



Importance of intertidal seagrass beds as nursery area for coral reef fish juveniles (Mayotte, Indian Ocean)

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ABSTRACT

The present study highlights the importance of intertidal seagrass beds as nursery areas for coral reef fish juveniles along four sites (Mtsoubatsou, Sohoa, Boueni, Ngouja) on the western coast of Mayotte Island. The results collected by underwater visual census from November 2012 to January 2013 showed that mean total fish density between adults and juveniles varied significantly at each site, with juveniles always being more abundant in seagrass beds than adults. Of the total fish assemblages sampled in seagrass beds, 73% were juveniles and few adults of large species were observed. Overall, our study highlights the important functional role of intertidal seagrass beds for fish assemblages, as they are the primary habitat for the juveniles of many fish species on Mayotte reefs. Seagrass beds, however, are very vulnerable ecosystems and are decreasing worldwide. Therefore it is of primary importance to protect seagrass beds within the Indo-Pacific.

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1. Introduction

Shallow tropical coastlines provide an exceptional environment with complex interactions often represented by several highly productive habitats, such as seagrass beds, mangroves, and coral reefs (Unsworth et al., 2008; Barnes et al., 2012). Numerous studies conducted in multiple biogeographical regions have confirmed the importance of seagrass beds as essential habitats for fish (e.g., Nagelkerken et al., 2001; Dorenbosch et al., 2005a, 2007; Nakamura, 2010). Seagrass beds support large numbers and a wide variety of coral reef and estuarine juvenile fish (commercial and non-commercial species), while the adults of these species are almost exclusively found on coral reefs (e.g., Pollard, 1984; Parrish, 1989; Jackson et al., 2001; Dorenbosch et al., 2005a; Nakamura et al., 2009a,b). Hypotheses explaining the high abundance of juvenile fish in this habitat are mainly based on lower predation risk, high food availability and higher interception rates of planktonic larvae (e.g., Parrish, 1989; Nagelkerken et al., 2000; Beck et al., 2001; Dahlgren et al., 2006; Lecchini et al., 2003,

2012). However, environmental stressors threaten these coastal habitats and human-induced disturbances further lead to significant habitat loss for fish juveniles (Moritz et al., 2018). Similarly to mangrove habitats, high rates of seagrass loss have also been observed throughout the world, due to human impacts linked to the growth of coastal human populations (e.g., eutrophication, pollution, sedimentation and destructive fishing practices) and natural disturbances (e.g., diseases and storms) (Gullström et al., 2002; Orth et al., 2006; Waycott et al., 2009).

Several studies have been conducted on the nursery role of seagrass beds for coral reef fish in Caribbean and Indo-Pacific regions (e.g., Nagelkerken et al., 2001; Lecchini and Galzin, 2005; Dorenbosch et al., 2005a, 2007). In the Western Indian Ocean (WIO), most research on seagrass fish assemblages has been conducted along the East African coast, Kenya, Tanzania and Mozambique (Berkström et al., 2013; Alonso Aller et al., 2014; Kruse et al., 2016; Chirico et al., 2017). Seagrass ecosystems, however, have received little scientific attention in the Island States of the WIO (Seychelles, Comoros archipelago, Reunion, Mauritius and Madagascar) where human pressure is high on the coast. The lagoon of Mayotte contains a variety of biotopes such as mangroves, seagrass beds and coral reefs. However, the spatial distribution of seagrass beds and mangroves is not homogeneous around the island. Intertidal seagrass beds are more developed

