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Habitat utilisation by juveniles of commercially important fish species in a marine embayment in Zanzibar, Tanzania

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Abstract – Habitat utilisation by juveniles of 13 commercially important fish species was studied in five habitats located in Chwaka Bay, Zanzibar: mangrove creeks, mangrove channel, sand/mud flats, a seagrass area close to mangroves, and a seagrass area far from mangroves. Fish samples were collected from each habitat using a seine net, and fish abundance and size were measured to determine habitat utilisation. The seagrass beds near to mangroves showed the most diverse fish assemblage of all habitats, possibly because it functions as a corridor between the mangroves and deeper parts of the embayment. Juveniles of *Cheilio inermis*, *Hipposcarus harid, Leptoscarus vaigiensis*, and *Scolopsis ghanam* inhabited seagrass beds only. Juveniles of *Gerres filamentosus* and *Monodactylus argenteus* were mainly found in the mangrove habitats. *Lethrinus variegatus*, *Pelates quadrilineatus* and *Siganus sutor* were found in more than two habitats, with highest abundances in seagrass beds. Juveniles of *Gerres oyena*, *Lethrinus lentjan*, *Lutjanus fulviflamma* and *Sphyraena barracuda* were the most generalist species and were found in all studied embayment habitats. Visual census surveys supported the seine net data showing that most fishes in the embayment habitats were juveniles or sub-adults. In terms of habitat utilisation by different size classes, five of the 13 species (*Lethrinus lentjan*, *L. variegatus*, *P. quadrilineatus*, *Siganus sutor* and *Sphyraena barracuda*) were found as small-sized individuals in shallow and turbid mangrove areas, whereas large-sized individuals were observed in deeper and less turbid seagrass beds. A possible explanation for this pattern could be an ontogenetic shift in habitat utilisation, although this could not be proven. The patterns observed in the present study show a high similarity to those observed in marine embayments in the Caribbean, indicating that similar mechanisms are at work which make these systems attractive juvenile habitats.

Key words: Tropical fish / Juvenile fish / Mangrove / Seagrass bed / Habitat utilization / Indian Ocean

Résumé – Utilisation de l'habitat par des poissons juvéniles d'espèces d'intérêt commercial dans une baie de Zanzibar, Tanzanie. L'utilisation de cinq types d'habitat, par des juvéniles de 13 espèces de poissons d'intérêt commercial, est étudiée dans la baie de Chwaka, à Zanzibar : criques de la mangrove, canaux de la mangrove, bancs de sable/vase, une zone d'herbier proche de la mangrove, et une autre zone d'herbier situé loin de la mangrove. Les échantillonnages ont été effectués au moyen d'une seine de plage pour chacun des habitats ; l'abondance et la taille des poissons ont été notées. Les herbiers situés près de la mangrove montrent les assemblages les plus variés, probablement parce qu'ils fonctionnent comme un couloir entre la mangrove et des zones plus profondes de la baie. Les juvéniles de *Cheilio inermis*, *Hipposcarus harid, Leptoscarus vaigiensis* et *Scolopsis ghanam* occupent uniquement ces herbiers. Les juvéniles de *Gerres filamentosus* et *Monodactylus argenteus* sont trouvés principalement dans les habitats de la mangrove. *Lethrinus variegatus*, *Pelates quadrilineatus* et *Siganus sutor* sont trouvés dans plus de deux habitats, avec des abondances plus importantes dans les herbiers. Les juvéniles de *Gerres oyena*, *Lethrinus lentjan*, *Lutjanus fulviflamma* et *Sphyraena barracuda* sont les espèces les plus généralistes et sont trouvées dans tous les habitats étudiés. Des campagnes de recensement visuel à partir des captures de la seine de plage montrent que la plupart des poissons sont des juvéniles ou sub-adultes. En terme de classes de taille, 5 des 13 espèces (*Lethrinus lentjan*, *L. variegatus*, *P. quadrilineatus*, *Siganus sutor* et *Sphyraena barracuda*) sont trouvés en tant qu'individus de petites tailles dans les zones peu profondes et turbides, tandis que les individus de grandes tailles sont observés dans les zones profondes et moins turbides des herbiers. Une explication plausible de ce schéma pourrait être un changement ontogénique dans l'utilisation de l'habitat. Les groupements observés, dans cette étude, montrent une grande similarité avec ceux observés dans les baies des Caraïbes, indiquant que des méchanismes identiques fonctionnent, et qui rendent ces habitats attractifs pour les juvéniles.

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1 Introduction

Lagoonal and bay habitats containing mangroves and seagrasses are known to be important habitats for juvenile fish, many of them commercially important to reef fisheries (Blaber and Blaber 1980; Parrish 1989; Nagelkerken et al. 2000b; Nagelkerken and van der Velde 2002; Dorenbosch et al. 2004a). It is suspected that they act as nurseries for juvenile fish, although some evidence has yet been provided (Beck et al. 2001; Chittaro et al. 2004). At a certain stage, most fish probably outgrow the protection of these habitats and likely migrate permanently from their nursery habitats to deeper water, such as adjacent coral reefs (Cocheret de la Morinière et al. 2002; Nagelkerken and van der Velde 2002; Nagelkerken et al. 2002; Dorenbosch et al. 2004a).

The present knowledge concerning the nursery potential of habitats with mangrove and seagrasses is mostly based on research conducted in North America, Australia and the Caribbean (see for example Robertson and Duke 1987; Thayer et al. 1987; Morton 1990; Nagelkerken et al. 2000a,b; Cocheret de la Morinière et al. 2002), with most studies carried out in estuaries. The general situation in the Indo-Pacific region may differ considerably from Caribbean islands, since bays and estuaries along the continental coastline in the former area are often characterised by turbid waters, a larger tidal range and a muddy substratum (Blaber 2000). Given that the functioning of mangroves as juvenile fish habitats is not the same in all areas across the globe (see for example Chong et al. 1990), it is of importance to study these areas separately to understand the potential variations in the role of mangroves as fish habitats.

