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Distribution of fish, crustacea and zooplankton at different distances from mangrove prop roots within a semi-isolated lagoon

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Although semi-isolated mangrove lagoons are common in the Caribbean, few studies have surveyed organisms of multiple trophic levels and taxa in these lagoons, which are characterized by a lack of adjacent seagrass and coral-reef habitats. In this study, visual surveys, minnow traps and plankton tows, which were deployed at abutting mangrove prop roots and on macro-algal beds 5 and 15 m away from the prop roots, were used to study assemblages of fish and their potential prey in a semi-isolated lagoon located on Utila, Honduras during the dry season. Assemblages of fish and macro-crustacea differed between the three distances from prop roots, while zooplankton abundances were highly variable and did not follow any distinct distribution patterns. Daytime visual surveys found that large lutjanid (snapper) juveniles, tetraodontid (pufferfish), and some species of brachyurans were more abundant near prop roots. Small lutjanid juveniles were also significantly more numerous near prop roots, but their potential prey, copepods, showed no such difference in abundance. However, 24-hour minnow trap catches found that mean fish abundance (although low) did not differ between near-mangrove transects and transects located in algal beds away from prop roots. Whereas it is well known that mangrove–seagrass habitats play a vital role for fish in open systems, low abundances of organisms in algal beds, particularly in the day time, in this study indicate that algal beds may not be as important to fish in a semi-isolated mangrove lagoon.

Keywords: mangroves, algal beds, semi-isolated lagoon, zooplankton, crustacea, fish, Caribbean

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INTRODUCTION

Mangrove forests not only provide valuable ecosystem services to humans by protecting coastlines from wave action and storms, sequestering carbon and nutrient runoff and preventing erosion, they also supply habitat for reptiles, terrestrial invertebrates and marine organisms (Scoffin, 1970; Granek & Ruttenberg, 2007; Nagelkerken *et al.*, 2008a; Miah *et al.*, 2011). Mangroves can be found fringing open coastlines, lining estuarine creeks and rivers and bordering semi-isolated (from the open ocean by barrier beaches) bays or lagoons (e.g. Nagelkerken *et al.*, 2000a; Layman & Silliman, 2002; Gratwicke *et al.*, 2006; Dorenbosch *et al.*, 2007). In each seascape, mangrove habitat may have varying degrees of connectivity to shallow habitats such as seagrass, sand, mud, coral reef patches and algal beds.

Semi-isolated mangroves are often overlooked in reef-associated literature. However, many regions in the Indo-Pacific and Caribbean house semi-isolated mangroves (e.g. Tongnunui *et al.*, 2002; Pittman, 2007). In isolated locations, high concentrations of suspended sediment can inhibit seagrass and coral establishment (Rogers, 1990; Hall *et al.*, 1999). In these cases, mud and macro-algae often dominate the bottom substrates of habitats adjacent to mangrove forests (Copeland, 1965; Shepherd *et al.*, 2009). Therefore, open mangrove fringing coastlines and semi-isolated mangroves may differ greatly with regards to type of adjacent habitat, which has been shown to affect abundances and species present in fish assemblages (Dorenbosch *et al.*, 2007; Pittman, 2007; Jaxion-Harm *et al.*, 2012).

While many species of macro-invertebrates and fish remain in mangroves throughout their lives (habitat specialists), others utilize multiple habitats during their lifespan (e.g. ontogenetic shifters) (as defined by Adams *et al.*, 2006; Jaxion-Harm *et al.*, 2012). Different habitats may offer organisms different levels of refugia and food (Dorenbosch *et al.*, 2009). Commercially important macro-crustacea, such as *Panulirus argus* (spiny lobster) in Belize, occupy mangroves as juveniles and coral reefs as adults (Acosta *et al.*, 1997). Likewise, many fish species use mangroves as a nursery ground (defined by Beck *et al.* (2001) as a habitat that contributes greater than average abundances to adult populations per unit area) before undergoing ontogenetic migration to coral reefs (Gratwicke *et al.*, 2006; Verweij *et al.*, 2007). Undoubtedly, there are many benefits to spending at least part of a lifecycle in mangroves, including abundance of food (Laegdsgaard & Johnson, 2001), retention of larvae (Paris & Cowen, 2004), and a combination of increased habitat complexity (Beukers & Jones, 1998), increased shade

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and turbidity (Helfman, 1981; Cocheret *et al.*, 2004) and reduced predation pressure (Laegdsgaard & Johnson, 2001).

Most studies deeming mangroves as important for both nursery and habitat specialist species have performed their research in mangroves in riverine systems or connected to seagrass and/or coral reefs (e.g. Nagelkeren *et al.*, 2000a; Mumby *et al.*, 2004; Jones *et al.*, 2010). Furthermore, very few studies survey both fish and invertebrates (macro and micro, e.g. Robertson & Blaber, 1992; Dorenbosch *et al.*, 2007) in mangrove habitat, despite the latter playing an important dietary role for fish (Layman & Silliman, 2002; Cocheret *et al.*, 2003). Little is known about how associations and connectivity of habitats commonly found in semi-isolated lagoons affect the faunal communities within. Assessing habitat and resource requirements is the first step in protecting species such as commercially important fish and crustaceans. Therefore, the aim of the current study is to survey fish, crustacean, and zooplankton distribution in mangroves and adjacent habitats within a semi-isolated lagoon to determine how abundant they are throughout the lagoon, and how important specific habitats are to the multiple trophic levels.