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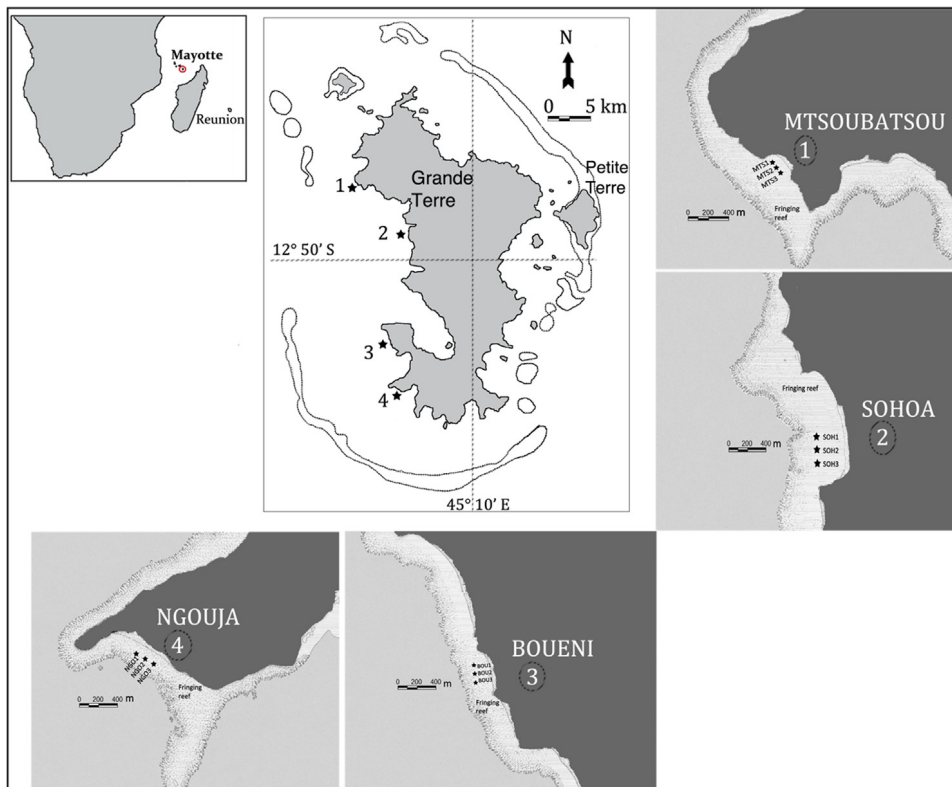


Fig. 1. Location of the four study sites along the western coast of Mayotte Island (Grande Terre).

on the western coast of the Grande Terre (Loricourt, 2005), while the largest mangroves are found at Boueni Bay (southern coast) and along the eastern coast (Jeanson et al., 2014). Moreover, the high rate of destruction of seagrass beds and mangroves at Mayotte may negatively impact seagrass-associated fish and fishery stocks (Madi Moussa et al., 2015; Madi Moussa, 2018). Thus far; no studies have investigated the intertidal seagrass beds of Mayotte and their potential as essential habitat for coral reef fish. The present study is the first one to focus on the seagrass fish assemblage at Mayotte Island, the 101st French department with a very high population density (690 habitant per km²). Specifically, the present study aims: (1) to describe the fish assemblage composition, (2) to determine the community structure of the ichthyofauna and (3) provide density of juvenile and adult fish that live in this biotope. Specifically, we addressed the following question: Do intertidal seagrass beds in Mayotte serve as important juvenile habitats for many reef species? The results of this study will allow us to better understand the role of seagrass beds and to assess the risk of its loss in order to guide the decisions of environmental managers.

2. Materials and methods

2.1. Study area

Mayotte is composed of two main volcanic islands, Grande Terre (360 km², culminating at a peak elevation of 660 m at Mount Bénara) and Petite Terre (14 km²). These islands are almost entirely surrounded by a 197 km barrier reef, with a large lagoon of 1500 km², one of the largest reef lagoons in the Indian Ocean. Mayotte lagoon is 3–15 km wide, with an average depth of 35 m (Guilcher, 1965) and up to 80 m deep in the pass reef. Grande Terre is surrounded by discontinuous well developed fringing reefs on nearly 186 km for 197 km of coastline (Chabanet,

2002). The present study was carried out between November 2012 and January 2013 on the fringing reef of Mayotte Island (Grande Terre - 12°50'S, 45°10'E - Fig. 1). Seagrass beds cover over 760 ha, which are mainly located on the eastern barrier reef (56%), (39%) along the western shore of the Grande Terre Island and (5%) around Mtsamboro and Karoni islets (Loricourt, 2005). Four different study sites have been chosen along this coast: Mtsoubatsou, Sohoa, Boueni, Ngouja (Fig. 1). The seagrass meadows on these sites are generally multi-specific (11 species identified by Loricourt, 2005) with the dominant genera per site respectively: e.g. Mtsoubatsou is dominated by *Halodule*, *Cymodocea* and *Thalassia*; Sohoa by *Syringodium*, *Halodule* and *Thalassia*; Boueni by *Thalassia*, *Halodule* and *Syringodium* and Ngouja by *Halodule*, *Syringodium*, *Thalassia* and *Cymodocea*. Overall, the mean height of seagrass leaves observed was low, about 10–15 cm and not very dense due to the herbivore pressure of green turtles (*Chelonia mydas*) (Ballorain et al., 2010). In addition, human induced disturbances (e.g. water pollution, erosion, sedimentation and trampling) may be also a factor responsible for the loss and fragmentation of seagrass beds (Duarte et al., 2004). Mtsoubatsou is isolated site under agriculture influence, Sohoa is situated near a village and the beach is strongly frequented by people during low tide, and Boueni is between two villages and this site is a privilege beach fishery. Ngouja is a natural zone established by Prefectural order No. 42/DAF/01 of June 11th, 2001.