In East Africa hardly any fish studies have been done in shallow tropical habitats, knowledge of the utilisation of mangroves and seagrass beds by fishes is limited to a few studies done in Kenyan estuaries (Little et al. 1988; van der Velde et al. 1995; De Troch et al. 1996; Kimani et al. 1996; Wakwabi 1999). Hence it is not clear how marine embayments in this region (and others) are utilized by juvenile fish. The scarcity of such studies world-wide could lead to an underestimation of the importance of such habitats, a situation that could lead to degradation and/or loss of these habitats (Morton 1990; Nagelkerken 2000).

In this study we present a detailed description of habitat use by juveniles of selected commercially important fish species that are found within a marine embayment in Zanzibar, Tanzania. The study was designed to answer the following key questions: (1) Do selected commercially important fish species use the bay habitats as juvenile habitats? (2) What is the spatial variation in habitat utilization by the selected fishes? (3) Which bay habitat contains the most species of juvenile fish? (4) Is the distribution of fish related to environmental variables?

2 Materials and methods

2.1 Study area

This study was carried out in Chwaka Bay, a shallow system on the east coast of Unguja Island, Zanzibar, Tanzania (Fig. 1). This embayment is an intertidal water body with an average depth of 3.2 m and an estimated area of 50 km^2 at high spring tide and 20 km^2 at low spring tide (Cederlöf et al. 1995). The region receives between 1000 and 1500 mm of rainfall per annum. Air temperatures are tropical and range from 27–30 °C. Predominantly north-easterly winds occur between October and March, and mainly south-easterly winds from March to October. There are two rainy seasons in Zanzibar: the extended rainy season that occurs during the months of March, April and May, and the short rainy season which extend from October to December (McClanahan 1988).

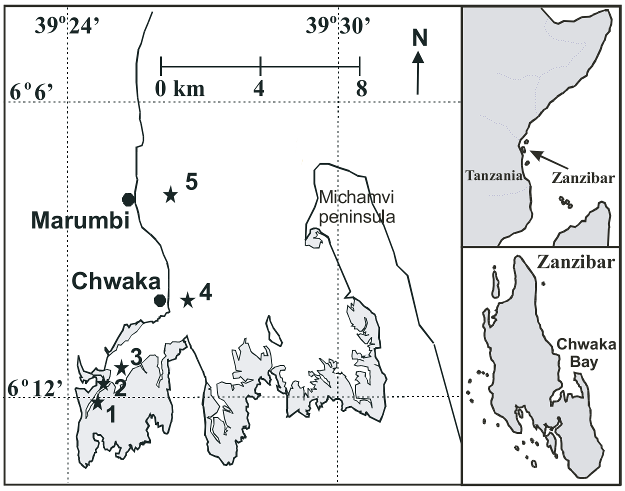

Fig. 1. Map of Unguja Island (Zanzibar) showing the location of Chwaka Bay and the sampled habitats. **1:** mangrove creeks, **2:** mangrove channel, **3:** mud/sand flats, **4:** Chwaka seagrass beds, **5:** Marumbi seagrass beds. Gray areas in Chwaka Bay indicate mangrove forest.

On the east side, Chwaka Bay is protected from high-wave action from the ocean by a reef system running along the coastline, as well as the Michamvi peninsula (Fig. 1). On the landward side, this embayment is fringed by a dense mangrove forest of approximately 3000 ha (Mohammed et al. 1995). The mangrove forest has a number of tidal creeks, with Mapopwe Creek (approximately 2 m deep) being the largest and acting as the main water exchange route between the forest and the embayment. All the creeks are intertidal in nature and none have any significant fresh water input from rivers or streams. Only during heavy rains, salinity gradients develop and these creeks temporarily acquire estuarine characteristics, with salinities as low as 5 psu (Johnstone and Mohammed 1995). The mangrove part of the bay is characterised by low water clarity (Table 1) and fluctuations in oxygen levels. On the seaward side, immediately adjacent to the forest, the embayment opens up onto large intertidal flats that are overgrown by mixed assemblages of algae and seagrasses, including scattered monospecific seagrass stands. The outer and middle parts of the embayment (about 4 m deep) are oceanic in character with salinities rarely below 35 psu (Table 1). Due to proximity of this part of the embayment to the open ocean, it is characterised by relatively high water clarity (Table 1). Furthermore, salinity and oxygen levels in this part of the embayment are relatively constant, even during the rainy seasons.

Table 1. Environmental characteristics (mean values and SD) of different embayment habitats, depth and seaward distance of different embayment habitats from the mangroves. Different fishing pressure intensities (− = rare or nearly absent, + = present but insignificant, ++ = regular and significant, + + + = irregular but intense) are also documented.

