were found ($P_1 = P_2 = P_3 > 0.05$) but these habitats differed significantly to seagrass in terms of salinity (p_1=<0.001; p_2=0.002 and p_3<0.001). Water depth was also significantly lower in sand flat, mudflat

Table 2. Two-factor ANOVA testing similarity of environmental factors (temperature, salinity, turbidity and water depth) between habitats (H) and replicates (R) for data collected at Saco da Inhaca during January–June 2003 (df=degrees of freedom, MS=mean squares, F=Fmax Hartley test)

Environmental parameter	Source	df effect	MS effect	F	P-level
Temperature	Habitat (H)	3	15.65934	5.65278	<0.001
	Replicate (R)	2	0.09730	0.035123	0.96540
	H x R	6	0.17986	0.064925	0.99891
Salinity	Habitat (H)	3	1.976024	6.3291	<0.001
	Replicate (R)	2	0.494958	1.583343	0.20667
	H x R	6	0.090427	0.289636	0.94161
Turbidity	Habitat (H)	2	0.00229	2.83880	0.14023
	Replicate (R)	6	0.00004	0.03248	0.96804
	H x R	2	0.00001	0.006541	0.9989
Depth	Habitat (H)	2	0.8402	78.2525	<0.001
	Replicate (R)	3	0.074848	6.9706	0.00111
	H x R	6	0.024989	2.3272	0.032832

and creek habitats (0.7-1.1m) compared to seagrass meadows (0.9-1.4 m, $p_1=p_2=p_3<0.001$). Turbidity was slightly higher in the creek compared to the other habitats. However, no differences were reported in the analysis (Table 2).

Shrimp catches and abundances

Four hundred and thirty-two (432) trawls were performed during the study period at the four habitats around Saco da Inhaca corresponding to a trawled area of 21,600 m². A total of 14,976 specimens belonging to five species of penaeid shrimps were captured: *Fenneropenaeus indicus, P. japonicus, P. semisulcatus*, and *Metapenaeus stebbingi*. One unidentified species of *Metapenaeus* was also found in the seagrass habitat but not included in the statistical analysis owing to the very low numbers collected.

Fenneropenaeus indicus, M. monoceros and *M. stebbingi* were the most common species captured during the study period, accounting for about 80% of the total catch (Fig. 2). In terms of distribution between the four habitats, *F. indicus, M. stebbingi* and *P. japonicus* were significantly more abundant in the sand flat habitat than in the other three habitats while *M. monoceros* was dominant in the mudflat. *Penaeus semisulcatus* was almost exclusively captured in the seagrass habitat.

Figure 3 shows shrimp densities throughout the study period. Different mean catch values can be depicted for each of the shrimp species for the study period. The shrimp mean densities per 50 m² were 27± 0.75 for *F. indicus*, 25± 0.45 for *M.*

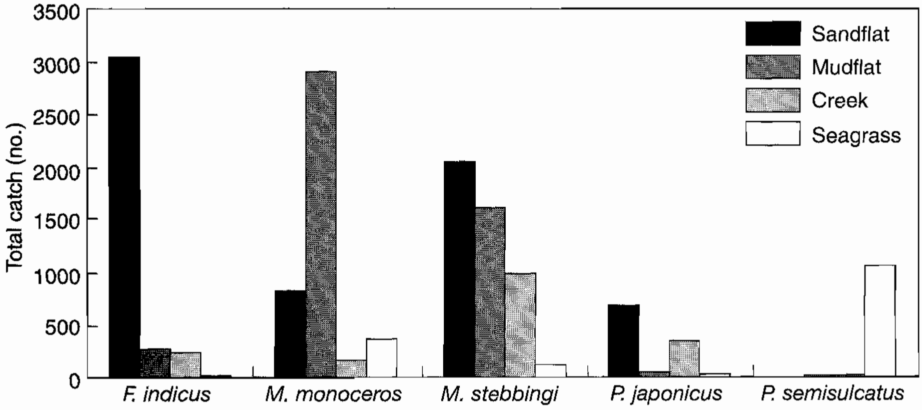

Fig. 2. Total numbers of penaeid juvenile shrimp species caught at each of the sampled habitats at Saco da Inhaca throughout the period from January-June 2002.

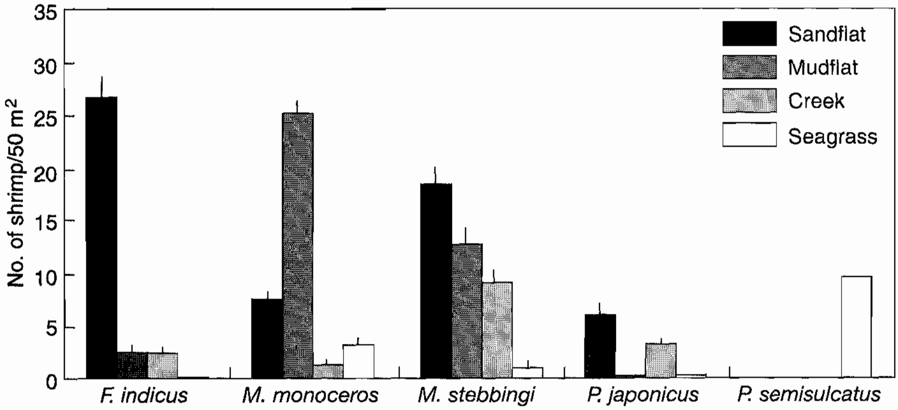

Fig. 3. Mean numbers (± S.E.) of juvenile shrimps captured in four habitats around Saco da Inhaca during the study period from January until June 2002. In each month, n = 72 tows (18 per habitat) were taken.

monoceros, 21± 0.31 for *M. stebbingi*, 7±0.31 for *P. japonicus*, and 10± 0.81 for *P. semisulcatus* for the whole study period. Significant statistical differences were found in shrimp abundance across the habitats (Table 3).