On the four chosen sites, the seagrass beds were situated between 60 and 200 m to the shore and between 150 and 250 m to the reef front. Tides characterizing Mayotte are semidiurnal and ranged between 0 and 4 m with a mean spring range of about 3 m. In all sites, the seagrass beds were partially or completely exposed at low tides.

2.2. Fish sampling surveys

Fish communities were sampled using underwater visual census from November 2012 to January 2013, covering the hot rainy

monsoon season. Due to the high patchiness of the seagrass habitat, sampling with belt transects was not efficient in the present study. Thus, three replicates of 20-min census were performed by snorkelling on the seagrass beds. The observer moved normally (2.5 m min⁻¹) to record all fishes, i.e. transient and more sedentary species, present within the seagrass bed patches area for 20-min. Each 20-min sampling slice was separated from each other by at least 50 m. For each site, the covered sampling area was the same and was approximately 200 m² for the 20-min and swimming speed was constant to standardize the sampling time. Individual fish were identified to species level and their total length (TL) was estimated to the nearest centimeter. Fishes that were difficult to identify visually to the species level were photographed for later identification using identification books (Smith and Heemstra, 1986; Taquet and Diringer, 2007). To classify juvenile and adult fish, the approach by Nagelkerken and Velde (2002) was used, where fish were recorded as juveniles when they were smaller than 1/3 of the maximum species length, obtained from identification books (Smith and Heemstra, 1986; Taquet and Diringer, 2007) and FishBase World Wide Web (Froese and Pauly, 2017). Sampling was repeated five times, twice a month during the first and the second fortnight of November and December and once in January at each site. The same diver conducted each census during daytime between 09.00 and 16.00 h at high tide, when the seagrass beds were fully flooded to reduce possible tidal range effects (Unsworth et al., 2007; Madi Moussa et al., 2015; Kruse et al., 2016).

2.3. Habitat and environmental data

Percentage cover of seagrass and other substrate (algal turf, live coral boulders, sand, dead coral rubble, habitability coefficient) were estimated at all sites using the Medium Scale Approach based on a semi-quantitative description (MSA - Clua et al., 2006). Habitability coefficient corresponds to estimating habitat complexity or heterogeneity that fish perceive, by using a semi quantitative scale (1 to 4) where 1 is not complex and 4 complex. The habitat complexity is linked to the number of components and their relative surfaces (Clua et al., 2006). To describe the habitat of each site, a diver swam along three 50 m transects placed randomly within the same area as the fish assessment, and divided in 20 non overlapping quadrates of 25 m², positioned on both sides of the transect lines. The cover of seagrass and other substrate measured on each quadrat were then averaged along each transect. These habitat description transects were surveyed once. Water clarity was measured using a horizontal Secchi disk and graduating tape. At each site, depth was measured before each census using a dive computer. Water clarity and depth were measured every time that fish transects took place.

2.4. Data analysis

One-way analysis of variance (ANOVA) was used to test differences in species richness, number of families, Shannon diversity (H'), Pielou evenness (J') indices, mean total fish density and environmental variables (water clarity, depth, habitability coefficient) between sites. Comparison of mean total fish density between juveniles and adults within sites was performed with a 2-way ANOVA with site (4 levels) and age class (juvenile and adult) as predictors. If the ANOVA results indicated significant differences between sites (probability level < 0.05), Tukey's (HSD) post-hoc tests were conducted to determine which of the means differed significantly. All analyses were performed using R version 3.3.2.

The total fish density obtained from the five time surveys for each of the three transects performed at each site was used to examine differences in juvenile and adult fish assemblages with

Table 1

Environmental characteristics (mean ± SD) of the four sampling sites located on the western shore of Mayotte.

| | Water clarity (m) | Depth (m) | Habitability coefficient |
|-------------|-------------------|-------------|--------------------------|
| Mtsoubatsou | 4.8 ± 0.40 | 1.58 ± 0.19 | 1.63 ± 0.25 |
| Sohoa | 5.8 ± 0.20 | 1.92 ± 0.15 | 1.67 ± 0.49 |
| Boueni | 4.8 ± 0.20 | 2.02 ± 0.10 | 1.60 ± 0.17 |
| Ngouja | 10.2 ± 1.06 | 1.98 ± 0.25 | 1.53 ± 0.38 |