Environmental factors	Mangrove creeks	Mangrove channel	Mud/sand flats	Chwaka seagrass beds	Marumbi seagrass beds
pH	8.0 (0.7)	7.9 (0.4)	8.1 (0.2)	8.2 (0.2)	8.2 (0.3)
Temperature (°C)	26.3 (2.5)	26.8 (3.0)	27.6 (2.2)	28.1 (2.1)	27.3 (2.4)
Salinity (psu)	30.9 (6.9)	29.9 (8.6)	32.2 (5.8)	33.8 (3.4)	35.5 (1.9)
Oxygen (mg L^{-1})	3.6 (1.2)	4.8 (1.1)	5.5 (2.6)	8.6 (4.6)	6.9 (4.3)
Water clarity (m)	1.0 (0.7)	0.9 (0.4)	0.7 (0.2)	2.8 (0.9)	9.4 (2.9)
Habitat structure	Mud Mangrove prop roots Few algae Few seagrasses	Mud Mangrove prop roots Few algae Few seagrasses	Mud and sand Brown algae Few seagrasses	Seagrasses Seaweed farms (red algae) Other algae	Seagrasses Calcareous algae (*Halimeda* spp.) Other algae
Distance from the mangroves (km)	0	0	2	6	8
Maximum depth (m)	2	2	2	4	4
Fishing Pressure	–	–	+	++	+++

2.2 Study design

Bimonthly sampling was conducted during the day at spring low tide (two spring tides per month) for a period of one year (November 2001 – October 2002). Fish samples were collected from five habitats in Chwaka Bay, including: (1) mangrove creeks, (2) mangrove channel, (3) intertidal mud/sand flats located within 2 km of the mangroves, (4) Chwaka seagrass beds located approximately 6 km from the mangroves, and (5) Marumbi seagrass beds situated about 8 km from the mangroves (Fig. 1). The mangrove creeks and the channel were characterised by mangrove prop roots (*Rhizophora mucronata*), with a muddy substratum harbouring few algae and seagrasses. The mud/sand flats were characterised by a higher cover of algae and some seagrasses. The seagrass habitats consisted of vast fields of *Enhalus acoroides* interspersed by patches of *Thalassodendron ciliatum* and calcareous algae *Halimeda* spp.

Fish samples were collected from each habitat using a seine net measuring 35 m in length, 3 m in height, and with a stretched mesh size of 1.8 cm. The sampled area of each haul was approximately 480 m^2. In each habitat, four replicate samplings were randomly conducted during each spring low tide. A consistent net deployment (purse seining) was used in all habitats, except the creeks where narrowness restricted similar deployment of the net. Instead, the mouth of the mangrove creeks (about 4 m wide) was closed by the net and the whole net laid out upstream along one side of the creek (about 30 m) and then closed, sampling an area of approximately 120 m^2.

To make sure that the net remained vertically stretched and touching the bottom, a metal chain was attached to the middle section of the sinker line. In addition, plastic floats were attached to the float line so that the entire water column was enclosed. Snorkelling observations during net deployment indicated that the lower part of the net remained on the bottom throughout the exercise and no fish were observed escaping under the net. Although some individuals belonging to the family Mugilidae were observed jumping over the net, it was concluded that the procedure was well designed for the study species.

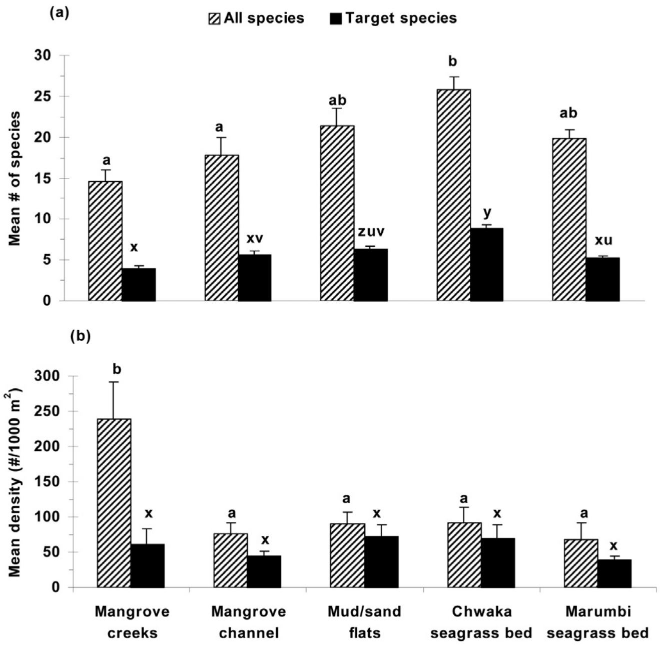

Fig. 2. Variations (+ SE) in (a) mean number of species and (b) mean densities along a gradient of habitats in Chwaka Bay for all species and for target species. Values that are significantly different (Gabriel's post-hoc test) have different letters (*a*, *b* for all species; *x*, *y*, *z*, *u* for target species). Mean number of species is calculated by pooling the 8 beach seine hauls of each month and taking the average of the different months.

To improve standardisation, the sampling was carried out by the same two fishermen, using the same net, and similar net deployment procedures. All fish sampled by the seine net were collected (see Figs. 2 and 3) but 13 commercially important fish species (Jiddawi and Stanley 1997, see Table 2) that were