MATERIALS AND METHODS

Site description

The current study was conducted in Oyster Bed Lagoon, Utila, which is one of the Bay Islands located 29 km off the coast of Honduras (Figure 1). Utila has very little tidal exchange (approximately ±20 cm) and no freshwater influence during the dry season (end of March to mid-August) (Gutshe *et al.*, 2005). Utila's hydrological and environmental factors make the island representative of most Caribbean islands (e.g. Nagelkerken *et al.*, 2000a; Aguilar-Perera & Appeldoorn, 2008). Oyster Bed Lagoon houses mangrove forests comprised solely of the red mangrove *Rhizophora mangle,* surrounding shallow bodies of water (with high suspended sediment levels, 4.3 mg/l in the dry season) that are semi-separated from the open sea. Oyster Bed Lagoon consists of two large bodies of water separated by a small (110 m long) canal (Figure 1). For the purpose of the study, the bodies of the water were named as Lower and Upper lagoon. The opening of the lagoon measures 75 m across and allows for exchange of water with the sea. The lagoon is shallow, with an average depth of 1.5 m and maximum depth of 3 m. The bottom of the lagoon is predominately mud or foliose macroalgae covered mud. The nearest seagrass and coral reef habitats are located on the sea-ward side of the lagoon's mouth, nearly 1 km away from surveyed sites. Small portions of the lower and upper lagoons have undergone mangrove loss from land reclamation (see Figure 1, personal observation). Two man-made canals have been cut and dredged to a water depth of 2–3 m on the west and north-west side of the lower lagoon.

A criterion for selection of sampling sites in Oyster Bed Lagoon was depth; 0.5 m was the minimum depth necessary to perform snorkel underwater visual censuses (UVC) and to deploy minnow traps. Depth measurements were taken every 5 m along the shoreline of the lagoon. Roughly 30% of the lagoon that met this requirement was divided into four sites separated by at least 150 m. Between 21 June and 11 August

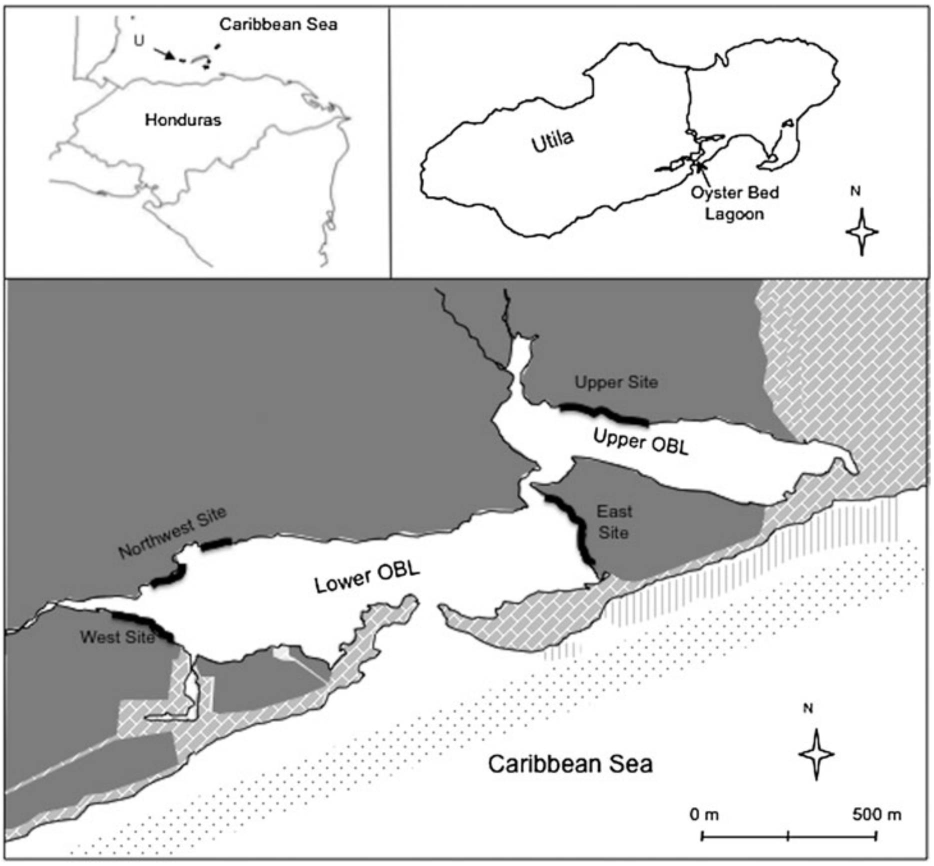

Fig. 1. Map of Oyster Bed Lagoon (OBL) (N16°06′25′W86°54′75′), Utila, Honduras, Central America. Sites are depicted with black shading. ▬ mangroves, ▨ cleared mangroves, ▥ seagrass, ⬚ coral.