Shrimp abundance differed between habitats. Tukey's HSD multiple comparison test showed that *F. indicus* abundance differed between sand and creek, between sand and mud and between sand and seagrass ($p_1=p_2=p_3 <0.001$), but no significant differences were found between seagrass and creek or between seagrass and mud ($P_1=P_2 >0.05$).

Metapenaeus monoceros also showed significant differences between habitats, with shrimp abundance in the sand flat significantly different from mud ($P_1<0.001$) and from creek ($P_2 < 0.001$) as well as between mud and creek ($P_3 < 0.001$). ANOVA showed that *M. stebbingi* also differed significantly in abundance between sandflat and creek ($P < 0.001$) and between sandflat and seagrass ($p < 0.001$), between creek and mud ($P < 0.05$) as well as between seagrass and creek ($P < 0.01$) but no differences were noted between sand flat and mud ($p>0.05$). For *P. japonicus* Tukey's HSD test also showed significant differences between sandflat and mud, between sandflat and creek, between mudflat and creek and between creek and seagrass ($P_1=P_2=P_3=P_4<0.001$) but no differences were detected between mud and seagrass ($p>0.05$). *Penaeus semisulcatus* was more restricted to seagrass meadows and very few specimens were captured in the other habitats. Its high density in seagrass differed significantly from its lower densities in each of the other three habitats ($p<0.001$).

Catches and environmental parameters

Multiple regression runs on shrimp catches (log-transformed data) and some of the environmental parameters provided useful data for the interpretation of the potential causes of variation in shrimp abundances between the four studied habitats (Table 4). *Fenneropenaeus indicus* abundance was strongly related to decreasing water depth and salinity and significantly related to increasing temperature and turbidity. Depth and salinity variation was negatively related to *P. japonicus* while no relationship was found with temperature and turbidity. *Penaeus semisulcatus* abundance was negatively related to temperature but positively to water depth and turbidity. The abundance of *M. monoceros* was significantly related only to turbidity, while *M. stebbingi* abundance was positively related to both temperature and salinity but negatively to depth (Table 4).

Table 3. Two-factor ANOVA on differences in density of shrimps in each habitat (H) sampled at Saco da Inhaca from January-July 2002. (df=degrees of freedom, MS=mean squares, F=Fmax Hartley test)

Shrimp species	Source	df effect	MS effect	F	P-level
F. indicus	Habitat (H)	3	18826.08	93.41824	<0.001
	Replicate (R)	2	197.81	0.98159	0.42775
	H x R	6	201.52	0.33440	0.91867
P. japonicus	Habitat (H)	3	891.5332	45.50179	<0.001
	Replicate (R)	2	22.9606	1.17186	0.37186
	H x R	6	19.5934	1.0740	0.37726
P. semisulcatus	Habitat (H)	2	2643.886	729.037	<0.001
	Replicate (R)	6	2.787	0.7685	0.50449
	H x R	2	3.627	0.1925	0.97886
M. monoceros	Habitat (H)	2	14427.51	145.1544	<0.001
	Replicate (R)	3	154.03	1.5497	0.28669
	H x R	6	99.39	1.1788	0.31651
M. stebbingi	Habitat (H)	2	6294.453	41.63491	<0.001
	Replicate (R)	3	24.009	0.15881	0.85663
	H x R	6	151.182	0.74885	0.610612

Table 4. Multiple regression coefficients (r^2) of shrimp catch and abiotic factors (temperature, salinity, turbidity and depth), F(4,427), ns-not significant, *-p < 0.05, **-p < 0.01, *-p < 0.01. (-), negatively correlated**

	Source of variation			
Species	Temperature (°C)	Salinity (‰)	Depth (m)	Turbidity (g/l)
F. indicus	0.87 ***	(-) 0.11*	(-) 0.27***	0.38***
P. japonicus	0.05 ns	(-) 0.18 ***	(-) 0.33 ***	0.09 ns
P. semisulcatus	(-) 0.26 **	(-) 0.05 ns	0.52 ***	0.35 ***
M. monoceros	(-) 0.01 ns	(-) 0.02 ns	(-) 0.11 ns	0.11 *
M. stebbingi	0.27 ***	0.34 ***	(-) 0.25 ***	0.03 ns

Shrimp sizes

A considerable number of very small shrimps dominated the catches throughout the study period. Cumulative length frequency histograms per habitat and species are presented in Figure 4 a & b. For *P. japonicus* and *M. monoceros* the number of specimens within the 3 mm CL group were higher than for any other size group in all habitats. For *F. indicus* the 3 mm CL class was most numerous in creeks and sand flat but in mudflat and seagrass the most abundant size group was 6 mm. For *M. stebbingi* catches of size class 3 mm occurred in creeks, sand flat and mudflat. In the seagrass the modal size class was 5 mm. *Penaeus semisulcatus* showed highest abundance in class 3 mm CL in the seagrass and no consistent mode could be identified in other habitats as too few specimens were captured (Fig. 4 a, b). There were distinct differences in the size distribution patterns of the species between the four habitats (Fig. 5). Mean carapace length of all juvenile shrimps captured varied between species and between the four sampled habitats ranging from 5.95 mm to 8.42 mm CL. Among the species captured in all habitats, *F. indicus* showed the largest mean CL (8.42±0.73 CL) and *M. stebbingi* the shortest mean CL (5.9±0.55 CL). The remaining two species, *P. japonicus* and *M. stebbingi* had a mean CL of 6.67± 0.53 and 5.95±0.55, respectively (Fig. 5). *Fenneropenaeus indicus, P. japonicus,* and *P. semisulcatus* showed similar associations between mean CL and habitat. Smaller shrimps were captured in sand flats and creeks while bigger sizes were caught in the mud and seagrass habitats. *Metapenaeus monoceros,* and *M. stebbingi* showed a consistent aggregation of smaller sizes in mud, sand and creeks (areas closer to mangroves) while the bigger shrimps were dominant in the seagrass meadow (Fig. 5).