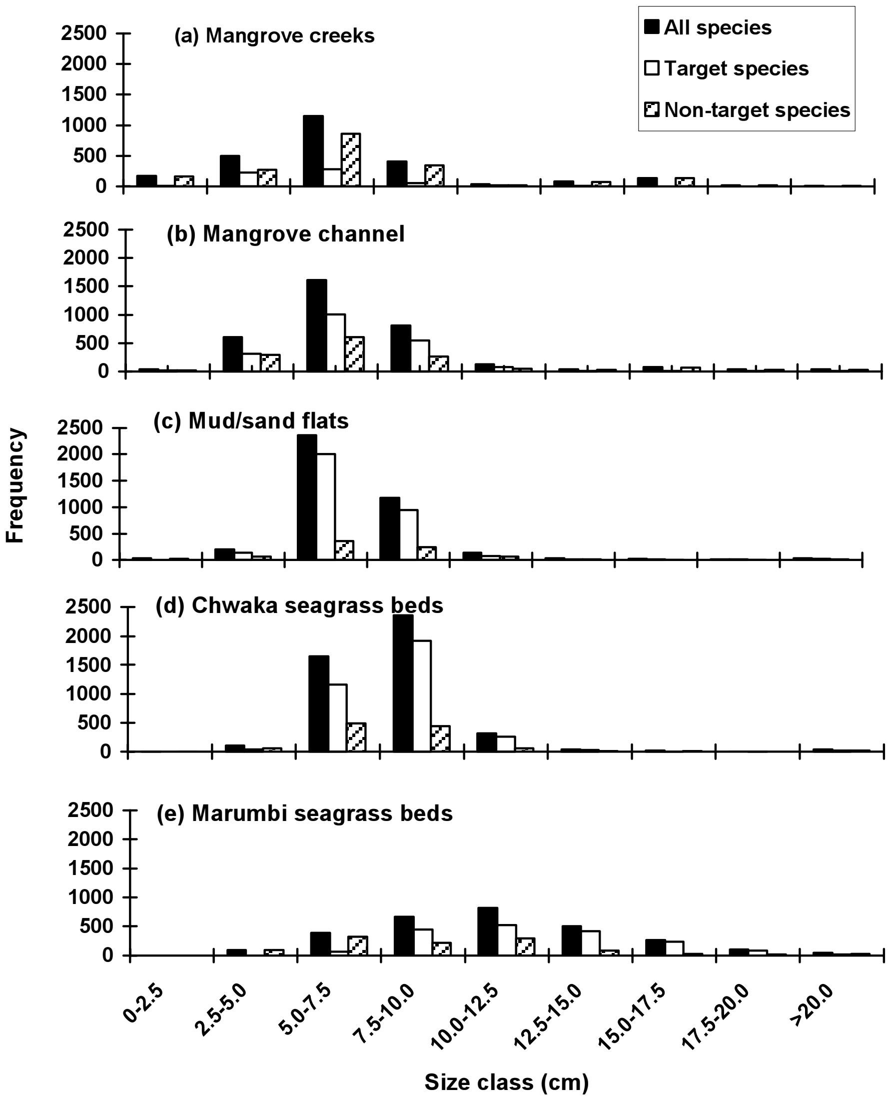

Fig. 3. Length frequency distribution of fish in different habitats in Chwaka Bay. Non-target species refers to all species minus target species.

most common and represented over 60% of the total catch are studied in more detail, so that the results can contribute to effective management and conservation of the fisheries in this embayment. The role of the studied embayment habitats as a feeding area by these fish species will be reported elsewhere. In the laboratory, fish fork lengths were measured to the nearest 0.1 cm and analysed in class intervals of 2.5 cm, except for two large-sized species (viz. *Sphyraena barracuda* and *Cheilio inermis*) where a 5 cm class interval was used.

In another study during September – December 2003, visual census surveys of the fish communities in the mangroves near Chwaka (different from the beach seine surveys) and in the seagrass beds of Chwaka and Marumbi were performed during neap tides in quadrats of 5 × 5 m using SCUBA. Visual census surveys could not be done within the mangrove creeks, mangrove channel and mud/sand flats habitats due to high turbidity in these habitats. Water depth at the Marumbi and Chwaka seagrass beds was on average 4.5 m. After marking the quadrat with a line, the observer waited 3 min to minimise fish disturbance in the quadrat, after which fishes were counted during 10 min. Fish surveys were performed by two independent observers that were simultaneously trained in fish identification and size class estimation prior to the surveys. Care was taken not to count fishes that moved in and out of the quadrats more than once.

The majority of juveniles collected in this study were larger than 2.5 cm in length and did not include larval stages. The smaller juveniles (<2.5 cm) and larvae tended to pass through the net, thus leading to an underestimation of the total density and size composition of early juveniles captured during this study. However, since the same mesh size was used throughout the embayment habitats, the selectivity of the net applies equally to all habitats, thus resulting in comparable data being collected. It is known that seine nets have a limitation in sampling adult fish, a problem that could result into them being underrepresented in this study. The visual census survey was used as an additional technique to determine whether adults are present in the embayment habitats.

Since variations in environmental variables can have profound effects on the distribution and consequently catches of

Table 2. Families, species names, common names, percentage composition of different categories of fish (following Nagelkerken and van der Velde 2002): small juveniles (<1/3 max. species' length), large juveniles and sub-adults (1/3–2/3 of max. species' length), and adults (>2/3 of max. species' length), maximum length an individual species can reach (source: Froese and Pauly 2004). Habitats where fishes were most abundant are also documented (1: mangrove creeks, 2: mangrove channel, 3: mud/sand flats, 4: Chwaka seagrass beds, 5: Marumbi seagrass beds, * habitat with high fish density).

Family	Species	Common names	% small juveniles in the bay	% large juveniles in the bay	% adults in the bay	Maximum size attained by adult fish (cm)	Habitat observed
Gerreidae	*Gerres filamentosus*	Whipfin silver biddy	100	0	0	35	1*, 2*, 3
Gerreidae	*Gerres oyena*	Common silver biddy	94.7	5.3	0	30	All, 2*, 3*, 4*
Labridae	*Cheilio inermis*	Cigar wrasse	55.8	44.2	0	50	4, 5*
Lethrinidae	*Lethrinus lentjan*	Redspot emperor	100	0	0	52	All, 1*, 2*, 3*, 4*
Lethrinidae	*Lethrinus variegatus*	Variegated emperor	26.4	73.4	0	20	2, 3, 4*, 5
Lutjanidae	*Lutjanus fulviflamma*	Blackspot snapper	87.1	12.9	0	35	All, 3*, 4*
Monodactylidae	*Monodactylus argenteus*	Silver moon	97.8	2.2	0	25	1*, 2*, 3
Nemipteridae	*Scolopsis ghanam*	Arabian monacle bream	87.0	13.0	0	30	4*
Scaridae	*Hipposcarus harid*	Candelamoa parrot fish	100	0	0	75	4*
Scaridae	*Leptoscarus vaigiensis*	Marbled parrotfish	45.3	54.7	0	35	4, 5*
Siganidae	*Siganus sutor*	Whitespotted rabbitfish	88.9	11.1	0	45	2, 3, 4*, 5*
Sphyraenidae	*Sphyraena barracuda*	Great barracuda	100	0	0	200	All*
Teraponidae	*Pelates quadrilineatus*	Fourlined terapon	93.6	6.4	0	30	1, 3, 4*