(within the dry season), 2008, UVC fish surveys were conducted at each of the four sites (West, North-west, Upper, and East) within six marked 2 × 30 m transects located at 0 and 5 m from prop roots. Between 3 July and 30 July of 2009 UVC surveys, fish/macro-invertebrate traps and plankton tows were deployed at three sites (West, North-west, and Upper; Figure 1) within four marked 2 × 20 m belt transects at 0, 5 and 15 m away from the prop roots. These transects differed in depth (the bottom gently sloped down from 50 cm adjacent to mangroves to a depth of 80 cm at 5 m and 100 cm at 15 m), but varied little in salinity (~37.5 ppm) or temperature (~32°C). Habitat characteristics in mangroves such as prop root density and percentage algal cover can be found in Jaxion-Harm *et al.* (2012) and Jaxion-Harm & Speight (2012).

Zooplankton survey

A plankton tow net, length 1.21 m × 0.54 m diameter, was constructed with 150 μm mesh size. Within each transect (three per 0, 5 15 m), the net was towed between 10:00 and 11:00 for 10 m at a depth of approximately 3 cm from the side of a two-person kayak, resulting in 2.289 m^3 of water sampled. Each sample was preserved with 70% alcohol for subsequent taxonomic identification and abundance measurements.

Macro-crustacea survey

Based on pilot studies, minnow traps (Cabellas's collapsible minnow traps; dimensions (H) 30 cm × (W) 30 cm × (L) 60 m with 6.5 cm openings on both ends) were an effective method for catching small crustaceans. Macro-crustacea are usually defined as 'able to be seen by the naked eye', and are often collected with mesh sizes of 0.5 or 1 mm (Vitaliano *et al.*, 2006); however, the mesh size of the minnow traps was 1.6 mm, therefore macro-crustacea in this study are defined as larger than 1.6 mm. Five minnow traps were placed in each transect at each distance (0, 5 and 15 m from prop roots) for a total of 20 traps per distance and 60 per site. Each minnow trap was baited with five pieces (approximately 2–3 g) of tuna-flavoured cat food before being deployed along the transect. Traps were checked every 24 hours between 14:00 and 16:00 for five days. All animals caught were identified, sized (prawn = tip of rostrum to tip of uropod; crabs = width of carapace) and released, before replenishing bait and redeploying.

Fish underwater visual census

Underwater visual census snorkel surveys were performed in each transect between 9:00 and 11:00 (see method details in Jaxion-Harm & Speight, 2012). All fish within primary prop roots and under overhanging roots were identified to the species level, and fork lengths were visually estimated to the nearest 5 cm. The snorkeller repeated the belt transect surveys at appropriate distances (5 or 15 m) from the prop roots. Fish were categorized into life stages according to Jaxion-Harm *et al.* (2012).

Statistical analyses

Abundances of macro-crustacea (and fish) per transect were calculated by aggregating individuals from the five traps in each transect (per distance, $N = 4$) and summing catches from the five days. Due to low abundances of small prawn/shrimp genera, all species outside of the larger-sized *Penaeus* genus were classified as 'other shrimp'.

Generalized linear models (R statistical software version 2.10.1) were used to compare pooled macro-crustacea catches (individual genera), abundances of individual dominant zooplankton taxa, densities of individual dominant fish species, mean fish density (all species totalled per 100 m^2), and fish species richness (number of species in a given area) amongst transects located 0, 5 and 15 m from mangroves. In all models, transects at the distances from prop roots (2008: $N = 6$ for fish surveys; 2009: $N = 4$ for macro-invertebrate and fish surveys and $N = 3$ for zooplankton surveys) were nested within the three categorical, random (not fixed) sites (m) (fish surveys 2008: $m = 4$; all surveys 2009: $m = 3$). Poisson error structures were used for count data, and fit of model was tested based on Akaike's information criterion (AIC) (Crawley, 2007). The most complex model with interactions between site and distance was tested, then simplified with deletions and amalgamating explanatory variables with similar parameter values, resulting in the minimum adequate model.

To determine if community structure differed amongst distance from prop roots, square-root transformed fish assemblage data were used with Bray–Curtis dissimilarities (sum of absolute differences divided by the total abundance) in an Analysis of similarity test (ANOSIM; Community Analysis Package (CAP), copyright PISCES 2008). An assemblage is defined as a 'phylogenetically related group within a community (collection of species in same place at the same time)' (Fauth *et al.*, 1996). Assemblage structure comparisons were displayed in a multidimensional scaling (MDS) plot with transects bearing similar communities clustering together. Goodness of fit in two dimensions was measured by stress tests (zero represents a perfect fit); acceptable levels are less than 0.2 (Clarke, 1993).

RESULTS

Zooplankton surveys

The plankton tow net caught a total of 18,257 organisms from 27 tows. Out of 14 main taxa (Table 1), four taxa accounted for approximately 99% of the mean zooplankton abundance: copepoda (98%), ostracoda (0.6%), amphipoda (0.2%) and gastropoda (0.2%). Copepods numerically dominated the catch; however, they displayed extremely high variation within site and distance, ranging from 134 to 2597 individuals per tow. There were no significant differences in total crustaceans or copepods (or any of the other taxa caught) amongst samples collected at the varying distances from prop roots. However, abundances of total crustaceans and copepods were significantly greater at the west site than at the north-west site ($N = 3$, $P < 0.01$).