The relative abundance of postlarvae also showed a distinct distribution with habitat. The majority of *F. indicus, P. japonicus, M. monoceros* and *M. stebbingi* specimens captured were postlarvae (sizes 1- ≤ 3mm) (Table 5). In general, postlarvae were more common in the sand flat, mudflats and creeks for all species except *P. semisulcatus,* which occurred almost exclusively in the seagrass. Fifty three per cent of total species caught during the study period were postlarvae and the remaining percentage were juveniles of dominant sizes (4-8 mm CL). *Fenneropenaeus indicus* postlarvae and juveniles occurred in almost similar proportions in the sand flat, but in other habitats juveniles were more common but found in negligible abundances (Table 5). *Metapenaeus monoceros,* both postlarvae and juveniles, were most abundant in mudflat habitats followed by sand flat where juveniles were higher in abundance. A small fraction was distributed between creek and seagrass habitats. *Metapenaeus stebbingi* was the only species occurring in similar abundance in mudflat and sandflat. It also occurred in a fairly high percentage in the creek but in negligible numbers in seagrass. *Penaeus japonicus* postlarvae and juveniles were numerous in the sand flat and creeks but they were captured in low numbers in the mudflat and seagrass. *Penaeus semisulcatus* postlarvae and juveniles occurred basically in the seagrass habitat, but the juveniles were 4 times more abundant than postlarvae (Table 5).

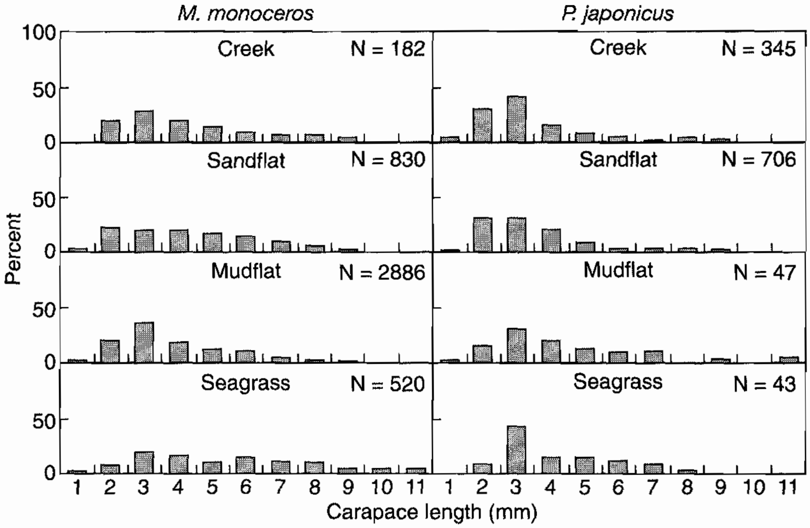

Fig. 4a. Length–frequency distributions (%) of *M. monoceros* and *P. japonicus* caught in the four habitats during the study period at Saco da Inhaca.

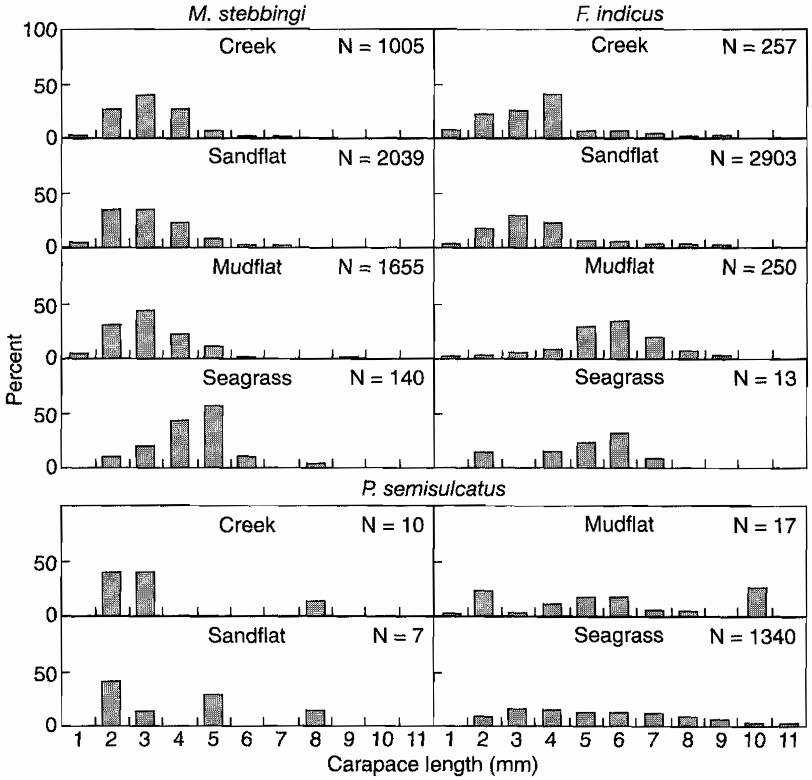

Fig. 4b. Length–frequency distributions (%) of *M. stebbingi, F. indicus* and *P. semisculcatus* caught in the four habitats during the study period at Saco da Inhaca