fish, these variables were recorded before each catch. Water temperature, pH, salinity and dissolved oxygen were measured using a temperature-compensated Multi Parameter Analyzer (Eijkelkamp, model 18.28). To determine water clarity, a line was extended to the maximum horizontal distance at which a snorkeller in the water could discern a black and white coloured stationary held Secchi disk (44 cm diameter).

2.3 Data analysis

Using the monthly environmental data, mean and standard deviations for each of the variables were determined (Table 1).

Mean species richness and mean density for the entire fish community were compared between different embayment habitats using a one-way ANOVA on log-transformed data, followed by multiple comparisons of means with a Gabriel's Post Hoc test, using the programme SPSS for Windows (Field 2000). To examine associations between fish densities in different embayment habitats and environmental variables, two analyses were done: 1) Multiple linear regression analysis for each target species (all size classes pooled), and 2) Correspondence Analysis (CA) on log-transformed data of the various size classes of all target species (ter Braak and Smilauer 1998). First of all, simple linear regressions were done among the environmental variables to detect co-linearity. Temperature was significantly correlated to oxygen; to prevent over-parameterisation we therefore excluded temperature from the model and used only oxygen as a variable. Distance was significantly correlated to salinity, and we used only salinity as a variable. We excluded pH from the model because this factor hardly varied within the habitats. The final multiple linear regression model thus included three independent variables (predictors): oxygen, salinity and water clarity. Each of the 13 target species was set as a dependent variable in 13 separate multiple regression analyses. Semi partial (Part) correlations are provided which show the correlations of the separate independent variables with the dependent variable, taking the effect of the other independent variables into account.

3 Results

The number of all fish species and of target species both showed a similar trend across the embayment habitats, increasing from the mangrove creeks to Chwaka seagrass beds and then decreasing in Marumbi seagrass beds (Fig. 2a). The pattern for densities of all fish species pooled was the same as that of target species alone, except in the mangrove creeks (Fig. 2b). The density of all species pooled was significantly higher in the mangrove creeks than in any other habitats (1-way ANOVA and Gabriel's post-hoc test, $p < 0.05$). Non-target species, which contributed most to the high fish densities in the mangroves, included members of the family Ambassidae, Apogonidae and Leiognathidae. The highest densities of the target species pooled were recorded on the mud/sand flats and in Chwaka seagrass beds, but the differences in their density over the habitat gradient was not significant (1-way ANOVA, $F_{4,53} = 2.127$, $p = 0.09$).

Considering target species alone, the majority of small juveniles (<5 cm) were found within the mangrove habitats (i.e. creeks and channel) although other size classes

Table 3. Mean density (# fish 100 m^{-2}) and standard error (between brackets) of different size classes (cm) of fish observed during visual census surveys (n = number of transects surveyed). The maximum size that can be reached by individual fish species is shown in Table 2.

	Chwaka mangroves (n = 9)				Chwaka seagrass beds (n = 31)				Marumbi seagrass beds (n = 29)			
Species	0–10	10–20	20–30	>30	0–10	10–20	20–30	>30	0–10	10–20	20–30	>30
Gerres filamentosus	-	-	-	-	-	-	-	-	-	-	-	-
Gerres oyena	-	-	-	-	-	-	-	-	-	-	-	-
Cheilio inermis	-	-	-	-	0.6 (0.4)	2.6 (1.2)	1.8 (0.8)	0.6 (0.4)	0.8 (0.3)	5.5 (1.2)	4.6 (1.3)	-
Lethrinus lentjan	-	-	-	-	3.0 (1.2)	0.3 (0.3)	-	-	1.9 (0.9)	16.1 (4.1)	-	-
Lethrinus variegatus	-	-	-	-	0.1 (0.1)	-	-	-	-	0.1 (0.1)	-	-
Lutjanus fulviflamma	-	0.4 (0.4)	-	-	-	0.8 (0.8)	-	-	-	0.3 (0.3)	-	-
Monodactylus argenteus	5.3 (4.9)	-	-	-	-	-	-	-	-	-	-	-
Scolopsis ghanam	-	-	-	-	2.1 (1.0)	1.0 (0.8)	-	-	-	4.0 (2.8)	-	-
Hipposcarus harid	-	-	-	-	10.8 (2.2)	11.6 (4.7)	0.1 (0.1)	-	-	-	-	-
Leptoscarus vaigiensis	-	-	-	-	3.0 (1.4)	9.9 (3.6)	0.6 (0.3)	-	3.9 (2.7)	28.1 (8.2)	4.6 (2.8)	-
Siganus sutor	-	2.7 (2.7)	-	-	3.5 (0.9)	1.7 (0.7)	0.6 (0.5)	-	2.6 (1.3)	11.7 (4.4)	-	-
Sphyraena barracuda	-	0.4 (0.4)	0.4 (0.4)	-	-	-	-	-	-	-	-	-
Pelates quadrilineatus	-	-	-	-	-	-	-	-	-	-	-	-

were also represented (Fig. 3a,b). Mud/sand flats and Chwaka seagrass beds mainly harboured intermediate sized juveniles (5–10 cm) while in Marumbi seagrass beds large-sized juveniles (>10.0 cm) dominated (Figs. 3c–e). Non-target species which mainly included small-body species did not show a distinctive pattern in size distribution over habitats (Fig. 3).

