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SHORT COMMUNICATION

MACROFAUNA ASSOCIATED WITH UNGROUNDED PROP ROOTS OF *RHIZOPHORA MANGLE* IN VERACRUZ AND QUINTANA ROO, MEXICO

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Introduction

The prop roots of the red mangrove (*Rhizophora mangle*) provide a solid substrate for diverse assemblages of marine organisms in areas typically characterized by soft bottoms (Bingham 1992, Farnsworth and Ellison 1996). Macrobenthic communities of mangroves have received little attention compared with other components of the ecosystem, largely due to sampling difficulties (Lee 2008). Mangrove root epifauna are likely used by predatory fish, especially juveniles. Thus, these organisms have the potential of being important links between mangroves and adjacent ecosystems. The fauna associated with red mangrove prop roots along Mexican Gulf of Mexico (GOM) and Caribbean shorelines has not been well described. The infauna of red mangrove associated sediments has been studied in GOM sites in the Río Carrizal Estuary, Tamaulipas, Mexico (Rabalais et al. 1989), Laguna de Términos, Veracruz, Mexico (Hernández-Alcántara and V. Solís-Weiss 1995) and Rookery Bay, Florida (Sheridan 1997). Red mangrove root epifauna in the GOM has been described only in Laguna de Tamiahua (Fajardo M. 1990). Although red mangrove root faunas have been described in some areas of the Caribbean, such as Puerto Rico (Mattox 1949, Kolehmainen and Wildner 1975) and Bahia de Buche, Venezuela (Sutherland 1980), in the northwestern Caribbean the mangrove root epifauna has only been described in Belize (Ellison and Farnsworth 1992, Farnsworth and Ellison 1996). The objective of this study was to describe macrofaunal community composition of ungrounded red mangrove prop roots in the southwestern GOM and the northwestern Caribbean, on the Yucatan Peninsula. The communities we describe are compared to others in Mexico, Central America and the wider Caribbean to address factors that may explain similarities and differences.

Study Area

Laguna La Mancha is located on the central GOM coast of Mexico about 51 km north of the city of Veracruz, in the state of Veracruz, Mexico (Figure 1). The lagoon is located behind a barrier peninsula with only one small outlet to the GOM that is closed during the dry season, October to May (Moreno-Casasola et al. in press). Freshwater enters the lagoon via the Río Caño Grande to the south and a small, ephemeral stream to the north; fresh groundwater is also a major water source for the lagoon. In Laguna La Mancha, salinity ranged from 18 ppt (Site 4) to 25 ppt (Site 3) during collections. Water depth ranges from 0.5 - 1.0 m (Contreras 1993).

The Caribbean study area was located within the Sian Ka'an Biosphere Reserve on the Yucatan Peninsula in the state of Quintana Roo, Mexico. Mangrove roots were collected from sites within a lagoon system behind a long (56 km) barrier peninsula (Figure 1). Laguna Campechén, Laguna Boca Paila, and Laguna San Miguel comprise the northern portion of the lagoon system. These lagoons are only connected to the more marine-influenced southern portion by a small mangrove channel and to the Caribbean through a single narrow opening (~100 m) at Boca Paila (Sanvicente-Añorve et al. 2002). The entire lagoon system is supplied with freshwater from subterranean sources and both Laguna Campechén and Laguna San Miguel are isolated from marine influence. Salinity in Laguna Boca Paila ranged from 19 ppt (Site 3) to 33 ppt (Site 5) during collections. Water depth within the lagoons is between 0.5 - 1.0 m except in channels near the inlet (Boca Paila) where tidal scouring has occurred (Tunnell et al. 1993). For the purposes of this paper, the northern portion of the lagoon system will be referred to collectively as Laguna Boca Paila.

Materials and Methods

Ungrounded prop roots of red mangroves were randomly collected from 5 sites in both Laguna La Mancha and Laguna Boca Paila that were selected because they varied in distance from the inlet. Collections were made at both sites during the transition from the wet to dry season: May 8-11, 1999 at Laguna Boca Paila and May 26, 1999 at Laguna La Mancha. Roots were collected from water depths < 1 m, ranging from 16-29 cm in Laguna La Mancha and 42-94 cm in Laguna Boca Paila. Roots were randomly selected by reaching into the root mass and grabbing a root. If it was ungrounded, it was collected. Working in one di-