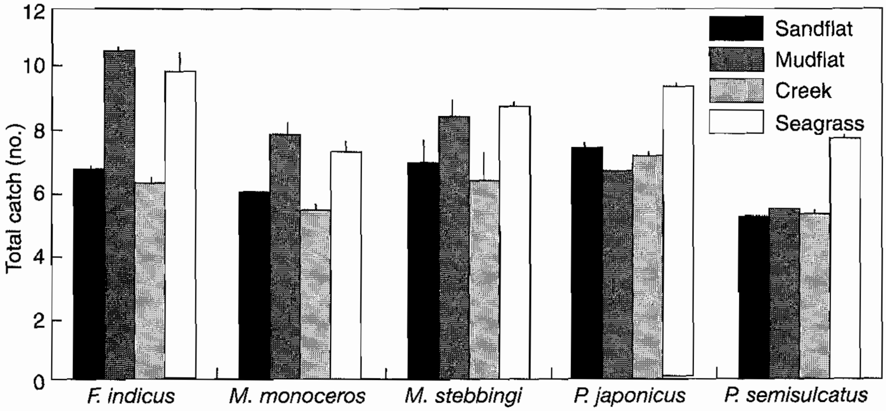

Figure 5. Mean carapace length (± S.E.) of the juvenile shrimp species captured in different habitats throughout the study period.

Table 5. Comparative relative abundance (%) of juvenile penaeid shrimp postlarvae (PL, ≤ 3 mm CL) and juveniles (JV, ≥ 3 mm CL) in each of the four sampled habitats (total n=14,976)

	Creek		Sand flat		Mudflat		Seagrass	
Species of shrimp	PL	JV	PL	JV	PL	JV	PL	JV
F. indicus	3	4	**44**	**41**	1	7	0	0
M. monoceros	2	2	8	11	**36**	**29**	3	9
M. stebbingi	13	7	**29**	13	**29**	11	1	2
P. japonicus	21	9	**39**	**23**	2	2	2	2
P. semisulcatus	1	0	0	0	0	1	**19**	**79**

DISCUSSION

Shrimp catches and distribution among the habitats

All species captured in the study area are of economic importance and comprise the same species captured in Maputo Bay by commercial trawling fisheries. *Metapenaeus stebbingi* comprised 32% of the catches while *M. monceros* was 29%, and *F. indicus*, 23%. Of the remaining 16%, 9% were *P.japonicus* and 7% were *P. semisulcatus*. This pattern of juvenile abundance does not reflect the pattern of abundance found for the adult population in the shrimp fisheries at Maputo Bay where *F. indicus* and *M. monoceros* comprise 80% of the total catches (Sousa, 1985;1987; Macia, 1990). This result suggests perhaps that the mortality of *M. stebbingi* before reaching the fishing areas is higher compared with the other two species, or perhaps this species prefers areas that are not fished commercially. However, it is also important to note that this result only refers to Saco Bay, which is one of the potential nursery areas for commercial shrimps. There are many other nursery areas around Maputo Bay such as estuaries and mangrove habitats that were not accounted for in this study but contribute to the commercial shrimp fishery. On the other hand the differences in the recruitment peak may be another source of differences in abundance between these species. *Fenneropenaeus indicus*, during the period of the study, seemed to have peaked before the first January sampling month, suggesting that a great proportion of recruiting post-larvae and juveniles were missed.

Penaeid shrimps were not evenly distributed among the sampled habitats in spite of their adjacent locations. This suggests different habitat preferences between the species and that the nursery habitat requirement for the juvenile penaeid species is not necessarily the same as for the adults. This result also emphasises spatial partitioning among the species captured, which reduces competition for space and food. In general, the shrimps were significantly more abundant in mud flats and sand-flats compared to other habitats. However, some species appear to be more widespread, foraging over much wider areas. This is the case for *M. stebbingi, M. monoceros* and to a lesser extent for *F. indicus* and *P. japonicus*. In contrast, *P. semisulcatus* showed a very restricted distribution pattern, suggesting habitat specialization from postlarvae to larger juvenile stages. With respect to substrate type, the distribution pattern of the five species sampled is similar to those reported by Hughes (1966), de Freitas (1986) and Abdurremane (1998) despite differences in the periods of tides when samples where collected.

Hughes (1966) and de Freitas (1986) found *F. indicus* in muddy areas within the mangrove swamps and channels, which might indicate a preference for mangrove areas. Abdurremane (1998) could not find *F. indicus* in her study and suggested that this species may enter the mangrove forest during high tide and is thus unavailable in daylight catches.

The distribution of juvenile shrimps within the mangrove forest and adjacent sand flat at Saco da Inhaca, has simultaneously been studied by Rönnbäck et al. (2002). *Fenneropenaeus indicus* and *M. monoceros* were found to make extensive use of the mangroves, but *F. indicus* was the most abundant species in the mangroves compared to intertidal sand flats while *M. monoceros* preferred sand flats. Their study showed a higher preference of *F. indicus* for mangrove habitats in comparison to sand flat habitat. The preference of this species for mangroves was more pronounced as individuals grew bigger than 4 mm. As larger shrimp are more powerful swimmers, the trend shows a more active choice of refuge. This may explain why Abdurremane (1998) did not catch *F. indicus* when using a sampling net of 5 mm aperture mesh size. Staples (1979) reported that *P. merguiensis*, a species closely related to *F. indicus*, became unavailable for capture at high tide in an Australian estuary as a result of migration towards the mangrove areas, where predation pressure is reduced. This finding may explain why *F. indicus* abundance increases near the fringing mangrove during the ebb tide.