Considering the embayment as a whole and using the beach seine data, 11 out of 13 target species were recorded mainly as small juveniles, with the other 2 species predominanthy occurring in the embayment as large juveniles (Table 2). No target species were recorded in the embayment as adults. Also visual census surveys revealed that the majority of the target fish species occurred in the embayment habitats as juveniles and sub-adults (Table 3). In contrast to the beach seine data, the visual census surveys showed presence of *Siganus sutor* in the mangroves, and absence of *Gerres filamentosus*, *G. oyena* and *Pelates quadrilineatus* in all habitats.

Correspondence Analysis showed a clear separation of species and size classes of the target species in the different habitats (Fig. 4). The Eigenvalues of the first and second CA axis were 0.66 and 0.37, respectively, indicating that a high proportion of the variation in species density data could be explained by the hypothetical axes. Four distinct groups could be identified. The first group occupied the mangrove habitats (creeks and channel) and were characterised by small-sized individuals of *Gerres filamentosus*, *G. oyena*, *Lethrinus lentjan, Monodactylus argenteus* and *Sphyraena barracuda*. In addition, the whole size range of *M. argenteus* was found in these habitats, together with large individuals of *Lutjanus fulviflamma*. The second group was found on the mud/sand flats and was characterised by small-sized individuals of *L. fulviflamma*, *Lethrinus variegatus, Pelates quadrilineatus, Siganus sutor, Sphyraena barracuda* and intermediate-sized individuals of *G. filamentosus* and *G. oyena*. Chwaka seagrass beds were occupied by the third group which was characterised by intermediate-sized individuals of *P. quadrilineatus* and *S. barracuda* and all size classes of *Hipposcarus harid* and *Scolopsis ghanam*. The last group, comprising mainly large individuals (≥10.0 cm) of *Cheilio inermis*, *Leptoscarus vaigiensis*, *Lethrinus lentjan*, *L. variegatus, Siganus sutor* and *Sphyraena barracuda* were found in Marumbi seagrass beds.

The density distribution of the various size classes of the target species was highly correlated to all environmental variables (Fig. 4). The size distribution of the target species as well as the environmental variables increased from the mangroves to the seagrass beds of Chwaka and Marumbi. At species level, salinity (and/or distance), oxygen (and/or temperature) and water clarity were correlated to the fish density distribution (Table 4), although few conditions were significant. Only two species (*C. inermis* and *L. variegatus*) showed significant results.

At the species level, several species showed a difference in habitat utilization for small versus large juveniles (Fig. 5, Table 2): (1) small-sized individuals of *Lethrinus lentjan, Pelates quadrilineatus* and *Sphyraena barracuda* were found in the mangrove habitats, whereas the large-sized individuals of these species were recorded in the seagrass beds (2) small-sized individuals of *L. variegatus* and *Siganus sutor*