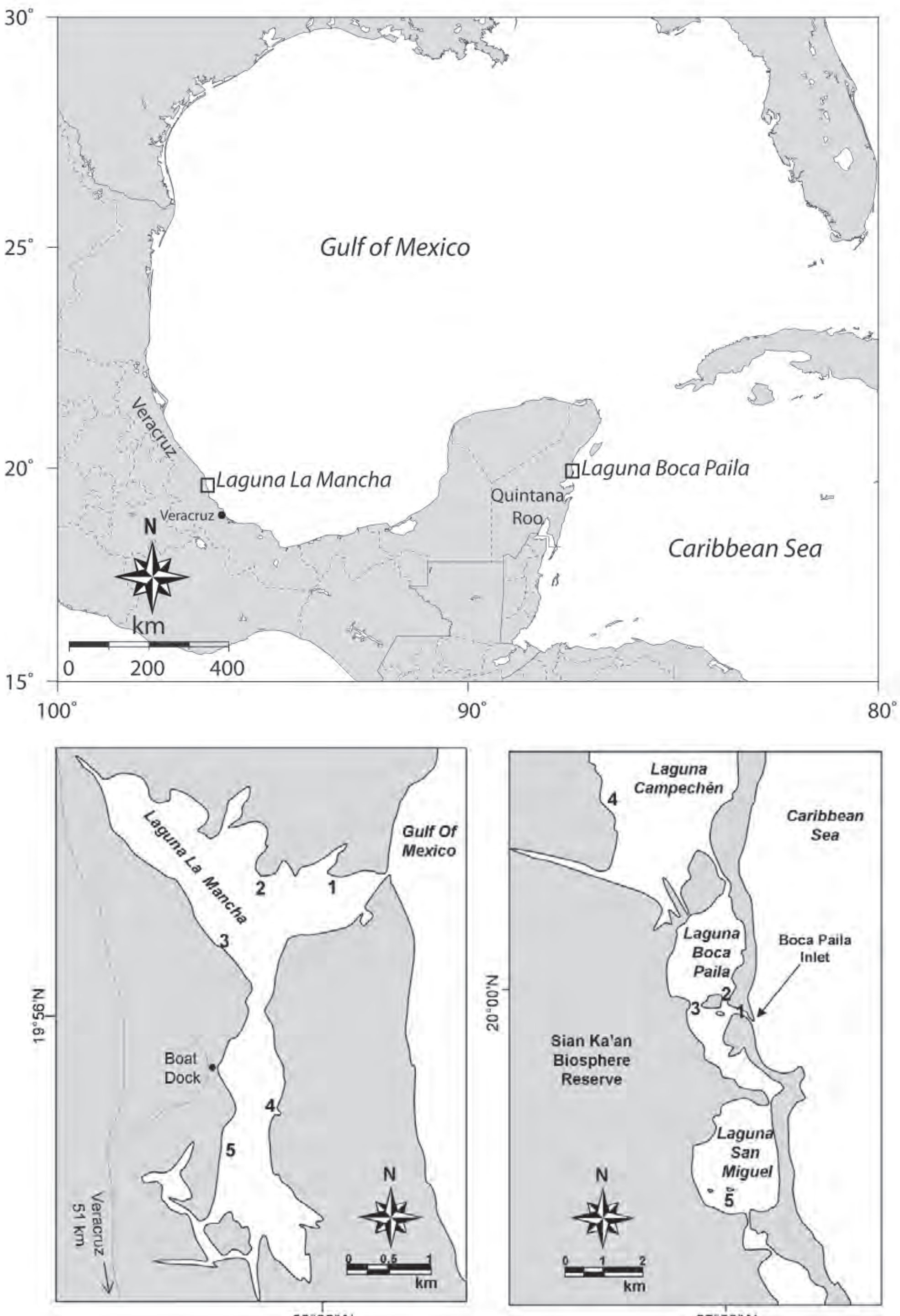

Figure 1. *Map showing the general locations of mangrove study areas within the Mexican Gulf of Mexico and Caribbean Sea. The approximate locations of sites where red mangrove roots were collected are shown within Laguna La Mancha, Veracruz (bottom left) and the northern lagoon system in the Sian Ka'an Biosphere Reserve, Quintana Roo (bottom right).*

rection along the edges of the mangroves at a site, 10 steps were taken, and another root was collected in the same way. This sequence was followed until 10 roots were collected at each site (50 roots total for each study area). Roots were collected by cutting with lopping shears just above the high tide line demarcated by the upper limit of dead barnacles. Before cutting the roots, a 0.5 mm mesh biobag was placed around the root to prevent fauna from escaping. All samples were fixed in 10% buffered formalin for 2 d then transferred to 45% isopropyl alcohol for storage until analysis.