Macro-invertebrate survey

Minnow traps were nine times more effective at catching macro-crustacea than at catching fish, with a mean catch rate of 1.77 ± 0.25 crustacea/trap. Traps caught six genera

Table 1. Taxa caught in plankton net towed at three distances (0, 5, 15 m) from mangrove prop roots in three sites. Values presented as mean abundance ± standard error.

Taxa	West			North-west			Upper		
	0 m	5 m	15 m	0 m	5 m	15 m	0 m	5 m	15 m
Copepoda	697.0 ± 307.1	889.3 ± 116.9	1322.3 ± 643.7	464.0 ± 195.6	421.7 ± 241.8	233.0 ± 48.8	702.3 ± 313.8	711.7 ± 212.4	533.3 ± 196.7
Amphipoda	2.0 ± 1.5	2.0 ± 1.2	0.7 ± 0.7	0.0	2.7 ± 2.7	0.3 ± 0.3	4.0 ± 3.1	1.0 ± 0.6	0.0
Hydrozoa	0.3 ± 0.3	0.7 ± 0.7	0.0	0.0	0.3 ± 0.3	0.0	1.0 ± 0.6	1.0 ± 1.0	0.0
Ostracoda	2.7 ± 2.7	2.7 ± 1.8	1.3 ± 0.9	5.3 ± 1.3	3.7 ± 3.2	1.7 ± 1.2	1.7 ± 1.2	8.0 ± 5.1	7.0 ± 3.8
Balanidae (L)	4.3 ± 3.4	0.0	1.3 ± 1.3	0.3 ± 0.3	2.0 ± 2.0	0.0	0.0	0.0	0.0
Brachyuran zoe (L)	0.0	2.3 ± 0.9	1.3 ± 0.3	0.0	0.7 ± 0.3	0.0	0.0	2.3 ± 1.9	3.3 ± 2.8
Polychaeta	0.3 ± 0.3	0.7 ± 0.3	1.0 ± 1.0	0.7 ± 0.3	0.0	0.3 ± 0.3	0.7 ± 0.7	2.7 ± 1.5	1.0 ± 0.6
Teleostomi (L)	1.7 ± 0.9	1.0 ± 0	0.7 ± 0.3	0.3 ± 0.3	2.0 ± 1.0	1.0 ± 0.6	0.0	2.3 ± 1.2	1.7 ± 0.3
Nematoda	1.3 ± 1.3	2.3 ± 0.9	0.3 ± 0.3	0.0	1.7 ± 1.7	0.0	0.3 ± 0.3	0.3 ± 0.3	0.7 ± 0.7
Gastropoda	2.3 ± 2.3	0.3 ± 0.3	0.0	0.0	2.0 ± 1.5	0.0	0.0	4.3 ± 2.2	3.7 ± 2.0
Appendicularia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7 ± 0.7	0.0
Isopoda	0.0	0.0	0.0	0.0	0.3 ± 0.3	0.0	1.0 ± 1.0	0.3 ± 0.3	0.0
Pantopoda	0.7 ± 0.7	0.3 ± 0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oligochaeta	0.7 ± 0.7	0.7 ± 0.3	0.3 ± 0.3	0.0	0.0	0.0	0.0	0.0	0.0

L, larval life stage.

of crabs and six genera of prawns/shrimps (Table 2). The majority of the crabs were *Callinectes* spp. (blue crabs, 19%) and *Panopeus* spp. (mud crabs, 74%), while *Penaeus* spp. (pink prawns, 45%) and *Palaemon northropi* (grass prawns, 42%; Rankin, 1898) were the most abundantly caught prawns/shrimp.

Assemblages of macro-crustacea caught in minnow traps at 0 m were grouped together in the multivariate plot, and determined to be significantly different from those at 5 m and 15 m (ANOSIM, both $P < 0.001$, $R = 0.78$, Figure 2A). Conversely, macro-invertebrate assemblages 5 m away from mangroves appear to overlap with assemblages in transects 15 m away. ANOSIM tests reveal that these macro-invertebrate assemblages are not significantly different from each other ($P = 0.707$).

Comparisons amongst macro-invertebrate catch abundances show significantly more *Panopeus* spp. and small prawns/shrimp (<2 cm) at 0 m ($N = 4$, $P < 0.001$), and no difference in abundances between traps 5 m and 15 m away from mangroves. *Penaeus* prawn and *Callinectes* crab spp. abundances were not significantly different amongst 0, 5 and 15 m.

Fish surveys

In 2008, visual surveys showed that the density of fish located in 0 m transects was more than three times the total density of fish located in transects 5 m away from the prop roots ($N = 6$, $P = 0.04$, Figure 3A). In 2009, surveys of additional transects at 15 m revealed there was no linear decrease in fish densities with distance from prop roots, and fish densities in 5 m and 15 m were not significantly different. In addition, species richness in 0 m transects was significantly higher than in 5 m and 15 m transects (2008: $N = 6$, $P < 0.001$ and 2009: $N = 4$, $P < 0.001$, Figure 3B). When multiple species in the community are grouped together, fish assemblages were significantly different between assemblages at 0, 5 and 15 m (all $P < 0.001$, $R = 0.376$). However, on a multivariate scale plot, fish assemblages in 5 m plots do not appear to cluster separately from assemblages in 15 m plots (Figure 2B).