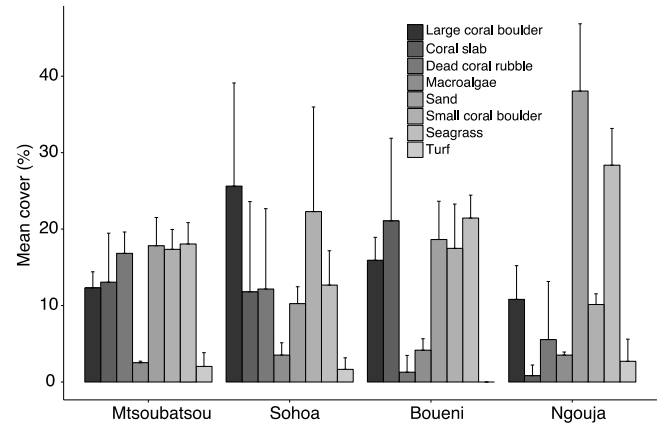


Fig. 2. Percentage cover of the different habitat variables used in the present study for the four sites. Error bars represent one standard deviation.

the non-metric Multidimensional Scaling (MDS). This analysis was performed on the Bray–Curtis similarity matrix, using fourth-root transformed data (to reduce the influence of abundant and rare species) via the PRIMER V.6 software (Plymouth Marine Laboratory). Stress values found by the MDS analysis correspond to a good ordination with no risk of drawing false inferences of sample relationships when the value is less than 0.1 (Clarke, 1993). A One-way (Site) ANOSIM (analysis of similarity) was used to investigate differences identified by MDS and cluster following SIMPER (similarity percentage) analysis, to determine the fish groups that contributed most to the dissimilarity between sites (Clarke and Warwick, 1994).

The relationship between juvenile and adult fish assemblages and environmental variables (water clarity, depth, habitability coefficient, sand, seagrass, turf, coral slab, live coral boulder and dead coral rubble) was studied by Canonical Correspondence Analysis (CCA) using total fish density data. The importance of each environmental variable was evaluated by Monte Carlo permutation tests during forward selection, and only significant variables were used in the CCA model. No collinearity between variables was observed and the statistical significance (at the 5% level) of the effect of each variable on the final analysis was determined using the Monte Carlo permutation test (ter Braak, 1986). This analysis was performed using the Canoco 4.5.1 program (ter Braak and Smilauer, 1998).

3. Results

3.1. Habitat and environmental data

A difference existed in both environmental characteristics and the seagrass habitat structure among the four sites (Table 1 and Fig. 2). The analysis of variance showed a highly significant influence of the water clarity ($F = 46.09$; $p < 0.001$). Tukey's HSD post hoc test indicated that the Ngouja site, where the maximum visibility value (mean ± SD, 10.2 ± 1.06 m) was observed, was responsible for this divergence. There was also a significant difference in mean depth between sites ($F = 10.07$; $p < 0.001$).

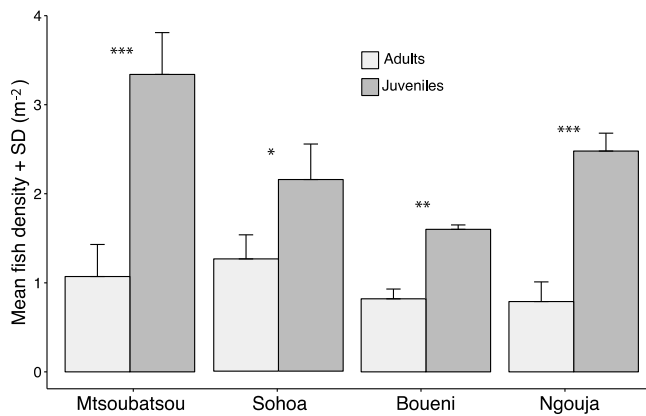


Fig. 3. Mean total fish density of adults and juveniles at the four study sites along the West coast of Mayotte. Error bars show SD. Meaning of codes: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

The post hoc test designated Mtsoubatsou as responsible for the difference observed with the lowest depth mean (Table 1). In contrast, no significant difference existed in the habitability coefficient among sites ($p > 0.05$). Concerning habitat categories, only six presented an average cover percentage greater than 10%: sand, seagrass, small coral boulders, large coral boulders, slab, dead coral and rubble (Fig. 2). For example, the percentage (mean \pm SD) sand cover fluctuated between $38 \pm 8.8\%$ at Ngouja and $10 \pm 2.2\%$ at Sohoa. The mean seagrass cover showed the highest values at the Ngouja site ($28.4 \pm 4.8\%$) and the lowest values at the Sohoa site ($12.7 \pm 4.5\%$). The lowest values of dead coral rubble were at Boueni site ($1 \pm 2.2\%$) and the highest values at Mtsoubatsou ($17 \pm 2.8\%$). At Mtsoubatsou, four habitat categories have relatively the same mean cover value (sand, small coral boulders, dead coral and rubble and seagrass around 17%–18%).