Metapenaeus stebbingi was the only species that was widespread over the habitats examined. Surprisingly this species was not reported by Hughes (1966) in his study at Saco da Inhaca, perhaps due to the period of the year when the samples were taken. Its pattern of distribution confirms the findings of de Freitas (1986) and Abdurremane (1998) for bare sand substratum, the firm muddy sand, mud and among the mangrove pneumatophore zone fringing the bay. *Penaeus japonicus* was mostly found in the sand flat and mudflat. Forbes & Benfield (1986), reported *P. japonicus* to occur in soft bottom and turbid water habitat in St. Lucia in South Africa. Hughes (1966) also did not report this species at Saco da Inhaca and de Freitas (1986) suggested that the species identified by Hughes as *P. semisulcatus*, occurring in the shallow pools on the intertidal flats adjacent to the *Dotilla* sand flats, was probably *P. japonicus* since it was uncharacteristic for this species to be abundant in the sand flats. The results of this study are consistent with de Freitas's observation and revealed that the most common species captured in the sand flats as well as in the "*Dotilla* sand flats" (Hughes, 1966) was *P. japonicus* and probably not *P. semisulcatus*, since during the whole sampling period few specimens were captured in any other habitat but seagrass. However, the period of the year and time of sampling could be another reason affecting these comparisons. *Penaeus semisulcatus* in this study was strongly associated with seagrass meadows as reported from Australia (Staples et al., 1985, Loneragan et al. 1998). Similar results are reported by de Freitas (1986) for Maputo Bay and by Abdurremane (1998) for Saco da Inhaca. This study therefore supports the nursery function previously attributed to the seagrass meadows.

In terms of the density of shrimps in general, the values obtained in this study are comparable to densities obtained from other geographic areas. (Staples et al., 1985, Haywood et al., 1995; Primavera, 1998; Kangas & Jackson, 1998). However, care should be taken when comparing catches at different locations and times of sampling, which may cause differences in shrimp abundances due to tidal height. Comparing the shrimp densities of *F. indicus* and *M. monoceros* captured by stake nets (Rönnbäck et al., 2000) with this result, the overall mean value obtained by these authors in the same sand flat for *F. indicus* and *M. monoceros* were of the same magnitude as the present study, but the mean values within the fringing mangroves were eight times greater for *F. indicus*. This result emphasizes the importance of mangrove habitats for *F. indicus* compared to the other species occurring at Saco da Inhaca. The comparison of these studies also showed that *M. monoceros* was more common in the sandflats compared to the mangrove area, which together with the results from this study suggests that the mudflats are relatively more important for this species than other habitats.

Size distribution

The results in this study revealed that mangrove-adjacent habitats at Saco da Inhaca are highly utilized by postlarvae and juvenile penaeid shrimps during the early stage of their life cycles. Catches were entirely dominated by shrimps of carapace length smaller than 5 mm (Fig. 4a,b) and shrimp found in the majority of habitats were not bigger than CL 8 mm, which stresses the importance of this area as a potential nursery for penaeid species. *Metapenaeus monoceros* showed a wider range of size distribution within the four studied (Fig. 4a,b) while *Penaeus semisulcatus* was the only species with fairly high numbers of juveniles compared to postlarval shrimps in the seagrass.

The size–frequency distribution reported by de Freitas (1986) in the coastal areas of Maputo Bay close to Maputo city for all species studied was beyond the sizes found in this study and ranged from 16–45 mm for the five species studied. Abdurremane (1998) reported size frequencies ranging from 5 to 17 mm which was much closer to the results obtained in this study, despite the lack of postlarvae in her study. The differences encountered in the size ranges between the three studies are probably due to mesh size differences or more likely due to differences in nursery function.

With the exception of *P. semisulcatus* all shrimp species with carapace length ≤ 3 mm occurred in higher numbers in the sand flat, mudflat and creek. It is clear that not all shrimp postlarvae settle in all sampled habitats at the same magnitude. It seems therefore, that once in the nursery area postlarvae select their preferred habitat for settlement. However, some species are more restricted to one or two main habitats where catches were higher. All shrimps of the same genus showed alternatively similar patterns of distribution of mean carapace lengths over the habitats. *Metapenaeus monoceros* and *M. stebbingi* were similar in their preference and behaviour, as well as in morphology.

Bigger shrimps of the genus *Penaeus* were found in the mud and the seagrass beds and smaller shrimps were found in the sand flat and creeks while *Metapenaeus* species were much bigger in the seagrass and much smaller in the other three habitats (Fig. 5). As the shrimps grow bigger they apparently move to deeper waters and the mud and seagrass are the deepest areas of the Saco. They act as transition habitats for these shrimps.

One of the factors that may contribute substantially to the pattern of distribution of smaller sizes in close proximity to mangroves could also be the water current. Smaller shrimps are expected to be less active swimmers than bigger shrimps, therefore may be a tendency for net transport to the mangrove edges and mud flats (Vance et al., 2002; Rönnbäck et al., 2002; Loneragan et al., 1998). Data collected during 14 months near the mangrove forest (sand flat habitat) at Saco da Inhaca, also found that sizes smaller than 3 mm CL dominated the catches (Macia, unpublished data).

Haywood et al. (1995) reported considerably higher densities of postlarvae and juveniles of *P. semisulcatus* in seagrass meadows at the Gulf of Carpentaria in Australia. Loneragan et al. (1998) have also shown the same pattern of distribution and abundance of postlarvae and juveniles of tiger shrimps *(P. semisulcatus)*; however, considerable numbers of postlarvae were found in seagrass together with larger-sized juveniles in the seagrass beds. In this study, this species showed a high number of postlarvae and juveniles occurring together (98%) in the seagrass habitat with only the remaining 2% percent of specimens captured in the other habitats.

Environmental parameters

There are many environmental parameters governing shrimp distribution in coastal areas. In this study salinity, temperature, turbidity and depth varied significantly between the habitats. The seasonal variation of these factors has been shown to influence shrimp abundance in the area as previously reported by Macia (unpublished) and other authors such as Dall et al. (1990) and Vance et al. (1996) for Australian shrimps. However, in this study sediment type and depth differences are most responsible for differences in shrimp abundances between habitats.