Nineteen species of fish were found in the 36 transects visually surveyed in 2009 (Table 3). Juvenile ontogenetic shifters constituted 77% of fish surveyed, while mangrove habitat specialists comprised the remaining percentage. Juvenile snappers, primarily *Lutjanus apodus* (13%, schoolmaster snapper; Walbaum, 1792) and *L. griseus* (11%, grey snapper; Linnaeus, 1758) dominated UVC surveys (Table 3). Results from the UVC reveal that there were significantly more small (<10 cm) and large (>10 cm) juvenile *L. apodus* at 0 m ($N = 4$, $P = 0.01$, $P < 0.001$, respectively) than in transects 5 m and 15 m away, but no difference in densities between 5 m and 15 m (Figure 4). All fish species, with the exception of lutjanids, gerreids and *Sphoeroides testudineus* in the surveys were less than 10 cm (total length). Lengths of *Sphoeroides testudineus* were not measured, as all fish were of similar length (estimated 8–12 cm). Results from UVC surveys revealed *Sphoeroides testudineus* (checkered pufferfish; Linnaeus, 1758) densities exhibit the same pattern in the Upper and North-west sites, with more fish located in 0 m transects compared to 5 m and 15 m transects ($N = 4$, $P = 0.01$; Table 3). In addition, both gobies and grunts were only found in 0 m transects at all sites (Table 3). In contrast, there was no

Table 2. List of the macro-crustacea caught in minnow traps deployed at three distances (0, 5, 15 m) from mangrove prop roots with corresponding densities (± standard error) per 100 m^2.

Family	Genus/species	West			North-west			Upper		
		0 m	5 m	15 m	0 m	5 m	15 m	0 m	5 m	15 m
Brachyura	*Callinectes* sp.	0.5 ± 0.5	0.75 ± 0.48	2.25 ± 048	0.25 ± 0.25	1.5 ± 0.5	2 ± 0.41	0.75 ± 0.25	2.75 ± 0.85	0.0
	Panopeus sp.	15.75 ± 1.18	1 ± 0.71	0.75 ± 0.25	9.75 ± 1.44	3 ± 0.41	2.5 ± 0.65	6 ± 0.82	3.25 ± 0.85	1 ± 0.71
	Stenorhynchus seticornis	0.0	0.0	0.0	0.75 ± 0.75	0.0	0.0	0.0	0.0	0.0
	Portunus ordwayi	0.0	0.0	0.0	0.0	0.75 ± 0.48	0.25 ± 0.25	0.0	0.0	0.0
	Portunus sebae	0.0	0.0	0.0	0.0	0.25 ± 0.25	0.25 ± 0.25	0.0	0.0	0.0
	Microphyrs bicornutus	0.25 ± 0.25	0.0	0.25 ± 0.25	0.75 ± 0.48	0.0	0.0	0.0	0.0	0.0
	Unknown decorator crab A	0.0	0.0	0.00.0	0.0	0.0	0.25 ± 0.25	0.0	0.0	0.0
Stomatopoda	*Gonodactylus* sp.	0.0	0.0	0.0	0.0	0.0	0.25 ± 0.25	0.0	0.0	0.0
Caridea	*Alpheus* spp.	0.75 ± 0.75	0.0	0.0	0.25 ± 0.25	0.0	0.5 ± 0.29	0.0	0.0	0.0
	Penaeus sp.	3.75 ± 1.93	3.5 ± 1.19	4.5 ± 1.85	7.5 ± 1.44	4 ± 2.35	3.25 ± 0.63	3 ± 1.08	3.25 ± 1.31	2.5 ± 1.55
	Palaemon northropi	23.25 ± 2.29	0.0	0.0	4 ± 0.71	0.0	0.25 ± 0.25	1.25 ± 0.75	0.25 ± 0.25	0.0
	Leander tenuicornis	0.25 ± 0.25	0.0	0.0	1.5 ± 0.87	2 ± 0.71	1 ± 0.41	0.0	0.0	0.0
	Cuapetes americanus	0.0	0.0	1.5 ± 0.65	0.5 ± 0.29	2.25 ± 2.25	0.25 ± 0.25	0.0	0.0	0.0
	Unknown shrimp A	3.75 ± 1.61	0.5 ± 0.5	0.25 ± 0.25	0.25 ± 0.25	0.25 ± 0.25	0.25 ± 0.25	0.75 ± 0.75	0.0	0.0