3.2. Spatial structure of the fish assemblage

From November 2012 to January 2013, 8,288 fish belonging to 99 species and 28 families were counted in the seagrass beds of the four sites (Table 2 and Supplementary material I). The mean total fish density varied significantly according to the sites ($F = 25.15$; $p < 0.001$), with the highest total fish density at Mtsoubatsou and lowest total fish density at Boueni (Tukey's HSD post-hoc test, $p < 0.001$). The three most encountered fish families were Pomacentridae, Labridae and Acanthuridae, representing 54% of the total fish composition. Total species richness varied from 34 species at Mtsoubatsou to 49 species at Ngouja (Table 2). The mean fish species richness differed significantly between sites ($F = 23.06$; $p < 0.001$), particularly between Mtsoubatsou and Sohoa (Tukey's HSD post-hoc test, $p < 0.001$). The average number of families significantly differed among sites (one-way ANOVA: $F = 18.97$; $p < 0.001$), and was higher in Ngouja seagrass beds (20 ± 0) than at Mtsoubatsou (14 ± 67) (Tukey's HSD post-hoc test, $p < 0.001$). The Shannon's diversity index showed a significant difference ($F = 6.445$; $p = 0.015$) between sites with the higher value at Sohoa (3.31) and the lowest at Mtsoubatsou (2.66). The evenness (J') did not vary among sites (Table 2), suggesting that the fish assemblage is balanced at the four sites.

3.3. Relationship of total fish density at juvenile and adult stages with environmental variables

Mean total fish density between age class (adult and juvenile) varied significantly at each site (two-way ANOVA, $F = 138.77$; $p < 0.001$), with juveniles always being more abundant in seagrass

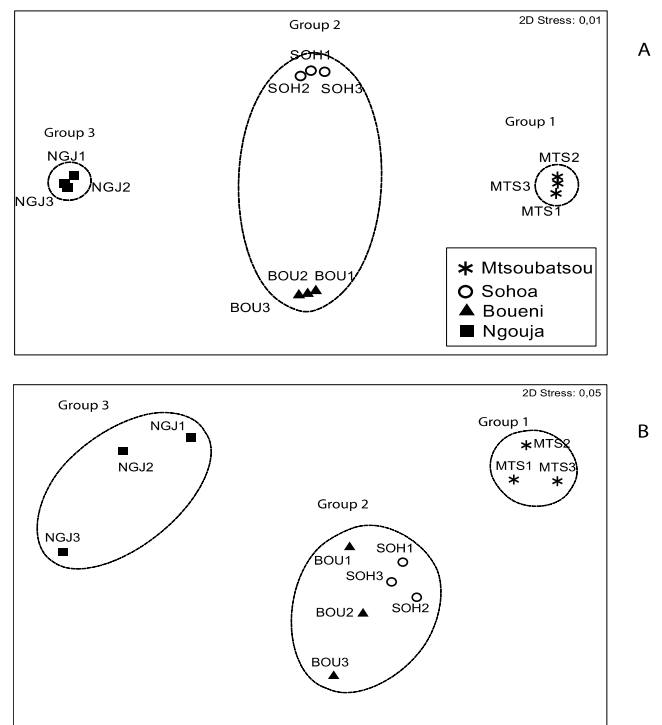


Fig. 4. Multidimensional scaling (MDS) of the similarity of fish assemblages obtained from the similarities (Bray–Curtis similarity) on the total fish density of each species (A) for all juveniles and (B) for adults. Assemblages were grouped according to site-transsects with a similarity level of 50% delineated in the MDS plot. Site code: MTS = Mtsoubatsou; SOH = Sohoa; BOU = Boueni and NGJ = Ngouja. Each point represents total fish density for the five time surveys for each transect.

beds than adults (Fig. 3). There were significant differences in the mean total fish density of juvenile between the sites (two-way ANOVA, $F = 7.64$; $p < 0.01$), while the mean total fish density of adults did not differ significantly (Tukey's HSD test; $p > 0.05$). Juveniles made up 73% of the total fish assemblage sampled in the seagrass beds and few adults of large species were observed.

