



Differences in root architecture influence attraction of fishes to mangroves: A field experiment mimicking roots of different length, orientation, and complexity

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ABSTRACT

Benthic structure plays an important role as shelter and feeding habitat for demersal fauna. While many studies have investigated the relationship between structural complexity of aquatic vegetation and the number of species or abundance of motile organisms, little is known of the attractiveness of submerged mangrove roots. We tested the importance of various root attributes in attracting fish species in a field experiment using different artificial mangrove units (AMUs) with PVC pipes mimicking roots to exclude interaction with other environmental and biotic factors. We manipulated length, vertical orientation, and three-dimensional structural complexity of root mimics in the AMUs to explore their effects on the fish community variables: fish abundance, number of species and community composition. Pipe length and three-dimensional structure did not have an effect on fish community variables. Vertical pipe orientation had a significant effect and AMUs with standing pipes showed higher total fish abundances and number of species than AMUs with hanging pipes. Also community composition differed greatly between AMUs with standing versus hanging pipes. At species level, demersal fish species mainly occupied AMUs with standing pipes and occurred only at very low abundances when hanging pipes dominated in the AMUs; in contrast, the semi-pelagic swimmer *Sphyraena barracuda* showed a trend of higher abundance in AMUs with mainly hanging pipes. When analyzed across all AMUs, fish abundances of demersal as well as semi-pelagic species decreased significantly with increasing interspatial pipe distance among AMUs, suggesting that distance to refuge may be the underlying mechanism for the observed patterns. The above findings are important in the context of the worldwide degradation of mangroves, because human alteration to mangrove vegetation affects its structure and thus composition and size of fish communities.

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1. Introduction

Demersal fish species are often attracted by structure-rich habitats (Chabanet et al., 1997; Jenkins and Sutherland, 1997; Scharf et al., 2006). One of the driving factors for this attraction is reduction of predation risk (Gotceitas and Colgan, 1989). However, fishes may face a trade-off as shelter habitats are often not the optimal feeding habitats (Crowder and Cooper, 1982). Various strategies have evolved to cope with this dichotomy, such as diel migrations between

structure-rich shelter habitats and food-rich foraging habitats (Hobson, 1973; Summerson and Peterson, 1984).

The tropical coastal seascape is a typical example of where such day–night feeding migrations occur (Ogden and Ehrlich, 1977; Nagelkerken et al., 2000a). Aquatic vegetation, such as mangroves, seagrasses and algae, provides optimal feeding and/or shelter opportunities for prey as well as small predators. The complex structure provided by the vegetation can reduce predation risk and offers high food abundance for associated fauna (Orth et al., 1984; Nagelkerken et al., 2008a). These two factors are assumed to be the underlying principles why habitats such as mangroves and seagrass beds are used as nurseries by many fish during their juvenile life phase (Beck et al., 2001; Nagelkerken, 2009; but see Grol et al., 2008). Once fish outgrow the shelter of the vegetation or reach maturity they permanently migrate to deeper offshore habitats, such as coral reefs

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(Cocheret de la Morinière et al., 2002; Nakamura et al., 2008; Verweij et al., 2008).

Due to the juxtaposition of various shallow habitats that provide different advantages for different species, many tropical coastal fishes show diel or tidal migrations among neighboring habitats (Nagelkerken et al., 2008b; Krumme, 2009). In the Caribbean, for example, various species of nocturnally-active fishes shelter in structure-rich habitats (mangroves, patch reefs, and undercut notches in shoreline fossil reefs; Ogden and Ehrlich, 1977; Verweij and Nagelkerken, 2007) during daytime and feed on open adjacent seagrass, algal and sand plains at night (Burke, 1995; Nagelkerken et al., 2000a).

Mangrove roots, one of factors that characterize the mangrove habitat, contribute to the attractiveness of this habitat by increasing its structural complexity. In the Caribbean, mangroves are continuously inundated due to small tidal ranges, and they harbor higher fish densities than adjacent habitats (Nagelkerken, 2009; and references therein). In contrast, Indo-Pacific mangroves are mostly of intertidal nature and due to the high tidal amplitude they are only temporarily accessible for feeding or shelter (Vance et al., 1996; Lugendo et al., 2007; Krumme, 2009).

Mangrove roots can be characterized on the basis of various structural properties, but so far very few studies have tested the role of these properties experimentally. Examples include those that tested the effect of root epibiont complexity (MacDonald et al., 2008), degree of shading (Cocheret de la Morinière et al., 2004; Verweij et al., 2006a), root density (Cocheret de la Morinière et al., 2004; MacDonald et al., 2009), and presence of decomposing leaves (Rajendran and Kathiresan, 1999) on fish communities. Equally few studies have assessed the effect that newly introduced complexity, such as in newly planted mangroves, has on fish or other marine communities (Bosire et al., 2004; Huxham et al., 2004; Bosire et al., 2008).