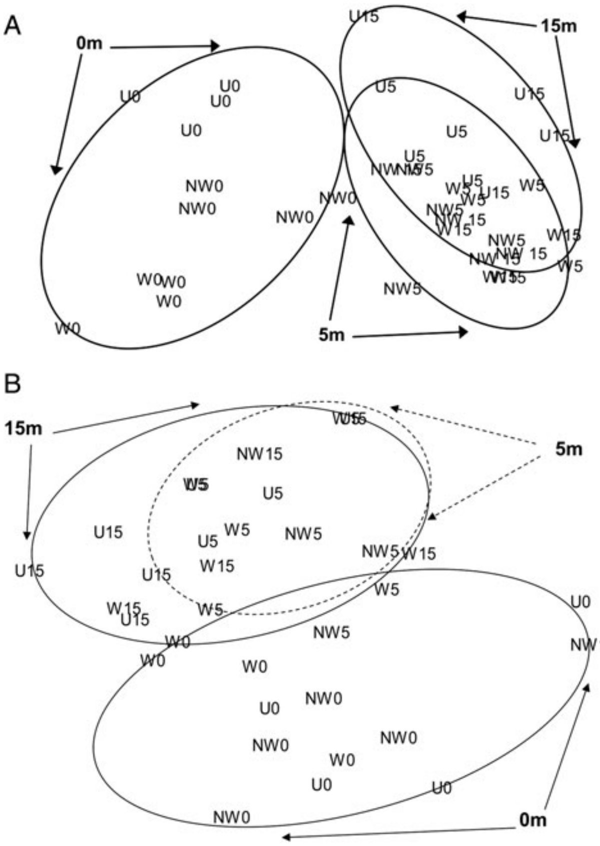

Fig. 2. Difference in (A) macro-crustacea and (B) fish assemblages located at 0 m, 5 m and 15 m from seaward edge of mangrove forests in Oyster Bed Lagoon, Utila. Assemblages are expressed in a multidimensional scaling ordination plot (Bray–Curtis dissimilarity coefficient) and each point represents the assemblage in one transect. Data point labels: U: Upper site; W: West site; NW: North-west site; 0: zero metres; 5: five metres; 15: fifteen metres from prop roots. Stress = 0.14.

difference in gerreid abundance (<10 cm and >10 cm) between 0, 5 and 15 m.

Minnow traps (24 hour catches) caught a total of 235 fish consisting of nine species. Pooled catches revealed no significant differences in total fish catch amongst distances (mean fish catch per five traps over five days = 6.45 ± 3.06).

DISCUSSION

Zooplankton distribution

The present study was the first to measure zooplankton abundance in Honduran mangroves. As found by the current study, copepods in Caribbean sites such as those in mangroves in Puerto Rico (Rios-Jara *et al.*, 1998) and a coral reef lagoon in Mexico (Álvarez-Cadena *et al.*, 2009) constituted over 90% of total zooplankton catches and displayed high degrees of density variation. Along with copepods, balanids and brachyurans were also abundant in these Caribbean studies (including the current study), while organisms from other groups were scarce. Zooplankton provide the trophic link between primary productivity and higher trophic guilds, and most carnivorous fish consume zooplankton during at least one stage (usually early juvenile) of their life history (Alheit

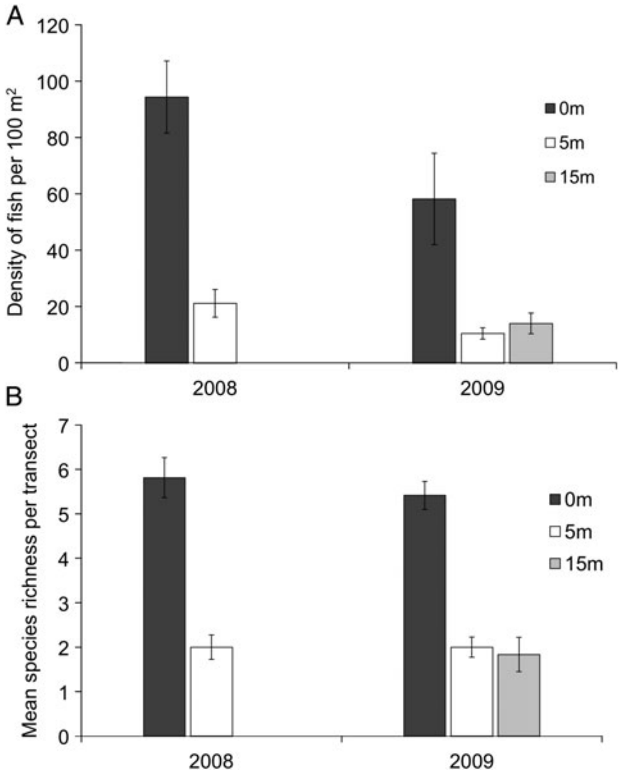

Fig. 3. Variation in numbers and diversity of fish with distances from the seaward edge of mangrove forests in Oyster Bay Lagoon: (A) density of fish per 100 m^2; (B) number of species per transect (2008: 60 m^2; 2009: 40 m^2). Values presented as mean ± standard error, $N = 4$ in 2008 and 3 in 2009.