In the laboratory, algae and fauna were removed from the roots, and fauna were separated from the algae. Both were stored in 45% isopropyl alcohol. Total algal biomass was determined for each root by drying algae at 100 °C in a preweighed pan for 72 h. Faunal organisms from each root were identified to the lowest practical taxon and counted. A lack of regional taxonomic sources meant that some polychaetes could only be identified to family, and some amphipod and polychaete genera could not be identified to species; these were designated as "A", "B", etc., when it was clear that there was more than one unidentifiable, but different species in the same genus. Other taxa, such as insects, were identified only to order, except for the dipteran family Dolichopodidae. In other cases, specimens were very small, appeared to be juveniles, or were missing parts preventing their identification to lower than family or genus. In most cases, taxa that were not identified to species represented relatively rare organisms that were present on only one or a few roots. Published references used to identify organisms included: polychaetes – Uebelacker and Johnson (1984); crabs – Felder (1973), Williams (1984), Chaney (1999); amphipods – Bousfield (1973), Barnard and Karaman (1991); isopods – Kensley and Schotte (1989). References used to determine phylogenetic order of organisms included polychaetes – Rouse and Pleijel (2001); gastropods – Rosenberg (2007); bivalves – Mikkelson and Bieler (2008); crustaceans – Martin and Davis (2001).

Root length (cm) was measured with a metric ruler. Diameter (cm) along the top and bottom of each root was determined with vernier calipers and mean diameter was calculated. Surface area (cm^2) of the root was estimated by using the length and mean diameter of each root. This was accomplished by using the formula for obtaining the surface area of a cylinder (π x diameter x length; Sheridan 1992). Estimated root surface area averaged 230.8 ± 113.6 cm^2 (mean ± sd) at Laguna La Mancha and 221.9 ± 143.9 cm^2 at Laguna Boca Paila with an overall mean of 226.3 ± 128.5 cm^2. Based on these estimates, we standardized invertebrate counts and algal biomasses to numbers or g dry weight per 100 cm^2.

Results

Forty-seven invertebrate taxa and 8,811 individuals were collected from roots in Laguna La Mancha (Table 1). The bivalves *Mytilopsis leucophaeta*, *Crassostrea virginica*, and *Ischadium recurvum* were the dominant species overall and constituted 98% of molluscs and 49% of all invertebrates collected. Roots were divided into those that were dominated by *C. virginica* (≥20/100 cm^2) and those that were not. Molluscs and amphipods were the most abundant groups regardless of root type. The amphipod assemblage was dominated by *Hyale prevostii*, *Melita nitida*, and *Amphilochus menehune*. *Cassidinidea ovalis* was the most abundant isopod. Polychaetes were not abundant. *Polysiphonia* sp. was the only algal genus present and algae were found on only seven roots. Roots dominated by *C. virginica* were more diverse than those that were not (44 taxa vs 35). In addition, many taxa, particularly polychaetes, bivalves, and amphipods, were more abundant on roots dominated by oysters. These roots were often colonized by oysters throughout their length, with no noticeable zonation. On roots with fewer oysters, the only apparent zonation was the concentration of barnacles at the top of the root in the intertidal zone.

In Laguna Boca Paila, 56,536 invertebrates were collected and 57 taxa were identified (Table 2). Most roots (88%) were colonized by algae and five species were identified: *Acetabularia crenulata*, *Batophora oersteddi*, *Anotrichium tenue*, *Bostrychia montagnei*, *Polysiphonia* sp. Mean algal biomass at Site 1 was 0.1494 g/100 cm^2, less than half the algal biomass recorded at the next lowest site (Site 5, 0.3181 g/100 cm^2) and only 12% of the highest mean algal biomass recorded (Site 3, 1.2594 g/100 cm^2). Algal biomass of individual roots with algae ranged from 0.0005 g/100 cm^2 to 2.2052 g/100 cm^2. Roots were divided into those that were dominated by algae (≥1 g dry weight/100 cm^2) and those that were not. Amphipods and isopods dominated both root types, although several species of amphipods, notably *Hyale plumulosa* and *Erichthonius brasiliensis*, were much more abundant on roots dominated by algae than on roots with little or no algal growth. Densities of *Sphaeroma terebrans* were similar on both root types. *Ischadium recurvum* and *M. leucophaeata* were the dominant molluscs and both were substantially more abundant on algae-dominated roots. The polychaete assemblage was comprised of 13 species but only *Capitellides*