Fish assemblage composition varied significantly among sites (Global $R = 1$, $p < 0.001$ for juvenile) and (Global $R = 0.861$, $p < 0.001$ for adult). The MDS plane highlighted three groups with a North–South gradient whatever the life stage considered (Fig. 4). The SIMPER analysis allowed for identification of the main species and ontogenetic stages responsible for the similarity within each group. *Stethojulis strigiventer* at juvenile stage and *Chrysiptera unimaculata*, *Stegastes fasciolatus* at adult stage were the most representative species of Group 1. *Rhinecanthus aculeatus* at juvenile stage and *Cryptocentrus strigilliceus*, *C. unimaculata*, *Halichoeres nebulosus*, *S. fasciolatus* at adult stage contributed most to the similarity within the Group 2. Similarity within Group 3 was mainly due to *Chrysiptera annulata* and *R. aculeatus* at juvenile stage and *Iniistius pentadactylus* at adult stage. Between juvenile fish assemblage, the first group was composed by *Abudefduf sparoides*, *Acanthurus triostegus* and *Acanthurus nigricauda* at juvenile stage. *Ostorhinchus angustatus*, *C. strigilliceus*, *Parupeneus macronemus*, *Lutjanus gibbus*, *Calotomus carolinus*, and *C. annulata* make up the second group. The third group was constituted by *P. macronemus*, *R. aculeatus*, *L. gibbus* and *Parupeneus barberinus*. A dissimilarity analysis by SIMPER showed that species, which contributed most to similarities within groups strongly contributed also to differences between groups.

The significant factors explaining variation in juvenile fish community structure were seagrass, water clarity, depth and

Table 2

Mean total fish density per square meter, mean number of species and families, Shannon's diversity and Pielou's evenness indices (mean ± SD) of the fish community at each site. For each site, the covered sampling area was 200 m².

| Sites | Mean total fish density | Mean number of species | Shannon's diversity index (H') | Pielou's evenness index (J') | Mean number of families |
|-------------|-------------------------|------------------------|--------------------------------|------------------------------|-------------------------|
| Mtsoubatsou | 4.5 ± 0.28 | 34 ± 0 | 2.7 ± 0.06 | 0.8 ± 0.02 | 14.7 ± 1.1 |
| Sohoa | 3.4 ± 0.29 | 43 ± 3 | 3.1 ± 0.18 | 0.8 ± 0.03 | 16.3 ± 1.1 |
| Boueni | 2.5 ± 0.24 | 39 ± 1 | 2.8 ± 0.12 | 0.8 ± 0.03 | 14.7 ± 1.1 |
| Ngouja | 3.3 ± 0.27 | 47 ± 2 | 2.9 ± 0.05 | 0.8 ± 0.02 | 20 ± 0.0 |

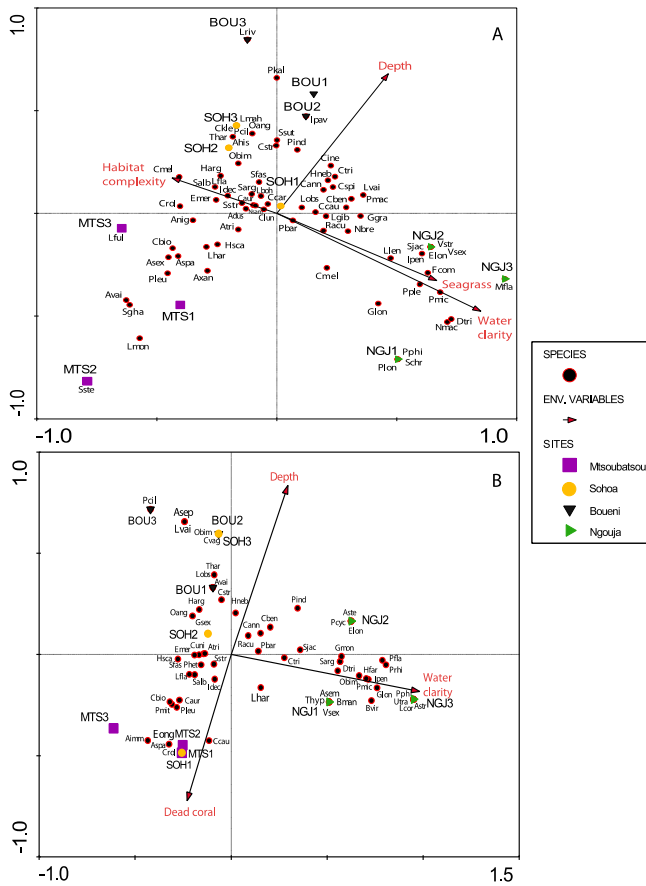


Fig. 5. Canonical Correspondence Analyses (CCA) of total fish density, environmental variables and sites for juveniles (A) and adults (B). Species are coded by the first letter of name of genus and the three first letters of species (see Supplementary material I). Site code: MTS = Mtsoubatsou; SOH = Sohoa; BOU = Boueni and NGJ = Ngouja.

habitat complexity, while dead coral, water clarity and depth were the variables explain more adult fish community. Correlation between spatial pattern of fish assemblages and the significantly important environmental variables was performed using CCA (Table 3). The CCA revealed that the four environmental variables explained 62.8% of the variation in species composition for juvenile and three variables for the adult 82.4%. The overall permutation test on the first two axes showed that the canonical significance correlation between fish assemblages and environmental variables for both life stages was highly significant ($p < 0.01$). The analysis of canonical and correlation coefficients revealed that the first axis was mostly explained by water clarity ($r = 0.81$ for juvenile and $r = 0.95$ for adult) while axis 2 was explained by depth ($r = 0.64$ for juvenile and $r = 0.73$ for adult) (Fig. 5).