& Scheibel, 1982; Cocheret *et al.*, 2003). In this study, copepod distribution was not linked to distance to mangrove forests. Distribution of zooplankton is often linked to hydrology, chlorophyll-*a*, salinity and sediment load (Jouffre *et al.*, 1991; Robertson & Blaber, 1992; Krumme & Liang, 2004; Costa *et al.*, 2009). In Oyster Bed Lagoon, current speed and direction is highly variable, which may explain the absence of a pattern in zooplankton assemblages at a distance to mangrove level (Cowie, unpublished data). In addition, the current study did not find a significant difference in salinity amongst site locations. It is suggested that future studies measure chlorophyll concentrations and sediment load at both the site and distance to mangrove level, as this may explain the significant difference in copepod abundances between the North-west and West sites.

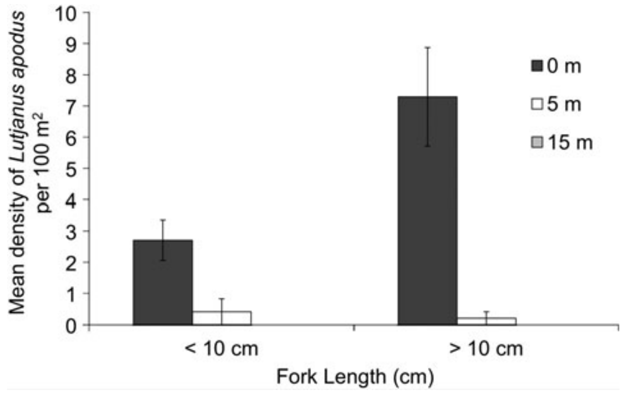

Fig. 4. Variation in numbers of small (<10 cm) and large (<10 cm) lutjanids with distances from the seaward edge of mangrove forests in Oyster Bay Lagoon. Densities per 100 m^2 presented as mean ± standard error.

Macro-invertebrate distribution

Knowledge of macro-invertebrate distribution from Caribbean mangroves is limited (e.g. Browder *et al.*, 1986; Sheridan, 1992). Numerically dominant decapods in this study, *Panopeus* and *Callinectes* crabs and *Penaeus* and *Paelomon* prawns corresponded with results from two other mangrove studies previously performed in Florida (Browder *et al.*, 1986; Sheridan, 1992). *Callinectes* crabs were found in both Floridian studies, but *Panopeus* crabs were only found in Browder's study. The second most abundant prawn species in the current study was *Paelomon northropi*, belonging to the family Paelomonidae, which was the most abundant decapod family in both Floridian studies.

In the present study, macro-invertebrate distribution indicates that different genera vary in their use of mangrove prop roots versus adjacent algae beds. However, reasons behind varying distribution are unknown and require further investigation.

Fish distribution

In the current study, daytime UVC surveys showed fish species richness and densities were greater in Oyster Bed Lagoon's prop roots than in adjacent algal beds. In Spanish Water Bay, Curaçao, and Antilles, Nagelkerken *et al.* (2000a) found twice the number of species and two hundred times higher densities of fish in mangroves compared to algal beds.

During the day, fish may use mangroves for both food and refuge. In Curaçao, Dorenbosch *et al.* (2009) found that grunts (Haemulidae) tethered to mangrove prop roots away from coral reefs had significantly higher rates of survival. Furthermore, with higher abundances of potential macro-invertebrate prey located in prop roots, it is likely that fish in the current study did not have to sacrifice growth for protection during daytime hours. However, diet analysis is needed in future studies to verify that macro-invertebrates present are the same species consumed by fish. Unlike open mangrove systems with adjacent seagrass beds, daytime densities of fish were low in adjacent algal beds compared to densities of fish in seagrass found in previous studies (Dorenbosch *et al.*, 2007; Jaxion-Harm *et al.*, 2012). In Spanish Water Bay, Curaçao, which contains mangroves, seagrass and algae, fewer species of fish were found in algal beds (Nagelkerken *et al.*, 2000a). Fish, particularly small juveniles, may prefer seagrass due to an abundance of small refuge gaps between blades (Gratwicke *et al.*, 2005). Reduced numbers of fish in algal beds in the current study may be due to dense thickets providing few refuge gaps. Future studies are needed to test predation of juvenile fish in mangroves versus mud/algae.

Fish distributions based on minnow trap catches in Oyster Bed Lagoon, which were deployed for 24 hours (i.e. encompassing both day and night), differ from daytime UVC results. Abundances of fish caught in the minnow traps were not significantly different amongst the three distances from prop roots, suggesting fish may leave the mangroves at night. In previous studies, fish have been found to migrate from mangroves to connected seagrass beds at night

Table 3. List of the fish visually surveyed at three distances (0, 5, 15 m) from mangrove prop roots with corresponding densities (± standard error) per 100 m², life-stage, and residency in mangroves.