The strong positive correlation encountered between *P. semisulcatus* and depth could partially explain the low abundance in the other three habitats compared to seagrass areas. On the other hand, the high density of *F. indicus* in the sand flats reflected the movement of this species from mangrove forests due to depth reduction. Therefore, its abundance does not seem to reflect a preference for the habitat, but perhaps its transition to the waterways in the bay caused by the ebbing tide. It is important therefore, to understand the shrimp dynamics in the area so as to interpret results correctly.

Other studies have emphasized the role of environmental parameters in determining the distribution of juvenile shrimps in coastal areas. Penn (1984) reported that *F. indicus* prefers soft sediment over hard. Grady (1971) found that the greatest catches of penaeid shrimps in the Gulf of Mexico were made over bottoms with fine substrata, either sand-silt or sand-silt-clay.

Branford (1981) showed that *P. semisulcatus* did not have a clear preference for different sizes of sediment, and Moller & Jones (1975) found *P. semisulcatus* burrowing in a range of different sediment particle sizes. Penn (1981) explained variation in abundance of *P. esculentus*—a species closely related to *P. semisulcatus*—in Australia as probably being due to depth variation. *Penaeus japonicus* is known to be inhibited from burrowing in fine sand and fine gravel thus their preferred particle range is from 500μm to 2μm (Otazu-Abril & Ceccadi, 1981). This finding may explain why *P. japonicus* was found in low quantities in the mud habitat. Substrate itself has other properties that may influence penaeids that burrow into it, for example, organic content that can affect feeding

Metapenaeus monoceros and *M. stebbingi* also showed a high abundance in the mud-flat habitat and sand-flat. Previous studies found that *M. monoceros* (Hughes 1966; de Freitas 1986) and other related species, e.g. *M. ensis* (Staples et al., 1985, Sasekumar et al., 1992), are widely distributed among coastal habitats and this may be associated with their ability to burrow. Joshi et al. (1979) showed that *M. monoceros* preferred mud substrates. and this preference may be associated with the predation avoidance or food availability. Macia et al. (2003) also found that predation of *M. monoceros* by *Terapon jarbua* in aquaria experiments was reduced on mud substrate compared to sand and shell debris substrate types. It has been reported that the amount of organic content constitutes an important factor determining penaeid shrimp abundance (Dall et al., 1990). In an attempt to assess the carbon sources of juvenile shrimps occurring at Saco da Inhaca, Macia (unpublished) found that *F. indicus* and *M. monoceros* isotope signatures were highly correlated to sediment signatures where they were collected. The results from this unpublished study also revealed that *M. monoceros* has a wide range of carbon signals which supports its wide distribution in the field.

CONCLUSIONS

The differences in habitat preference by penaeid shrimp species seen from this study emphasise their spatial partioning to reduce competition for space and food. Previous studies have reported a similar findings (Staples et al., 1985; de Freitas, 1986; Primavera, 1998; Rönnbäck et al., 2002) and a tidal migration has been described for the shrimp *Palaemon peringueyi* between seagrass beds and channels (Emmerson, 1987). This study also showed that areas adjacent to mangroves such as the intertidal sand flat, mudflat, creek and seagrass were crucially important for all commercial species captured in the area. Even species associated with mangroves, species such as *F. indicus*, utilize the adjacent habitats during low tide. This finding is of crucial importance for management and the protection of nursery areas. Mangrove conservation should therefore include the adjacent areas. Therefore, the utilization of adjacent habitats during low tide needs to be addressed in future studies, to determine whether juvenile shrimps leave the Saco area completely during low tide.

Penaeus semisulcatus was influenced significantly by seagrass presence and depth variation. Water depth and sediment type, among others, were the factors most responsible for differences in shrimp abundances between habitats. However, water currents, as suggested by Vance et al. (2002), Loneragan et al. (1998) and Dall et al. (1990) may also have an important influence on shrimp abundance.

Size–frequency distributions among habitats show that the proportions of smaller shrimps are greater closer to the mangrove areas than further away from the mangroves. Bigger shrimps occur in the subtidal areas, which probably act as a transition area during migration periods.

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REFERENCES

Abdurremane, Z. (1998) Distrubição e abundância de camarão juvenile no Saco da Inhaca. Tese de Licenciatura, Universidade Eduardo Mondlane, Maputo. 53 pp.

Branford, R. J. (1981) Sediment and distribution of Penaeid shrimp in the Sudanese Red Sea. *Est. Coast. Shelf Sci.* 13: 349-354.

Chong, V. C. (1995) The prawn-mangrove connection-fact or fallacy? *In:* Seminar on Sustainable Utilization of Coastal Ecosystems for Agriculture, Forestry and Fisheries in Developing Regions held in Kuala Lumpur, Malaysia. Japan International Research Center for Agricultural Science (JIRCAS). pp. 3-20.

Chong, V. C., Sasekumar, A., Wolanski E. (1996) The role of mangrove in retaining penaeid prawn larvae in Klang Strait, Malaysia. *Mang. Salt Mars.* 1: 11-22.

Coles, R. G., Lee Long, W. J., Squire, B. A., Squire, L. C. & Bibby, J. M. (1987) Distribution of seagrasses and associated juvenile commercial Penaeid shrimps in North-eastern Queensland Waters. *Aust. J. Mar. Freshw. Res.* 38: 103-119.

Dall, W., Hill, B. J., Rothisberg, P. C. & Staples, D. J. (eds.) (1990) The biology of the Penaeidae. *Adv. Mar. Biol.* 27: 1-489.

de Boer, W. F., Rydberg, L. & Saíde, V. (2000) Tides their effects on the intertidal ecosystem of southern bay, Inhaca Island, Mozambique. *Hydrobiologia* 428: 187-196.

de Boer, F. W. & Longamane, A. F. (1996) The exploitation of intertidal food resources in Inhaca Bay, Mozambique, by shorebirds and humans. *Biol. Conser.* 78: 295-303.

de Boer, F. W. (2000) Biomass dynamics of seagrasses and the role of mangrove and seagrass vegetation as different nutrient sources for an intertidal ecosystem in Mozambique. *Aq. Bot.* 66: 225-239.