In other habitat types, three-dimensional complexity of shelter has been shown to be an important variable with respect to habitat preference by fishes and the associated predation risk (Orth et al., 1984; Adams et al., 2004; Almany, 2004; Scharf et al., 2006), and fish often favor shelter holes that are near their body size (Hixon and Beets, 1993). The importance of three-dimensional structure for the associated fish community remains unclear for mangrove roots. Mangrove roots differ in length, circumference, and vertical orientation, creating a complex three-dimensional habitat. Few studies have considered the potential effects of such variables and they often simply refer to 'the protective value of mangrove roots' for fishes. Consideration is typically given to the role of root density alone. One of the exceptions was a study comparing fish communities among roots of different species of mangroves (Rönnbäck et al., 1999). They found higher fish densities among standing pneumatophores than among hanging prop-roots, and found no relationship with root surface area. However, field studies in mangroves typically suffer from interactive effects with a variety of other biotic and environmental factors. The spatial and temporal utilization of mangrove habitats by fish depends on factors such as tidal amplitude, time of inundation, geomorphology of the habitat, food abundance, predator abundance, competition, habitat complexity, water temperature, salinity, turbidity, water depth, distance to mangrove fringe, and so on (Nagelkerken et al., 2008a). This makes it very difficult if not impossible to determine which properties of mangrove root structure themselves attract fishes.

In the present study, we used artificial mangrove units (AMUs) in which only root architecture differed among treatments to avoid interactive effects with other biotic and environmental variables. We investigated the role of previously unstudied properties of mangrove root structure that are related to their architecture. Using the same total root density, we investigated the role of (1) root length (three lengths), (2) vertical root orientation (hanging, standing, or running from bottom to top in the AMUs), and (3) three-dimensional root

complexity (different mixtures of hanging and standing roots of different lengths) on various fish community variables (abundance, number of species, and community structure).

Although the relationships between complexity of various types of bottom structures and fish densities have been examined in various habitat types, study of the mangrove habitat is conceptually different in that the inundated mangrove area forms a clearly confined three-dimensional habitat. In contrast to benthic living structure formed by, for example, coral reefs, seagrass beds and algal plains that have an overlying column of 'open water', the canopy of overlying mangrove trees creates a dark water column which in itself can act as shelter for fish irrespective of the presence or complexity of roots (e.g., Cocheret de la Morinière et al., 2004). Hence, in the presence of shade typically-observed relationships between fish and structure may be altered. As the degree of shading and total density of structure was equal among AMUs used in this study, the null-hypothesis was therefore that there would be no differences in fish community variables among AMUs with root mimics of different architecture.

2. Materials and methods

2.1. Study area

The study was carried out in Spanish Water Bay on the Caribbean island of Curaçao, Netherlands Antilles. This semi-enclosed marine embayment has a maple-leaf shape with a connecting channel to the sea, a total surface area of approx. 3 km², and is for the main part <6 m deep. The shoreline of the bay is fringed by *Rhizophora mangle* L. trees of which the prop-roots are always inundated. Monospecific *Thalassia testudinum* Banks ex. König seagrass beds are located in front of the mangroves at depths of 0.4–3 m. Between about 3 and 6 m depth, the bay consists of subtidal muddy/sandy seabeds with some degree of algal cover, followed at 6 m by a deep channel (max. 11–18 m deep) in the central parts of the bay. The bay has no freshwater input other than rainwater, and shows relatively little seasonal variation in salinity and water temperature (see details in Nagelkerken et al., 2000b). The study site (12° 4' 24" N, 68° 50' 59.5" W) was located on a muddy patch at about 1 m depth situated between a shoreline mangrove stand of 50 m long and a seagrass bed (see 'site 2' of Nagelkerken et al., 2000b, or site 'mangroves 1100 m' of Nagelkerken and Faunce, 2008). The annual mean tidal amplitude on Curaçao is about 30 cm (de Haan and Zaneveld, 1959). Water clarity was relatively high at the study site and ranged between 3 and 5 m (horizontal Secchi disk distance), allowing visual surveys of the fish assemblages.

2.2. Study design

Artificial mangrove units (AMUs) were constructed using iron rods (Ø 6 mm) welded to form an open framework of 1.0 m wide, 1.0 m long and 0.8 m high. Mangrove prop-roots (*R. mangle*) and pneumatophores (*Avicennia germinans* L.) were mimicked by dull yellow-brown colored PVC pipes (Ø 1.5 cm, of varying lengths) hanging down from the top of the AMUs or standing up from the substratum, respectively. The PVC pipes were evenly distributed at 10 cm apart in the AMUs at a density of 64 pipes per m², based on a previous study where fish abundances were found to be highest at this level of structural complexity (Cocheret de la Morinière et al., 2004). Hanging PVC pipes were attached to the top of the AMUs using rope, while standing pipes were attached to a metal grid on the substratum.

To mimic the dark mangrove habitat, the top of the AMUs was covered with black shading fabric (polyethylene monofilament) to create an approx. 78% darker environment in the AMUs than on the surrounding mud flats. The thickness of the fabric was based on a previous study with AMUs where fish abundances were found to be greatest at this level of light intensity (between shade levels C and D