Table 3

Results of the canonical correspondence analysis performed on community structure of fishes for juvenile and adult. Significant factors were selected using backward elimination permutation tests (number of permutations = 999). The robustness of the analysis was tested using a Monte Carlo test.

| | Juvenile | | Adult | |
|---|----------|---------|--------|---------|
| | Axis 1 | Axis 2 | Axis 1 | Axis 2 |
| Correlations of environmental variables with ordination axes | | | | |
| (1) Dead coral | - | - | -0.222 | -0.629 |
| (2) Seagrass | 0.637 | -0.309 | - | - |
| (3) Water clarity | 0.813 | -0.451 | 0.949 | -0.158 |
| (4) Depth | 0.444 | 0.644 | 0.285 | 0.727 |
| (5) Habitat complexity | -0.418 | 0.164 | - | - |
| Summary statistics for ordination axes | | | | |
| Eigenvalues | 0.320 | 0.141 | 0.472 | 0.198 |
| Species-environment correlations | 0.956 | 0.946 | 0.966 | 0.870 |
| Cumulative percentage variance | | | | |
| of species data | 30.6 | 44.0 | 30.7 | 43.6 |
| of species-environment relation | 51.0 | 73.4 | 57.3 | 81.3 |
| Sum of all eigenvalues | 1.048 | | 1.537 | |
| Sum of all canonical eigenvalues | 0.628 | | 0.824 | |
| Summary of Monte Carlo test | | | | |
| | F | P-value | F | P-value |
| Significance of first canonical axis | 3.082 | 0.004 | 3.542 | 0.003 |
| Significance of all canonical axes | 2.620 | 0.001 | 3.078 | 0.002 |

4. Discussion

Many studies, which have recognized the importance of shallow coastal habitats such as mangroves and seagrass beds, as an important juvenile habitat, found that mangroves enhance the fish assemblage in adjacent seagrass beds (Nagelkerken et al., 2001; Lecchini, 2005, 2006; Lugendo et al., 2005; Unsworth et al., 2008, 2009). These seagrass beds might in turn also contribute to the adult fish density on adjacent coral reefs (Dorenbosch et al., 2005a; Nakamura and Sano, 2004a,b). Our results were similar to those of studies that have shown that seagrass beds are important juvenile habitat for coral reef fish (Dorenbosch et al., 2005a,b; Nakamura, 2010).

With a total of 99 species from 28 families, the ichthyofauna recorded on the intertidal seagrass beds of Mayotte appeared similarly diversified than other sites located in the Western Indian Ocean. Even though Harmelin-vivien (1983) found up to 157 fish species in multi-specific seagrass beds in Tulear, Madagascar, Chirico et al. (2017) identified 111 taxa from 31 families along Kenyan coast, while Alonso Aller et al. (2017) identified 114 species from 33 families around Unguja Island in Zanzibar, Tanzania. Differences in fish community richness between these studies can be explained by various environmental factors such as seagrass height, structural complexity and water depth. For example, differences in fish community structure between the seagrass beds of Tulear and our study may be due to the difference in height of seagrass leaves and the depth of the study sites. On Tulear, fish were sampled between 0 and 6 m depth and the height of seagrass leaves varied from 20 to 40 cm, while