TABLE 1. *Density (#/100 cm^2, with se in parenthesis) of taxa associated with ungrounded red mangrove roots collected from Laguna La Mancha, Veracruz on the Mexican Gulf Coast.*

	Oyster-dominated (n = 35)	**Bare (n = 15)**
Nemertea	0.5 (0.2)	0.1 (0.1)
Polychaetes		
Capitella capitata	1.8 (0.8)	1.2 (0.4)
Maldanidae Species A	0.3 (0.1)	0.2 (0.1)
Laeoneris culveri	9.3 (7.0)	0.4 (0.3)
Nereis falsa	20.5 (9.4)	3.9 (1.0)
Ehlersia sp.	0.1 (0.1)	0.1 (0.1)
Alciopidae Species A		0.2 (0.1)
Dorvilleidae Species A	0.2 (0.2)	0.1 (0.1)
Eunicidae Species A	0.1 (0.1)	
Marphysa sanguinea	2.5 (2.3)	
Serpula sp.	0.6 (0.2)	0.5 (0.4)
Boccardia hamata	2.7 (2.2)	0.6 (0.3)
Streblospio benedicti	0.2 (0.1)	
Gastropods		
Neritina virginea	1.0 (0.7)	0.3 (0.2)
Boonea impressa	3.1 (2.3)	
Bivalves		
Geukensia demissa	0.1 (0.1)	0.1 (0.1)
Ischadium recurvum	65.8 (15.4)	15.2 (4.6)
Isognomon bicolor	0.1 (0.1)	
Crassostrea virginica	83.4 (15.4)	14.1 (3.7)
Lucinidae Species A	0.1 (0.1)	
Mytilopsis leucophaeata	111.0 (22.5)	50.5 (24.1)
Bankia sp.	2.7 (0.8)	1.6 (1.1)
Barnacles		
Balanus spp.	47.2 (10.9)	23.7 (6.7)
Amphipods		
Amphilochus menehune	18.2 (4.7)	17.7 (7.4)
Amphithoe Species A	7.9 (3.8)	0.4 (0.4)
Corophium volutator	17.8 (4.8)	9.4 (3.5)
Gammarus mucronatus	3.2 (2.9)	1.2 (1.1)
Gammarus Species A	0.1 (0.1)	0.1 (0.1)
Ericthonius brasiliensis	1.0 (0.5)	1.7 (1.7)
Hyale plumulosa	0.6 (0.6)	
Hyale prevostii	33.1 (13.9)	38.6 (31.6)
Parhyale fascigera	0.1 (0.1)	
Elasmopus sp.	1.3 (0.9)	
Melita nitida	24.9 (6.1)	4.7 (1.4)
Orchestia gammarella	0.1 (0.1)	
Isopods		
Aega sp.		0.1 (0.1)
Cassidinidea ovalis	31.8 (6.4)	12.3 (3.5)
Uromunna caribea	0.7 (0.2)	1.1 (0.8)
Tanaids		
Hargeria rapax	12.5 (8.6)	11.5 (6.5)
Crabs and Shrimp		
Macrobrachium sp.	0.4 (0.2)	2.3 (1.3)
Brachyuran larvae	0.5 (0.3)	1.5 (1.5)
Micropanope nuttingi	0.1 (0.1)	
Panopeus herbstii	0.4 (0.2)	
Pachygrapsus gracilis	13.2 (2.4)	4.6 (1.1)
Armases ricordi		0.1 (0.1)
Insects		
Coleoptera	0.3 (0.2)	0.1 (0.1)
Diptera		
Dolichopodidae	0.3 (0.2)	0.4 (0.3)

TABLE 2. *Density (#/100 cm^2, with se in parenthesis) of taxa associated with ungrounded red mangrove roots collected from Laguna Boca Paila, Quintana Roo, on the Mexican Caribbean coast.*