as used by Cocheret de la Morinière et al., 2004). The fabric was cleaned off epibionts daily to maintain the same relative light intensities among AMUs throughout the study period. For a rough characterization of the light regime across habitats, light intensity was measured at the end of the study period on three different days between 11:00 and 14:00 h in the centre of an AMU with solely standing PVC pipes (40 cm high), in the centre of an AMU with solely hanging PVC pipes (40 cm long), at the fringe of the adjacent mangrove forest, and on the adjacent seagrass bed, using a Li-Cor light meter held at 40 cm above the substratum. Mean (± 1 SD) light intensity was similar for the AMU with standing pipes (see Fig. 1; AMU 2: $239 \pm 47 \mu\text{E m}^{-2}\text{s}^{-1}$), the AMU with hanging pipes (AMU 6: $265 \pm 62 \mu\text{E m}^{-2}\text{s}^{-1}$), and the fringe of the adjacent mangrove forest ($163 \pm 114 \mu\text{E m}^{-2}\text{s}^{-1}$) (1-way ANOVA followed by a Tukey HSD post-hoc, $p > 0.458$). Compared to these three values, light intensity was significantly higher on the adjacent seagrass bed ($1150 \pm 354 \mu\text{E m}^{-2}\text{s}^{-1}$; $p < 0.038$).

Three aspects of root architecture were studied: pipe length (10, 40, and 80 cm), vertical pipe orientation (hanging, standing, and full length), and three-dimensional pipe complexity (different mixtures of hanging and standing pipes of different lengths). To this end, seven different AMUs (i.e., seven 'treatments'; see Fig. 1) were constructed, containing: (1) standing pipes of 10 cm length, (2) standing pipes of 40 cm length, (3) an equal mixture of standing pipes of 10, 40 and 80 cm length, (4) pipes of 80 cm length that spanned the entire height of the AMU, (5) an equal mixture of hanging pipes of 10, 40 and 80 cm length, (6) hanging pipes of 40 cm length, and (7) hanging pipes of 10 cm length. To exclude an interaction with the factor 'food', as in access to benthos, the substratum (and bottom metal framework) of all AMUs was covered with a thin white cotton sheet. The cotton sheet, the iron rods of the AMUs, and the PVC pipes were cleaned off epibionts at the end of every other day.

The seven AMUs were positioned in a row oriented parallel to the adjacent mangroves (distance: 1.6 m) and adjacent seagrass bed (distance: 2.0 m). The AMUs were placed at a depth of about 1 m, so that at low tide the top of each AMU was just submerged. The AMUs were placed in random order (i.e., 'configuration') at a distance of 1 m from one another, left undisturbed for four days the first time, after

which the censuses started. Observations were performed during daytime at three 'time intervals': 10:00–10:45 h, 11:30–12:15 h, and 13:00–13:45 h. During each time interval all AMUs were censused in their consecutive order, after which the observer waited 5 min before starting a new round of observations for all AMUs. Per time interval, each AMU was censused eight times in this manner (i.e., eight 'observation rounds'). All AMUs were censused during the three time intervals for three consecutive days (i.e., 'days' 1–3) during which the configuration of the AMUs remained unchanged. At the end of day 3 their configuration was randomly changed and the AMUs were left undisturbed for one day before the entire 3-day observation cycle started over again. This cycle was repeated for a total of eight times (i.e., eight 'replicates' with each having a different AMU configuration), resulting in a total of 576 observations per treatment during the entire study period.

The visual censuses were performed during November–December 2003, using snorkeling gear. All fishes within the AMUs were identified, enumerated, and their size estimated in classes of 2.5 cm total length (Table 1). Juvenile *Scarus iseri* ranged in length between 5 and 15 cm and were therefore easy to distinguish from their congeneric and similar-looking *Scarus taeniopterus*. The position of each fish within the AMU was noted as bottom, centre, or top. Fish abundance estimations were first practiced thoroughly in the field before the experiment started.

2.3. Statistical analysis

All analyses were done using the statistical program SPSS 16.0. Prior to statistical analysis, fish abundances were summed per treatment for each configuration (i.e., 8 observation rounds \times 3 time intervals \times 3 days = 72 observations) in order to maintain discrete values to enable a Poisson regression (McCullagh and Nelder, 1989); this resulted in eight replicates of different configurations for each treatment. The 72 observations per configuration were pooled for three reasons: (1) we were not interested in time or day effects, (2) by pooling these values we did not have to make the (questionable) assumption of independence of data among time intervals within days or among days at the same time intervals, and (3) increasing