the seagrass bed height on the western shore of Mayotte did not exceed 10–15 cm and the depth varied from 0 to 2.5 m at our study sites. Nakamura and Sano (2004b) suggested that using the seagrass as shelter might lead to higher survival rates of juvenile fish in seagrass beds because of the increased the availability of living space and by providing abundant food resources for these juvenile fish. Hence, when fish become too large for optimal protection by the seagrass height, they often migrate to adjacent coral reefs (Nagelkerken et al., 2000). During our study, depth appeared as one of the factors explaining the fish assemblage composition and total fish density (Table 3 and Fig. 5). In the Caribbean, spatial variation in species abundance was related to variation of depth among sites (Kopp et al., 2012). Chabanet (2002) also observed this same trend in fringing reef sites of Mayotte where the lowest number of species were recorded at the shallowest sites, whereas the highest one was found at 3 m. However, our study highlighted four environmental variables correlated to fish community structure and species distribution in seagrass beds (water clarity, seagrass bed cover, depth and habitat complexity). Water clarity was the principal factor promoting leaf growth (see references in the review of Gullström et al., 2002), while seagrass bed cover may have allowed juvenile to reach maturity by serving as shelter (Nakamura and Sano, 2004c). The relation between the higher density of juveniles and the four variables might be explained by the increase in space for shelter and food resources at Mayotte (even though not statistically tested). Thus, in Mayotte, an apparently more homogenous diversity of fish assemblages was observed in the south, where sand and seagrass cover may display higher values, than in the north where diversity appeared more variable and where the intertidal seagrass beds were mixed equally, by dead coral rubble, small coral boulders and sand. However, more investigations would be required in order to confirm the possible link between juveniles' density and habitats variables.

In polyspecific seagrass beds of Tulear, Harmelin-vivien (1983) found that the five most common dominant families were Labridae, Goobiidae, Apogonidae, Pomacentridae and Lutjanidae. In the present seagrass beds, Pomacentridae, Labridae, Acanthuridae, Lutjanidae and Mullidae were the dominant families. *Abudefduf sparoides*, *S. strigiventer*, *A. triostegus*, *L. gibbus* and *P. macronemus* being the most abundant species belonging to these families. Nakamura and Sano (2004a) recorded Goobiidae and Labridae to be the most dominant families and found that *S. strigiventer*, *Cheilio inermis* and *Cryptocentrus caeruleomaculatus* were the most abundant species in the seagrass beds of the Amitori bay in Japan. In many studies in the western Indian Ocean region, seagrass beds have been reported to harbor the high number of juveniles of various reef fish species (Dorenbosch et al., 2005a,b; Lugendo et al., 2005; Gullström et al., 2008). Accordingly, this is a reason why seagrass beds have been referred to as nursery areas (Pollard, 1984; Parrish, 1989). Dorenbosch et al. (2005a) suggested that utilization of seagrass habitats as a juvenile habitat by coral reef fishes in some regions of the Indo-Pacific can be as important as seagrass beds and mangroves in the Caribbean. The dominance of juveniles in the intertidal seagrass beds in this study (73% of all fishes sampled) is consistent with other study done within the Indian Ocean (Gullström et al., 2008). According to the classification of fish species realized by Dorenbosch et al. (2005a), 4 of the 8 species of nursery groups were found on juvenile life stages in this study (*Lutjanus monostigma*, *Mulloidichthys flavolineatus*, *Scolopsis ghanam* and *Siganus sutor*). For all groups, the dominance of juvenile fish in this area, suggested that the seagrass beds in the present study might have a nursery function for these fishes. Dorenbosch et al. (2005a) found that juveniles of species of generalists and reef generalists are clearly able to use other available habitats, in particular reef habitats although

their highest juvenile densities were observed in seagrass beds. Hence, the patterns of abundance and distribution of seagrass fish assemblages may be influenced by several factors as the spatial arrangement of the habitats, ontogenetic shifts and competition and feeding mechanisms (Dorenbosch et al., 2005a,b; Gullström et al., 2008; Kimirei et al., 2011).

Overall, our study highlighted that intertidal seagrass beds of Mayotte played an important functional role for fish assemblages, as the juvenile habitat of many reef species. Mean total density of juvenile and adult fishes indicated that most species utilized the seagrass beds as a nursery area, but some small species also used them as part of their adult habitat. We found here that about 73% of the total number of fish sampled in seagrass beds juveniles. This result was similar to the one found by Gullström et al. (2008) on Zanzibar Island, where 75% of all fishes sampled in seagrass areas were juveniles. Some Lutjanid juveniles (*Lutjanus fulviflamma*, *L. fulvus* and *L. monostigma*) observed in the mangrove on the eastern coast (Madi Moussa, 2018), also used this habitat, suggesting that lacking mangrove in the western shore, seagrass bed was an alternative habitat before the ontogenetic habitat shifts in the coral reef. As observed by Kimirei et al. (2011) *L. fulviflamma* used seagrass beds and mangroves as their principal juvenile habitats. Our study demonstrated the influence of certain environmental variables (water clarity, seagrass cover depth and habitat complexity) on fish distribution in the seagrass beds. Seagrass beds, however, are very vulnerable ecosystems and are decreasing worldwide (Orth et al., 2006; Waycott et al., 2009). Therefore it is of primary importance to protect seagrass beds within the Indo-Pacific (Unsworth and Cullen, 2010).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at <https://doi.org/10.1016/j.rsma.2019.100965>.

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