	Algae-dominated (n = 23)	Not algae-dominated (n = 27)
Cnidarians		
Actiniara (anemone)		0.5 (0.4)
Nemertea	0.4 (0.2)	0.1 (0.1)
Polychaetes		
Capitellides jonesi	11.8 (4.5)	3.2 (1.9)
Ceratonereis mirabilis	0.3 (0.3)	1.9 (1.9)
Ceratonereis singularis		0.5 (0.3)
Neanthes acuminata		0.8 (0.6)
Nereis pelagica	0.4 (0.4)	0.5 (0.3)
Platynereis dumerilii	0.7 (0.4)	1.2 (0.7)
Syllidae Species A		0.2 (0.2)
Lysidice ninetta	0.1 (0.1)	
Marphysa sanguinea	1.3 (0.7)	0.1 (0.1)
cf. *Neovermilia capensis*	17.4 (9.4)	8.9 (4.8)
Aonides paucibranchiata	0.1 (0.1)	0.1 (0.1)
Minuspio cirrobranchiata	1.3 (1.1)	0.7 (0.5)
Gastropods		
Cerithiidae Species A	0.6 (0.6)	0.9 (0.6)
Echinolittorina lineolata	0.1 (0.1)	0.6 (0.3)
Littoraria angulifera	0.1 (0.1)	
Janthina sp.		0.1 (0.1)
Bullidae Species A	0.2 (0.2)	
Bivalves		
Ischadium recurvum	106.4 (70.2)	48.1 (28.6)
Isognomon alatus	0.1 (0.1)	0.4 (0.2)
Isognomon bicolor	1.3 (1.3)	
Mytilopsis leucophaeata	23.9 (10.8)	12.9 (7.9)
Teredo sp.	0.6 (0.4)	7.1 (2.9)
Barnacles		
Balanus spp.	10.0 (5.8)	11.9 (6.6)
Amphipods		
Amphilochus menehune	149.2 (91.8)	94.5 (47.2)
Amphithoe Species B	109.1 (79.4)	2.6 (2.3)
Amphithoe Species C		0.2 (0.2)
Cymadusa filosa	0.1 (0.1)	3.9 (3.3)
Corophium Species A	5.4 (5.1)	27.8 (12.9)
Corophium Species B	3.9 (3.5)	25.9 (11.3)
Ericthonius brasiliensis	548.1 (231.4)	169.9 (117.0)
Hyale plumulosa	1569.1 (541.2)	276.0 (147.8)
Parhyale fascigera	100.0 (45.5)	107.5 (43.6)
Lysianassa alba	37.8 (16.4)	40.1 (28.1)
Maera inaequipes	1.6 (0.9)	14.7 (7.3)
Melita nitida	34.8 (15.9)	8.2 (3.3)
Isopods		
Cyathura cubana	9.2 (5.3)	13.0 (7.2)
Excorallana tricornis tricornis	6.7 (2.4)	10.0 (4.3)
Cassidinidea ovalis	2.2 (1.2)	17.5 (6.6)
Sphaeroma terebrans	103.4 (40.4)	96.2 (26.0)
Dynamenella perforata	0.3 (0.2)	1.4 (1.1)
Munnidae Species A	6.4 (1.7)	21.3 (8.4)
Uromunna caribea	32.0 (12.1)	12.4 (4.3)
Tanaids		
Tanais sp.	8.6 (3.5)	24.3 (8.3)
Hargeria rapax	97.4 (30.5)	32.6 (13.9)
Crabs and Shrimp		
Palaemonetes sp.	1.3 (0.6)	0.8 (0.5)
Paguridae Species A		0.1 (0.1)
Brachyuran larvae	2.8 (1.0)	0.4 (0.2)
Majiidae Species A		0.2 (0.2)
Panopeus herbstii	11.1 (3.9)	2.0 (1.6)
Grapsidae Species A		0.1 (0.1)
Pachygrapsus gracilis	2.5 (1.1)	0.7 (0.5)
Sesarma curacaoense		0.2 (0.1)
Insects		
Hemiptera	0.1 (0.1)	0.1 (0.1)
Diptera		0.1 (0.1)
Hymenoptera		0.1 (0.1)

jonesi and cf. *Neovermilia capensis* were common. Roots dominated by algae were less diverse than those that were not (45 taxa vs 54). Roots dominated by algae were typically covered from top to bottom, often with very luxuriant growth. Like Laguna La Mancha, the only noticeable zonation pattern was the concentration of barnacles at the top few centimeters of the root where it entered the water.