Emmerson, W. D. (1987) Tidal migration and feeding of the shrimp *Palemon pacificus* (Tsimpson). *S. Afri. J. Sci.* 83: 413-412.

Forbes, A. T. & Benfield, M. C. (1986) Tidal behaviour of post-larval penaeid prawns (Crustacea: Decapoda:Penaeidae) in a southeast African estuary. *J. Exp. Mar. Biol. Ecol.* 102: 23-34.

de Freitas, A. J. (1986) Selection of nursery areas by six Southeast African Penaeidae. *Est. Coast. Shelf Sci.* 23: 901-908.

Garcia, S. & Le Reste, L. (1981) Life cycle, dynamics, exploitation and management of coastal penaeid shrimp stocks. FAO Fisheries Technical Paper. pp. 203-215.

Grady, J. S. (1971) The distribution of sediment properties and shrimp catch on two shrimp grounds on the continental shelf of the Gulf of Mexico. *In:* Proceedings of the Gulf and Caribbean Fisheries Institute, 23rd Annual Session. pp. 139-148.

Guerreiro, J., de Freitas, S., Paula, J., Fidalgo, P. & Macia, A. (1996) Sediment macrobenthos of an Eastern-African mangrove. *Cah. Biol. Mar.* 37: 309-327.

Haywood, M. D. E, Vance, D. J. & Loneragan, N. R. (1995) Seagrass and algal beds as nursery habitats for tiger prawns (*Peaneus semisulcatus* and *P. esculentus*) in a tropical Australian estuary. *Mar. Biol.* 122: 213-223.

Hughes, D. A. (1966) Investigations of the nursery areas and habitat preferences of juvenile shrimps in Mozambique. *J. of Appl. Ecol.* 3: 349-354.

Joshi, P. K., Kulkarni, G. K. & Nagabhushanam, R. (1979) Studies on the behaviour and substratum preference in juveniles of the marine prawn, *Metapenaeus monoceros* (Fabricius). *Hydrobiologia* 65: 195-198.

Joubert, L. S. (1965) A preliminary report on the penaeid shrimps of Durban Bay. South African Association for Marine Biological Research, Oceanographic Research Institute. Durban. Investigational report of the Oceanographic Research Institute. 11: 1-32.

Kangas, M. I. & Jackson, W. B. (1998) Sampling juvenile *Penaeus latisulcatus* Kishinouye with a water-jet net compared with a beam-trawl: spatial and temporal variation and nursery areas in Gulf St Vincent, South Australia. *J. Mar. Freshw Res.* 49: 517-523.

Kensley, B. (1972) Shrimps and prawns of southern Africa. South African Museum, Cape Town. 68 pp.

Kuipers, B. R., Maccurrin, B. J., Miller, M., Van Der Veer, H. W. & Witte, J. I. J. (1992) Small trawls in juvenile flatfish research: their development and efficiency. *Neth. J. Sea Res.* 29(1-3): 109-117.

Laegdsgaard, P. & Johnson, C. R. (1995) Mangrove habitat as nursery: unique assemblages of juvenile fish in subtropical mangroves in eastern Australia. *Mar. Ecol. Prog. Ser.* 126: 67-81.

Loneragan, N. R., Kenyon, R. A., Staples, D. J., Poiner, I. R., Conacher, C. A. (1998) The influence of seagrass type on the distribution and abundance of post-larval and juvenile tiger prawns (*Penaeus esculentus* and *P. semisulcatus*) in western Gulf of Carpentaria, Australia. *J.Exp. Mar. Biol. Ecol.* 228: 175-195.

Macia, A. A. Jr. (1990) Estudo de duas espécies de camarão (*Fenneropenaeus indicus* e *Metapenaeus monoceros*) capturadas nas pescarias artesanal e semi-industrial da Baía de Maputo.Tese de licenciatura. Universidade Eduardo Mondlane, Maputo. 53 pp.

Macia, A., Abrantes, K., & Paula, J. (2003) Thorn fish *Terapon jarbua* (Forskål) predation on juvenile white shrimp *Fenneropenaeus indicus* H. Milne Edwards and brown shrimp *Metapenaeus monoceros* (Fabricius): The effect of turbidity, prey density, substrate type, and pneumatophore density. *J. Exp. Mar. Biol. Ecol.* 291: 29-56.

Macia, A. (Unpublished). Seasonal variation in abundance of four juvenile penaeid shrimps in a mangrove adjacent sand flat, the Saco da Inhaca, Southern Mozambique.

Macnae, W. & Kalk, M. (1969) A Natural History of Inhaca Island, Mozambique. Witwatersrand University Press, Johannesburg. 163 pp.

Macnae, W. (1974) Mangrove forests and fisheries. IOFC/DEV/74/34, FAO, Rome. 35 pp.

Moller, T. H. & Jones, D. A. (1975) Locomotory rhythms and burrowing habits of *Penaeus semisulcatus* (de Haan) and *P. monodon* (Fabricius) (Crustacea: Penaeidae). *J. Exp. Mar. Biol. Ecol.* 18: 61-77.

Otazu-Abril, M. & Ceccadi, H. J. (1981) Contribution à l'etude du comportement de Penaeus japonicus (Crustacé Décapode) en élevage, vis-à-vis de la lumière et du sediment. *Tethys* 10: 149-156.

Palha de Sousa, L. (1989) Distribuição e biologia das espécies de camarão de águas pouco profundas. *Rev. Inv. Pesq.* 18: 43-46.