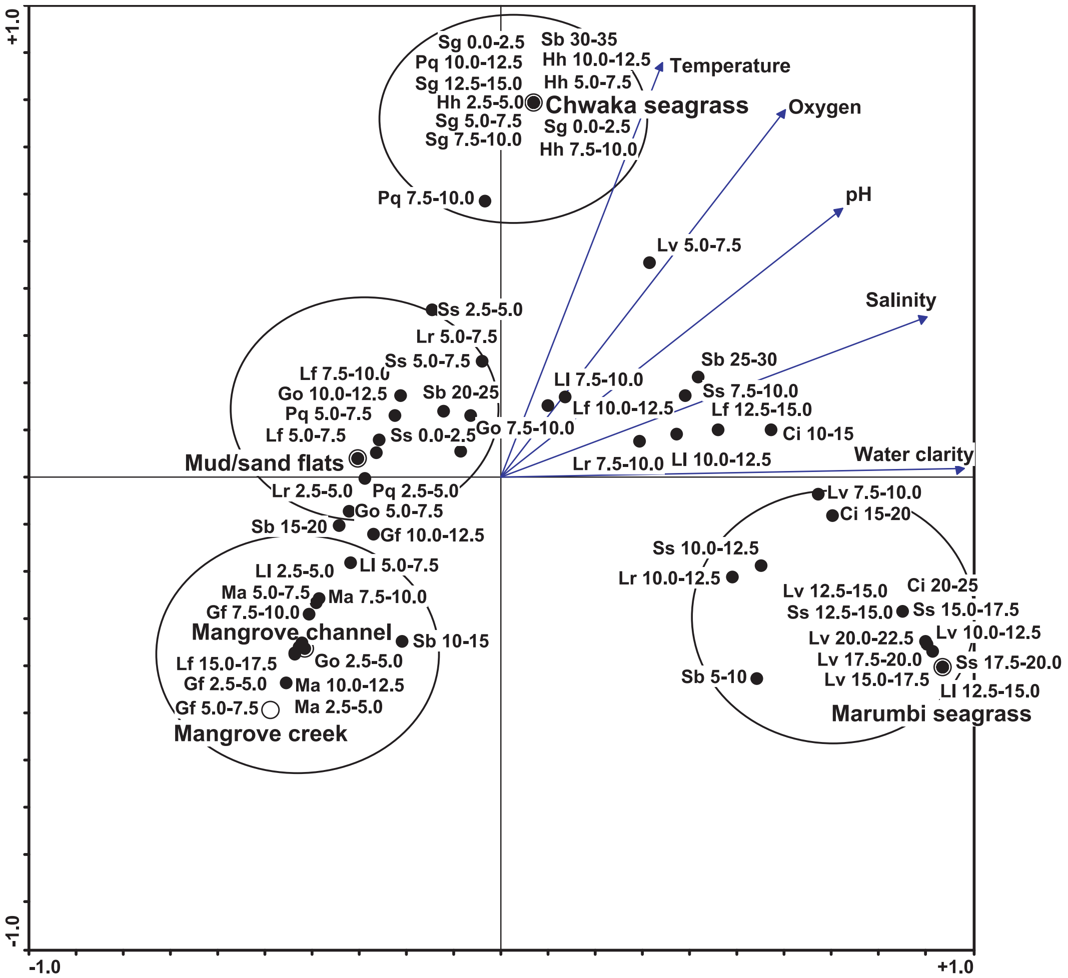

Fig. 4. Correspondence Analysis (CA) graph showing habitat utilisation of different size classes of target fish species and their relationship with environmental variables. Go: *Gerres oyena*, Gf: *Gerres filamentosus*, Ma: *Monodactylus argenteus*, Sb: *Sphyraena barracuda*, Ci: *Cheilio inermis*, Ll: *Lethrinus lentjan*, Lr: *Lethrinus variegatus*, Lv: *Leptoscarus vaigiensis*, Ss: *Siganus sutor*, Sg: *Scolopsis ghanam*, Hh: *Hipposcarus harid*, Pq: *Pelates quadrilineatus*, Lf: *Lutjanus fulviflamma*.

Table 4. Results of the multiple linear regression analysis, showing the R^2 and p-value of the full model, and the part (semi partial) correlation of the separate environmental variables. * significant at $0.01 < p < 0.05$, ** significant at $p < 0.01$.

	Part Correlation			R^2	p
Species	Salinity	Oxygen	Water clarity		
Cheilio inermis	0.009	0.036*	0.426**	1.000	0.001**
Gerres filamentosus	−0.651	0.153	0.453	0.994	0.101
Gerres oyena	0.249	0.087	−0.620	0.689	0.671
Hipposcarus harid	−0.027	0.604	−0.212	0.828	0.513
Leptoscarus vaigiensis	0.013	−0.050	0.454	0.997	0.074
Lethrinus lentjan	0.493	−0.718	−0.551	0.853	0.476
Lethrinus variegatus	−0.310*	0.807*	0.202	1.000	0.024*
Lutjanus fulviflamma	0.379	0.276	−0.640	0.972	0.214
Monodactylus argenteus	0.068	0.215	−0.538	0.874	0.442
Pelates quadrilineatus	0.341	0.291	−0.625	0.927	0.339
Scolopsis ghanam	−0.027	0.604	−0.212	0.828	0.513
Siganus sutor	0.129	0.198	0.135	0.866	0.456
Sphyraena barracuda	0.894	−0.415	−0.882	0.979	0.183

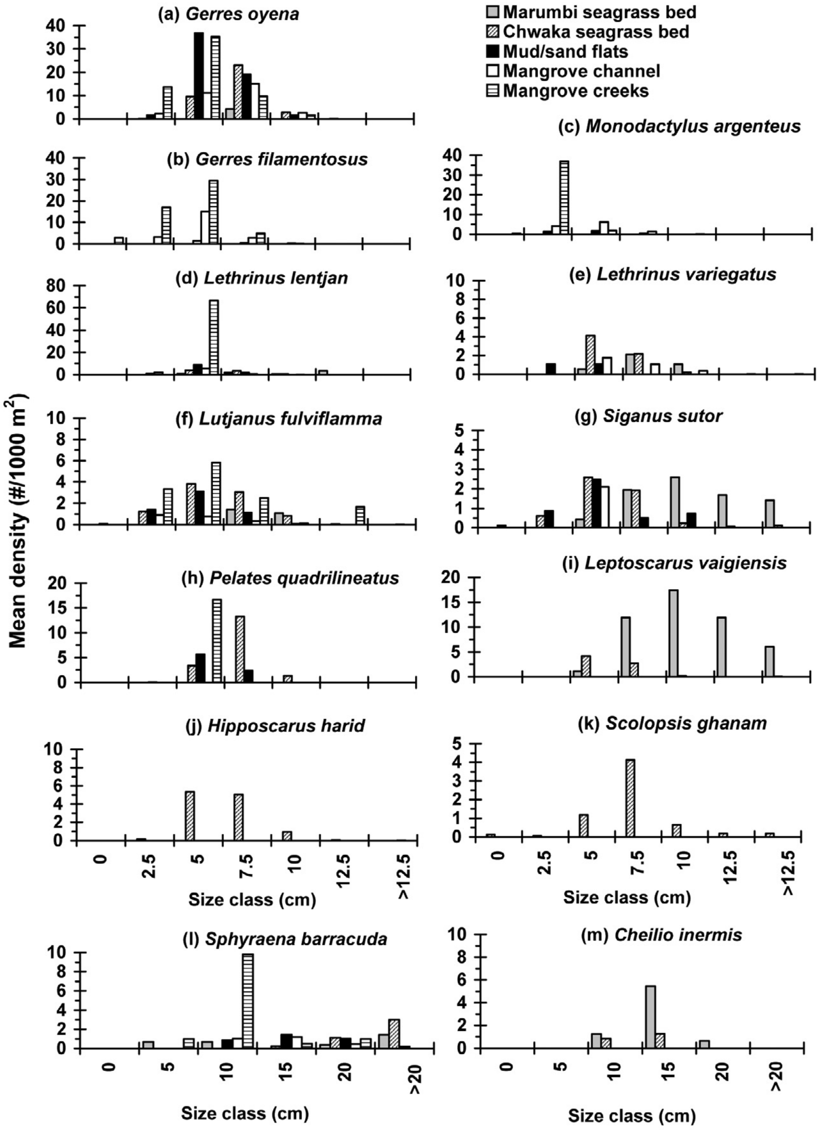

Fig. 5. Mean densities per size class of the target fish species in the five embayment habitats.

were found in the mangroves and mud/sand flats, whereas the large individuals were recorded in the seagrass habitats. The other target species did not show such a pattern, with all life stages found in the mangroves (*Gerres filamentosus*, *Monodactylus argenteus*), seagrass beds (*Cheilio inermis*, *Hipposcarus harid*, *Leptoscarus vaigiensis*, *Scolopsis ghanam*), or in a variety of habitats (*G. oyena*, *Lutjanus fulviflamma*).