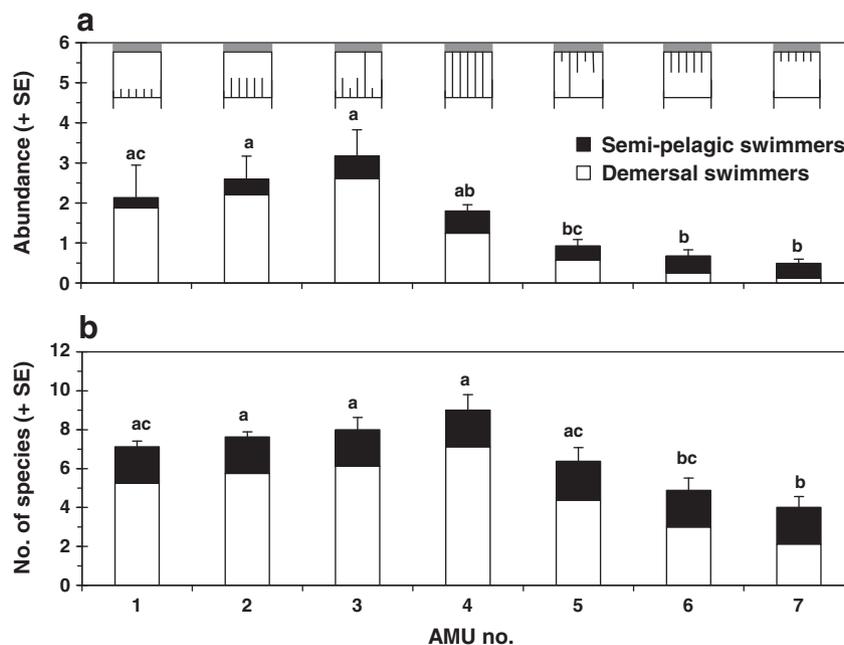


Fig. 1. Mean total fish abundance (a) and total number of species (b) for different artificial mangrove units (AMU). Standard errors (SE) depict the variation among the eight temporal replicates as described in the Materials and methods section. Different letters above bars indicate significant differences (Poisson regression, $p \leq 0.05$). Pictographs (not drawn to scale) represent the different treatments (i.e., pipe length, vertical orientation, and three-dimensional complexity).

Table 1

Mean size (total length) and density (m^{-2}) of fish species with different life modes (D = demersal, SP = semi-pelagic) and results of the regression analyses between fish abundances / no. of species and interspatial pipe distance. – = negative relationship.

Fish species	Mean length \pm 1 SD (cm)	Life mode	Mean density across AMUs	R ² -values regression
<i>Acanthurus chirurgus</i>	8.0 \pm 1.1	D	0.001	–
<i>Chaetodon capistratus</i>	4.4 \pm 1.2	D	0.03	–0.86**
<i>Eucinostomus jonesi</i>	8.0 \pm 2.1	D	0.001	–
<i>Haemulon chrysargyreum</i>	11.1 \pm 0.6	D	0.005	–
<i>Haemulon flavolineatum</i>	10.0 \pm 1.8	D	0.74	–0.93***
<i>Haemulon sciurus</i>	31.6 \pm 9.3	D	0.04	–0.69*
<i>Halichoeres bivittatus</i>	13.8 \pm 0.0	D	0.001	–
<i>Lutjanus analis</i>	11.5 \pm 1.7	D	0.003	–0.66*
<i>Lutjanus apodus</i>	24.0 \pm 0.8	D	0.05	–0.09
<i>Lutjanus mahogoni</i>	8.2 \pm 1.3	D	0.05	–0.83**
<i>Mulloidichthys martinicus</i>	11.5 \pm 1.4	D	0.04	–0.82**
<i>Ocyurus chrysurus</i>	10.2 \pm 2.0	SP	0.20	–0.83**
<i>Scarus iseri</i>	7.5 \pm 1.6	D	0.28	–0.78**
<i>Sparisoma chrysopterygum</i>	9.7 \pm 1.9	D	0.02	–0.45
<i>Sphyrna barracuda</i>	12.1 \pm 7.3	SP	0.22	–0.87**
Total fish abundance				–0.89**
Total number of species				–0.94***

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

observation times reduces within sample variation. The total number of species per treatment was calculated as the total across the 72 pooled observations and plotted as such; total fish abundance per treatment was plotted as the average of the eight replicates.

To test for differences among treatments, a Poisson regression with a log-link function was performed for abundance of the complete fish fauna, total number of species, and for abundances of the four most abundant species. As the observed counts tended to be overdispersed compared to Poisson variance, a correction was applied using the scaled deviance as an estimate for the dispersion parameter (McCullagh and Nelder, 1989). Post-hoc comparisons were made by calculating differences of least squares means, using a Bonferroni correction for multiple comparisons.

The specific design of the various AMUs enabled us to also examine the effect of variation in distance among pipes on fish community variables. Shortest distance between neighboring standing pipes was calculated for all AMUs with standing pipes, while distance from the substratum to the nearest hanging pipes was used when standing pipes were absent (i.e., AMUs 6 and 7). Conversely, for the semi-pelagic *Sphyrna barracuda* the distance between hanging pipes (for AMUs 3–7), and distance between the top of the AMUs and standing pipes when hanging pipes were absent (for AMUs 1 and 2) was used. The relationship between interspatial pipe distance and fish abundance and total number of species, respectively, was tested using regression analysis. The curve estimation function in SPSS 16.0 was first used to determine which type of curve provided the best overall fit, which proved to be a power function ($\ln(x)$, $\ln(y)$).

The structure of the fish assemblage was compared among AMUs and natural mangroves using Bray–Curtis cluster analysis (single linkage). As the adjacent mangrove stand was not sampled during the study period, earlier census data ($N = 5$) from the same mangrove stand in Spanish Water Bay (length \times width = 25 \times 2 m) were used instead, viz. Dec. 1997 and Aug. 1998 (Nagelkerken et al., 2000b) and June–July 2005 (Nagelkerken and Faunce, 2008). The sampled mangrove area (50 m²) approached that of each treatment to which it was compared (72 replicates \times 1 m² = 72 m²).