Penn, J. W. (1984) The behaviour and catchability of some commercially exploited penaeids and their relationship to stock and recruitment. *In:* Gulland, J. A. & Rothschild, B. J. (eds.) Penaeid shrimps - their biology and management. Fishing News Books. Farnham, England. pp. 173-186.

Penn, J. W. (1981) A review of mark-recapture and recruitment studies on Australian penaeid shrimp. *Kuw. Bull. Mar. Sci.* 2: 227-247.

Primavera, J. H. (1998) Mangroves as nurseries: Shrimp Populations in Mangrove and Non-mangrove Habitats. *Est. Coast. Shelf Sci.* 46: 457-464.

Primavera, J. H. (1997) The role of structures and substrate on fish predation on penaeid shrimps. *J. Exp. Mar. Biol. Ecol.* 215(2): 205-216.

Primavera, J. H. (1996) Stable carbon and nitrogen isotope ratios of penaeid juveniles and primary producers in a riverine mangrove in Guimaras, Philippines. *Bull. Mar. Sci.* 58: 675-683.

Primavera, J. H. & Lebata, J. (1995) Diel activity patterns in Metapeneaus and Peneaus juveniles. *Hydrobiologia* 295: 295-302.

Robertson, A. I. & Blaber, S. J. M. (1992) Plankton, epibenthos and fish communities. *In:* Robertson, A. I. & Alongi, D. M. (eds.) Tropical Mangrove Ecosystems (Coastal and Estuarine Studies No. 41. American Geophysical Union, Washington DC. pp. 173-224.

Robertson, A. I. & Duke, N. C. (1987) Mangroves as nursery sites: comparison of abundance and species composition of fish and crustaceans in mangroves and other near shore habitats in tropical Australia. *Mar. Biol.* 96: 193-205.

Rönnbäck, P., Macia, A., Amqvist, G., Schultz, L. & Troell, M. (2002) Do penaeid shrimps have a preference for mangrove habitats? Distribution pattern analysis on Inhaca Island, Southern Mozambique. *Est. Coast. Shelf Sci.* 55(3): 427-436.

Rönnbäck, P., Troell, M., Kautsky, N. & Primavera, J. H., 1999. Distribution pattern of shrimps and fish among Avicennia and Rhizophora microhabitats in Pagilao mangroves, Philippines. *Est. Coast. Shelf Sci.* 48: 223-234.

Stoner, A. W. (1995) A nursery ground for four tropical penaeus species: Lagna Joyuda, Puerto Rico. *Mar. Ecol. Prog. Ser.* 42: 133-141.

Sasekumar, A., Chong, V. C. M., Leh, U. & D'Cruz, R. (1992) Mangroves as habitat for fish and prawns. *Hydrobiologia* 247: 195-207.

Sousa, M. I. (1985) Actividade de pesca de emalhe e de arrasto na Baía de Maputo. *Bololetim de Divulgação (IIP)* 10: 19-41.

Sousa, M. I. (1987) Estimativa da captura total de peixe e camarão das capturas de emalhe e arrasto na Baía de Maputo. *Boletim de Divulgação (IIP)* 17: 4-9.

Staples, D. J. (1979) Effects of changes in catchability on sampling of juvenile and adolescent banana shrimps, *Penaeus merguiensis* de Man. *Aust. J. Mar. Freshw Res.* 30: 511-519.

Staples, D. J., Vance, D. J. & Heales, D. S. (1985) Habitat requirements of juvenile penaeid shrimps and their relationship to offshore fisheries. *In:* Rothlisberg, P. C., Hill, B. J. & Staples, D. J. (eds.) Second Australian National Shrimp Seminar NPS, Cleveland, Australia. pp. 47-54.

Subramaniam, S. P. (1990) Chwaka Bay (Zanzibar, East Africa) as nursery ground for penaeid shrimps. *Hydrobiologia* 208: 111-122.

Vance, D. J. (1992) Seasonal migration pattern of post larval and juvenile banana prawns *Penaeus merguiensis* in the major rivers of the Gulf of Carpentaria. Australia. *Aust. J. Mar. Freshwater Res.* 30: 143-157.

Vance, D. J., Haywood, M. D. E., Heales, D. S., Kenon, R. A., Loneragan, N. R. & Pendrey, R.C. (2002) Distribution of juvenile penaeid prawns in a mangrove forest in a tropical Australian estuary, with particular reference to *Penaeus merguiensis*. *Mar. Ecol. Prog. Ser.* 228: 165-177.

Vance, D. J., Haywood, M. D. E., Heales, D. S., Kenon, R. A. & Loneragan, N. R., (1998) Seasonal and annual variation in abundance of postlarvae and juvenile banana shrimps *Penaeus merguiensis* and environmental variation in two estuaries in tropical northeastern Autralia: a six-year study. *Mar. Ecol. Prog. Ser.* 163: 21-36.

Vance, D. J., Haywood, M. D. E. & Staples, D. J. (1996) How far do prawns and fish move in mangrove? Distribution of banana prawn *P.merguiensis* and fish in tropical mangrove forest in northern Australia. *Mar. Ecol. Prog. Ser.* 131: 115-124.

Williams, A. B. (1958) Substrates as a factor in shrimp Distribution. *Limn. Ocea.* 3: 283-290.

Young, P. C. & Carpenter, S. M. (1977) Recruitment of postlarval Penaeid Prawns to Nursery areas in Moreton Bay, Queensland. *Aust. J. Mar. Freshw. Res.* 28: 745-773.

Zimmerman, R. J. & Zamora, G. (1984) Selection of vegetated habitat by brown shrimp, *Penaeus aztecus*, in a Galveston Bay salt marsh, United States. *Fish. Bull.* 82: 325-336.