4 Discussion

Most fish caught in the present study were juveniles, indicating that an Indo Pacific marine embayment may have similar a function as juvenile habitats as Indo Pacific estuaries. In addition, both tropical marine embayments as well as estuaries are dominated by relatively few species when compared to fish diversity in adjacent coastal waters.

The density of juveniles of all species pooled was about 3 times higher in the mangroves than in any of the other habitats. Similarly, in tropical Queensland (Australia), Robertson and Duke (1987) observed 4–10 times higher densities of fish in mangroves than in adjacent habitats. The high density of fish in mangroves is probably explained by the high structural complexity formed by the prop-roots (Robertson and Duke 1987; Thayer et al. 1987; Cocheret de la Morinière et al. 2004). However, the low density of target species (i.e. commercially important species) as opposed to the high density of non-target species in the mangrove creeks indicates that the majority of fish found in the mangroves are not commercially important. This does not necessarily lessen the importance of mangroves, as the density of target species was equal in all habitats and non-target species are important in supporting food webs that include commercially important species. For example, in Dampier region of Australia, Blaber (1986) observed that 60% of the diet of commercially important species such as *Caranx* *ignobilis*, *Carcharhinus limbatus*, *Scomberoides comersonianus* and *Scomberomorous semifasciatus* was composed of permanently resident mangrove species. Therefore, as argued by Robertson and Duke (1987), the value of mangroves is not limited to a possible nursery potential alone.

The high number of fish species encountered in Chwaka seagrass beds, when compared to the other habitats, may possibly be explained by its geographical location between the mangroves and the deeper part of the embayment/coral reef. Fish species from adjacent habitats may school together in the seagrass channels of Chwaka during low tides. These channels are always inundated with water and fishes are known to occupy transient habitats during certain phases of tidal cycles (Chong et al. 1990; Forward and Tankersley 2001; Dorenbosch et al. 2004b). The Chwaka seagrass beds could also form a corridor for fishes if they would undertake an ontogenetic migration from the mangroves to deeper parts of the embayment. Higher numbers of species in seagrass habitats compared to mangrove habitats have been reported in other studies (Little et al. 1988; van der Velde et al. 1995; Pinto and Punchihewa 1996), but the opposite situation has also been documented (Robertson and Duke 1987; Thayer et al. 1987; Laegdsgaard and Johnson 1995).

Individuals of the fish species that were found in mangrove areas were smaller in size when compared to individuals of the same species that were found in seagrass areas. This suggests either a possible habitat shift with growth, with some species appearing to utilise the sand/mud flats as intermediate life stage habitats or it could also be a result of tidal migration in search for more beneficial habitats during low tides. Although the present study did not focus on the adult life stages, the almost total absence of adults in the studied embayment habitats suggests that these large fish must be present elsewhere, possibly in the deeper parts of the embayment or on the adjacent coral reef. There is a possibility that adult fish were able to escape the seine net more readily than juveniles, which could result into their under representation, however, visual census surveys (which target the entire size range) indicated that the deeper parts of the seagrass beds consisted mainly of juveniles.

Most species occurred in multiple embayment habitats, but some species were most abundant in just one habitat. *Gerres filamentosus* and *Monodactylus argenteus* showed a strong preference for mangrove areas and may be attracted to the brackish water that was sometimes present in this habitat (Froese and Pauly 2004). *Cheilio inermis* and *Leptoscarus vaigiensis* are typical seagrass-associated species (Froese and Pauly 2004) and were only recorded in seagrass beds during this study. Similarly, in Mhlathuze estuary, South Africa, Weerts and Cyrus (2002) reported the occurrence of Labridae and Scaridae only in eelgrass habitats.

Most studies on utilisation of neighbouring tropical shallow-water marine habitats by juvenile reef fish species have been done in the Caribbean. It is striking that many results of the present study in the western Indian Ocean are highly comparable to those of similar studies done in marine embayments in the Caribbean. In both regions, 1) marine embayment habitats were dominated by juvenile fish with an almost complete absence of adults (Nagelkerken et al. 2000a), 2) marine embayment habitats showed highest juvenile fish densities in mangroves (Nagelkerken and van der Velde 2002); 3) some marine embayment habitats were used specifically as an intermediate life-stage habitat (Nagelkerken et al. 2000b; Nagelkerken and van der Velde 2003), and 4) multiple marine embayment habitats could be used by juvenile fish simultaneously (Nagelkerken et al. 2000a) .These similarities indicate that irrespective of the geographical location, the same mechanisms are at work which make shallow-water marine embayment habitats favourable juvenile habitats.

5 Conclusion

The questions posed at the beginning of this study can be answered as follows: (1) All studied fish species used one or more embayment habitats as juvenile habitats. (2) Several species occurred as small juveniles in the mangrove areas and as large-sized juveniles in the seagrass areas. (3) Chwaka seagrass beds appeared to be the most widely utilised habitat probably due to its intermediate location between the mangroves and the deeper parts of the embayment. (4) Only two of the 13 species showed a significant correlation between density and the selected environmental variables, suggesting that the latter do not play a major role in the fish density distribution.

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