3. Results

3.1. Effect of pipe length

Pipe length did not have a significant effect on total fish abundance (Fig. 1a), abundance of the four most abundant species (Fig. 2), total

number of species (Fig. 1b), or community composition (Fig. 3). This was revealed by the similarity between the 10 and 40 cm standing pipes (AMUs 1 vs. 2) and between the 10 and 40 cm hanging pipes (AMUs 6 vs. 7). The only response to increasing pipe length was that demersal as well as semi-pelagic species were sometimes also observed in the central part of AMUs 2–6 as their longer pipes also created shelter in the centre of the cages (Fig. 2).

3.2. Effect of vertical pipe orientation

Vertical pipe orientation had a significant effect on all fish community variables. Total fish abundance (Fig. 1a), abundance of *Haemulon flavolineatum*, *iserti* and *Ocyurus chrysurus* (Fig. 2), and total number of species (Fig. 1b) were (significantly) higher for standing than for hanging pipes (AMUs 1 vs. 7, 2 vs. 6, and 3 vs. 5, respectively). Fish species with a demersal life mode were responsible for these differences between standing and hanging pipes (Fig. 1) as species that are typically semi-pelagic swimmers (see Table 1) showed no significant difference between the former and the latter in terms of their total abundance (Poisson regression, $p = 0.064$) or their total number of species ($p = 0.991$).

Community composition also differed between standing and hanging pipes (Fig. 3). AMUs 1–3 with predominantly standing pipes clustered together (at 89% similarity) and were dominated in terms of relative abundance by demersal *H. flavolineatum*. AMUs 6 and 7 with solely hanging pipes clustered together (at 84% similarity) and were dominated by semi-pelagic *S. barracuda*. AMUs 4 and 5 were more dissimilar to the above two clusters (66% and 68% similarity, respectively) and had a fish community consisting of a variety of common species.

3.3. Effect of three-dimensional complexity

Three-dimensional complexity did not have a significant effect on fish community variables. Neither total fish abundance (Fig. 1a), nor abundance of the four most abundant species (Fig. 2), nor number of species (Fig. 1b) were higher for three-dimensionally complex compared to less complex AMUs that had the same mean pipe length (i.e., 40 cm) across cages; this was the case for standing pipes (AMU 3 vs. 2) as well as hanging pipes (AMU 5 vs. 6).

3.4. Effect of interspatial pipe distance

For demersal fish species, interspatial pipe distance increased in two dimensions: (1) it increased horizontally with decreasing density of standing pipes (i.e., from AMU 4 to 5), and (2) in absence of benthic structure it increased vertically with decreasing length of hanging pipes (i.e., from AMU 6 to 7); the same was true for the relationship between semi-pelagic swimmers and hanging and standing pipes, respectively. Total fish abundance as well as the total number of species both showed a significant decrease with increasing interspatial pipe distance (Fig. 4). Also at species level, such a relationship existed with high R² and significant p-values (Table 1).

4. Discussion

Fish community variables (i.e., abundance, number of species, and community composition) differed significantly among AMUs, rejecting the null-hypothesis of no differences among AMUs due to an equal degree of shading and the same overall density of structure. For each of the three community variables, AMUs could be clustered into the same three groups: AMUs 1–3 with predominantly standing pipes of 10 and 40 cm length, AMUs 4 and 5 with hanging pipes that reached the bottom, and AMUs 6 and 7 with hanging pipes of 10 and 40 cm length that did not reach the bottom. This finding clearly shows that aside from degree of shading or root density (Cocheret de la Morinière