Family	**Species (group)**	**West**			**North-west**			**Upper**		
		0 m	**5 m**	**15 m**	**0 m**	**5 m**	**15 m**	**0 m**	**5 m**	**15 m**
Atherinidae (silversides)										
	Atherinidae school present	P	P	0	0	P	0	0	0	0
Chaetodonidae (butterflyfish)										
	Chaetodon capistratus (J)	0.00	0.00	0.00	2.50 ± 1.77	0.00	0.00	1.25 ± 0.72	0.00	0.00
Gerreidae (mojarras)										
	Eucinostomus spp. (J, A)	8.75 ± 4.84	7.50 ± 2.04	10.00 ± 5.30	0.00	2.50 ± 1.02	1.25 ± 1.25	3.75 ± 2.98	5.63 ± 1.20	14.38 ± 3.13
	Gerres cinereus (J)	1.88 ± 1.88	0.00	0.00	1.25 ± 0.72	0.63 ± 0.63	0.00	0.63 ± 0.63	0.63 ± 0.63	2.50 ± 2.50
Gobiidae (gobies)										
	Lophogobius cyprinoides (MHS)	0.63 ± 0.63	0.00	0.00	0.00	0.00	0.00	0.63 ± 0.63	0.00	0.00
Haemulidae (grunts)										
	Haemulon sciurus (J)	0.00	0.00	0.00	2.50 ± 1.77	0.00	0.00	0.00	0.00	0.00
	Haemulon flavolineatum (J)	0.00	0.00	0.00	1.88 ± 0.63	0.00	0.00	0.00	0.00	0.00
	Haemulon aurolineatum (J)	0.00	0.00	0.00	0.00	0.00	0.00	1.88 ± 0.88	0.00	0.00
	Haemulon parra (J)	0.00	0.00	0.00	0.00	0.00	0.00	0.63 ± 0.63	0.00	0.00
Lutjanidae (snappers)										
	Lutjanus apodus (J, A)	11.88 ± 2.13	0.00	0.00	5.63 ± 2.13	0.63 ± 0.63	0.00	12.50 ± 2.28	1.25 ± 1.25	0.00
	Lutjanus griseus (J, A)	3.75 ± 1.25	1.25 ± 1.25	1.88 ± 0.63	8.75 ± 2.39	1.25 ± 1.25	0.00	7.50 ± 1.02	0.00	1.88 ± 1.88
	Ocyurus chrysurus (J)	0.00	0.00	0.00	1.88 ± 0.63	0.00	0.00	0.00	0.00	0.00
	Lutjanus cyanopterus (J)	0.00	0.00	0.00	0.00	0.00	0.00	1.25 ± 1.25	0.00	0.00
Mullidae (goat fish)										
	Pseudupeneus maculatus (J)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.63 ± 0.63
Rivulidae (killifish)										
	Rivulus marmoratus (MHS)	0.00	0.00	0.00	0.00	0.00	0.00	15.63 ± 15.63	0.00	0.00
Scaridae (parrotfish)										
	Scarus iseri (J)	1.25 ± 0.72	0.00	0.00	0.00	1.88 ± 1.88	1.25 ± 1.25	3.13 ± 3.13	0.00	0.00
Sciaenidae (drums)										
	Drum (J) *Pogonias cr cromis*	0.00	0.00	0.00	0.00	0.00	0.00	37.50	0.00	0.00
Sphyraenidae (barracudas)										
	Sphyraena barracuda (J)	0.00	0.00	0.63 ± 0.63	0.63 ± 0.63	0.63 ± 0.63	0.00	0.00	0.00	0.00
Tetraodontidiae (pufferfish)										
	Sphoeroides testudineus (MHS)	3.75 ± 1.25	3.75 ± 1.61	2.50 ± 1.02	10.63 ± 1.57	3.75 ± 1.61	0.63 ± 0.63	20.63 ± 2.13	0.63 ± 0.63	1.88 ± 1.20

J, juvenile (ontogenetic shifters); A, adult (ontogenetic shifters); MHS, mangrove habitat specialist; *P*, present.

(Nagelkerken *et al.*, 2000b, 2008b; Luo *et al.*, 2009), and catches from our minnow traps suggest fish also migrate to neighbouring algal beds. At night, fish may use the protection of darkness to leave the protection of prop roots. Piscivores mostly use visual cues to find their prey; therefore, predation risk is likely to be lower during the night (McMahon & Holanov, 1995). Although the majority of macro-crustacea in the current study were found under the prop roots, potential fish prey (see Layman & Silliman, 2002), paeneid prawns and small *Callinectes* crabs, were plentiful in both prop roots and algal beds.

In conclusion, fish and macro-invertebrate assemblages were significantly different between prop roots and adjacent (both 5 m and 15 m away from prop roots) algal beds. However, zooplankton did not follow any distinct distribution patterns. Lutjanids dominated fish surveys, and *Panopeus* crabs dominated minnow trap catches. Many Caribbean studies have found positive correlations between mangroves and adult reef populations of fish species such as *Lutjanus apodus* (schoolmaster snapper), *Gerres cinereus* (Yellow fin mojarra; Walbaum 1792), and *Sphyraena barracuda* (great barracuda; Edwards, 1771) (Mumby *et al.*, 2004; Dorenbosch *et al.*, 2007; Harm *et al.*, 2008). Since these species depend on mangrove habitat during their juvenile life stage, and mangroves in this study are connected to adjacent mud and algae, it is important to study how these fish use this habitat continuum in order to provide necessary data for conservation management of semi-isolated mangrove lagoons. Observations from the current study imply that these fish use both mangrove prop roots and adjacent algal beds, but have a higher dependence on prop roots during daytime hours. However, future diet studies and nocturnal surveys are needed in order to make direct correlations between distribution of macro-invert prey and their predators—carnivorous fish.

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