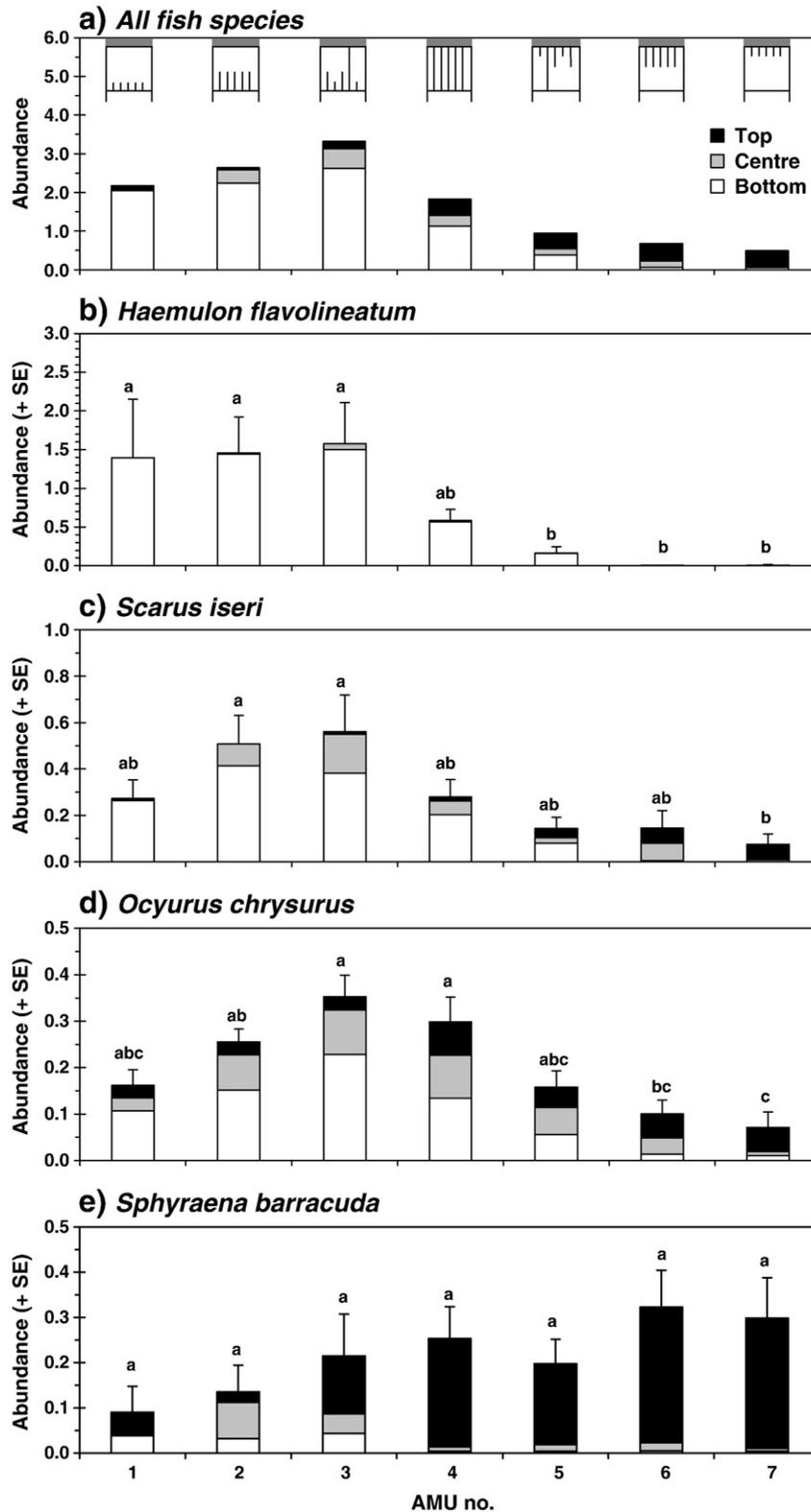


Fig. 2. Mean abundance of all fish species (a) and of the four most abundant fish species (b–e) for different artificial mangrove units (AMU). For each AMU, the position of fishes at the bottom, centre or top of the AMU is depicted. SE for panel a is shown in Fig. 1a. Refer to legend of Fig. 1 for other details.

et al., 2004), root architecture may also affect fish community variables. This concept has been tested earlier for fish in, for example, algal, coral, and seagrass habitats (Jenkins and Sutherland, 1997; Bartholomew, 2002; Gratwicke and Speight, 2005), but has rarely been tested for mangrove root systems. The current study shows that

not all aspects of root architecture had a significant effect on the associated fish community.

No response in fish community variables was found for differences in pipe length. This was probably due to lack of a difference in density of structure, meaning a similar distance to nearest refuge (see further

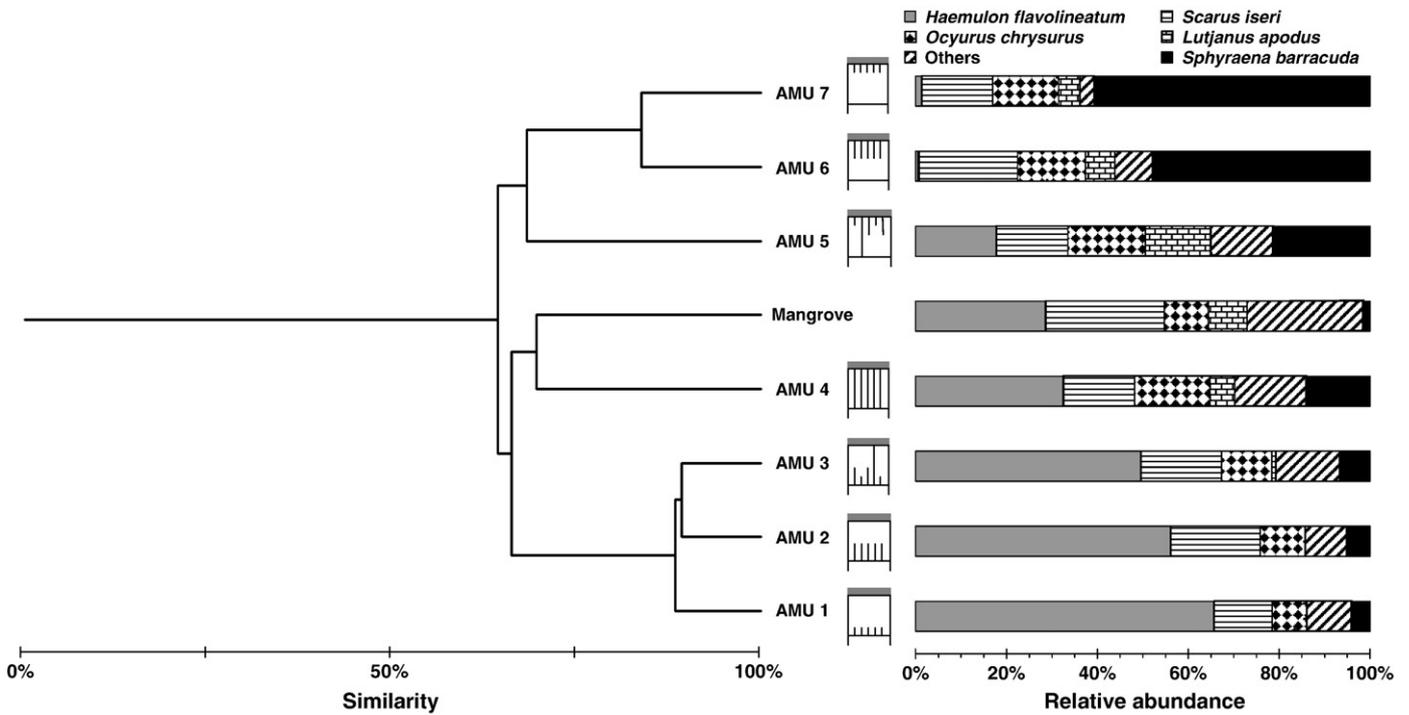


Fig. 3. Bray-Curtis cluster analysis of fish abundances in different artificial mangrove units (AMU) and adjacent mangroves. For each AMU as well as for the mangroves, relative abundances of the five most common and of other fish species are shown.

below). Likewise, a lack in response was observed for demersal fish (in terms of density) to small changes in height of structure in studies using experimental blocks, sponges, or seagrass as structure, as long as density of structure remained unchanged (e.g., Lindholm et al., 1999; Gratwicke and Speight, 2005; Horinouchi, 2007).

Three-dimensional pipe complexity did not explain the observed differences among AMUs for any of the three fish community variables either. The results indicate that the most heterogeneous

AMUs (measured as three-dimensional complexity) were not the most attractive to fishes. In contrast, MacDonald et al. (2008) found highest fish densities and number of species on mimics of mangrove root epibionts with highest three-dimensional structure. This contrast is not surprising, however, as in their study total surface area of structure strongly increased with increasing three-dimensional structure, whereas in our study it did not because a high three-dimensional structure was created by combining very short and long

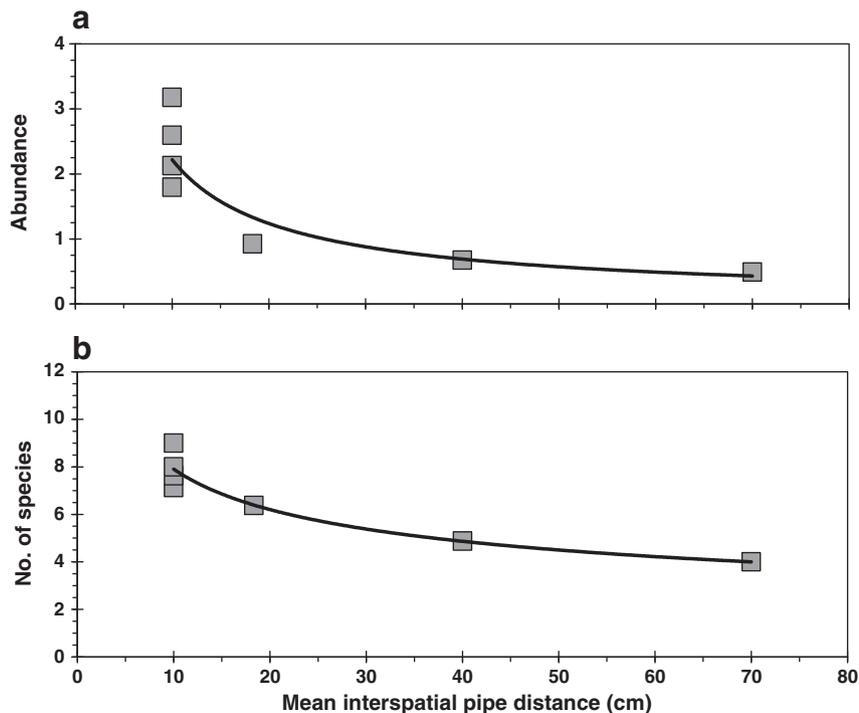


Fig. 4. Mean total fish abundance (a) and total number of species (b) as a function of interspatial pipe distance across all AMUs. Best-fitting regression lines are drawn through the data points; R²- and p-values are reported in Table 1.

pipes, which on average, had the same mean length (and thus surface area) as AMUs with lower three-dimensional structure. Likewise, Rönnbäck et al. (1999) found no relationship between fish abundance and root complexity (measured as total root surface area).

Vertical pipe orientation (i.e., hanging vs. standing) was a strong explanatory factor for observed differences in fish community variables among AMUs. Abundances and number of species of demersal fish always showed significantly higher values for AMUs with standing as opposed to hanging pipes, which compares well with the results of a descriptive study that found higher total fish densities in standing *Avicennia* than in hanging *Rhizophora* live roots (Rönnbäck et al., 1999). Two species showed a deviating pattern according to their life style: the semi-pelagic swimmer *O. chrysurus* conformed to the patterns of demersal species, whereas the demersal *Lutjanus apodus* conformed to the pattern of the semi-pelagic *S. barracuda*. This is not an artifact of the experiment, but related to their ecology. Large-sized *O. chrysurus* are pelagic feeders, but semi-pelagic swimming juveniles as observed here (see sizes in Table 1) are predominantly benthic feeders (Cocheret de la Morinière et al., 2003) and utilize benthic refuge when threatened (pers. observ.). Conversely, the demersal *L. apodus* is typically known to seek shelter in-between hanging prop-roots higher up in the water column at the size observed in the present study (MacDonald et al., 2009).

Interspatial distance between pipes, which translates to distance to refuge from an ecological perspective, was a strong predictor for abundance of demersal as well as semi-pelagic species. The fact that demersal fish species did not respond significantly to changes in mean pipe length or three-dimensional complexity as long as total density of benthic structure remained unchanged is probably because average distance to refuge remained the same in these treatments. The same was true for the semi-pelagic *S. barracuda* in relation to hanging pipes, indicating the importance of life style. It is important to note that even though shelter usage by fish is often species-specific (e.g., Orth et al., 1984; Laegdsgaard and Johnson, 2001; Cocheret de la Morinière et al., 2004), interspatial distance of refuge structures could explain all major differences in abundances of the various species when data were analyzed across all AMUs. This may also explain why in another experiment (Verweij et al., 2006a) demersal fish species that were sheltering and not feeding showed a similar attraction to AMUs with only artificial seagrass compared to AMUs with artificial seagrass and hanging pipes, and why attraction to these two AMUs was mostly higher than to AMUs with hanging pipes alone, especially in absence of shade. Indeed, field observations show that schools of demersal grunts typically seek shelter deeper within *Rhizophora* mangrove stands where roots grow all the way to the bottom as opposed to the mangrove fringe where the roots often hang partially downwards (pers. observ.). This finding suggests that distance to nearest structure may be the underlying mechanism explaining the distribution of benthic and of semi-pelagic fishes across the different AMUs. This does not mean that the large number of studies that found strong correlations between structural complexity and fish abundance is invalid, but simply that they studied attributes of structure that operate at a different hierarchical level.

Distance to refuge has been shown to be important on, for example, reefs and seagrass beds where fish forage or dwell in open spaces close to structured habitat to which they can flee in case of increasing risk of predation (e.g., Holt et al., 1983; Eklov and Diehl, 1994; Ross et al., 2007; Horinouchi et al., 2009). A new finding in this study is firstly that refuge distance also seems to operate within mangrove-root systems; it was expected that due to the overall high structural complexity and darkness of this habitat such a mechanism would not provide a lower anti-predation risk. Secondly, this mechanism of staying close to shelter operates in two dimensions, i.e. distance to horizontal structures and distance to vertical structures. This is supported by the fact that some species showed a

partial shift in space utilization towards the centre of the AMU when structure was provided there by usage of longer pipes (i.e., *O. chrysurus* and *S. iseri*; data not shown but also the case for: *Chaetodon capistratus*, *Haemulon sciurus*, and *Mulloidichthys martini-cus*), and that some species with a benthic feeding mode utilized hanging structure with absence of bottom structure (*O. chrysurus* and *S. iseri*), and vice versa for fishes with a semi-pelagic life style (*S. barracuda*). It is evident that fish favor positions at short distances to mangrove roots as such structure restricts pursuit by swimming predators and interrupts predator visual fields (Savino and Stein, 1989; Christensen and Persson, 1993).

The purpose of the present study was to provide an understanding of the importance of various attributes of mangrove root architecture on fish community variables. To avoid interactive effects with a variety of environmental and biotic factors, such as typical for natural mangroves, artificial roots were used. Food can be an important factor attracting fish to mangroves (Laegdsgaard and Johnson, 2001; Verweij et al., 2006a,b), but because the AMUs were cleaned off food and the bottom was covered this factor did not play a role in explaining the differential attraction to the AMUs. AMUs were placed next to one another and their configuration changed frequently so that they were exposed to the same local environmental and biotic variables. The above arguments support the fact that the conclusions of the present study are likely not affected by other interacting factors. Artificial units have been used extensively in the past to successfully mimic microhabitats and study various attributes of structure in relation to fish preferences (e.g., mangroves: MacDonald et al., 2008; seagrass: Horinouchi, 2007; reefs: Gratwicke and Speight, 2005).

The fish community of the adjacent mangrove was highly similar to that of AMU 4 with pipes running from top to bottom. Nagelkerken and Faunce (2007) also found a high and significant correlation between fish density in AMUs and the adjacent habitat, suggesting that the AMUs attracted fishes from the surrounding environment. If indeed the results from the AMUs can be extrapolated to mangrove roots, the present study suggests that architecture of mangrove roots, specifically their vertical orientation and interspatial distance, can regulate number of fishes and species within mangrove habitats. With ongoing anthropogenic effects on mangrove forests (Duke et al., 2007), such as (selective) cutting, the mangrove root habitat is often altered which may lead to negative effects on the associated fish community. Moreover, Nagelkerken and Faunce (2008) showed that for mangrove-associated fish species, the presence of root structure is more important in attracting fish than the occurrence of mangroves in shallow water or in wave-sheltered areas, underscoring the importance of root structure. Similarly, the ongoing loss of benthic cover on coral reefs has been held responsible for recent significant declines of Caribbean fish populations (Paddack et al., 2009). Maintaining a diverse suite of mangrove tree species with different root properties may thus be critical for a diverse and abundant mangrove fish community. This becomes even more important when considering that many mangroves function as temporary nursery habitats that subsidize coral reef populations of various ecologically and economically important fish species (see reviews by Nagelkerken, 2007, 2009).

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