Discussion

The main differences between the Laguna La Mancha and Laguna Boca Paila were the dominance of bivalves, particularly oysters, on root faunas in Laguna La Mancha and the widespread colonization of roots by algae in Laguna Boca Paila, with dominance by crustaceans, especially amphipods and the root boring isopod *S. terebrans*. Neither site exhibited noticeable faunal zonation, probably because waters were shallow and tidal fluctuation low. The sponges, tunicates and hydroids that are characteristic of many mangrove root faunas (e.g., Ellison and Farnsworth 1992, Sutherland 1980) were conspicuously absent from both sites. In addition, the faunas we describe include many more polychaetes and amphipods. Tube-dwelling sabellids and serpulids were the only polychaetes reported from roots in Belize (Ellison and Farnsworth 1992). Mattox (1949) noted the presence of the spionid *Polydora* in addition to a sabellid (*Sabella*) and a serpulid (*Hydroides*). Neither Mattox (1949) or Ellison and Farnsworth (1992) reported any amphipods.

Oyster-dominated roots were found only in Laguna La Mancha. Oyster coverage increased available surface area and provided more attachment sites for sessile organisms such as mussels and serpulid polychaetes as well as refuge for motile species (e.g., *Pachygrapsus gracilis, Nereis falsa*). The habitat complexity added by the oysters increased species richness and organisms were generally more abundant. For example, although the difference in polychaete species richness between root types was minimal (11 vs 9), the three most abundant species on oyster-dominated roots were 4.5 to 23 times more abundant than on bare roots. Abundance of some amphipod species was similar between bare and oyster-dominated roots (e.g., *Amphilochus menehune*, *H. prevostii*). However, most amphipod species were substantially more abundant on oyster-dominated roots and species richness was greater (12 vs 8). The fauna from Laguna La Mancha was very similar to that found in Laguna Tamiahua (Fajardo M. 1990), about 200 km to the north. Both lagoons are sites of artisanal oyster culture, which contributes greatly to oyster dominance of root faunas.

Algae-dominated roots were found only in Laguna Boca Paila. Where salinity, turbidity and water temperature were low (especially at Site 3 near the cenote) algal growth flourished, providing habitat for a plethora of small, motile invertebrates, mainly amphipods. Species richness was lower on algae-dominated roots than on roots with less algae but many species that were present on both types of roots were more abundant on algae-dominated roots. This was particularly true of the polychaetes, most bivalves, and about half of the amphipod species. All species of isopods identified were found on both root types. Abundance of the root-boring isopod *S. terebrans* was similar on both root types so algae did not appear to inhibit their colonization. However, with the exception of *Uromunna caribea*, the rest of the non-boring isopod species were more abundant on roots that were not dominated by algae.

Mangroves adjacent to offshore coral reefs are supplied with invertebrate larvae produced by reef inhabitants. Rützler (1969) noted that the sessile fauna of mangroves at Low Isles near the Great Barrier Reef "clearly belonged to the reef fauna proper." Root faunas on red mangrove prop roots in many lagoons isolated from coral reefs lack this diverse invertebrate larval supply and are often dominated by boring isopods, oysters and mussels (Perry 1988, Fajardo M. 1990). In Belize, epibiont species richness increased as proximity to the barrier reef increased, especially with regard to algae, sponges, hydroids, and ascidians; cover of these groups was also greater at sites nearer the reef (Ellison and Farnsworth 1992). In the Gulf of Nicoya, Costa Rica, the root-burrowing isopod *Sphaeroma peruvianum* and encrusting barnacle *Balanus* spp. were the dominant faunal components whereas sponge and tunicate coverage of roots was very low (Perry 1988). Bivalves, sponges, and tunicates were common faunal components in Puerto Rican mangrove lagoons with little oceanic communication (Mattox 1949) and in Bahía de Buche, a protected bay fringed by mangroves on the northern Venezuelan coast (Sutherland 1980).

The lack of sponges, tunicates and hydroids on mangrove roots in Laguna La Mancha and Laguna Boca Paila was likely due to a combination of isolation from larval sources (especially in the GOM) and salinities that are generally lower than marine. Salinity is an important determinant of mangrove faunal composition (Walsh 1967, Ellison and Farnsworth 1992). In all studies of mangrove root fauna in which sponges, hydroids and/or tunicates were prominent, salinities were marine (Mattox 1949, Sutherland 1980, Perry 1988, Bingham 1992, Ellison and Farnsworth 1992). Salinities in Puerto Rican mangrove lagoons typically mirrored those of the adjacent Atlantic Ocean (Mattox 1949). In Placencia Lagoon, Belize, where salinities were < 30 ppt and variable, only two sponge species were identified, the red alga *Bostrychia* was abundant, and no ascidians or cnidarians were reported (Ellison and Farnsworth 1992). Survival of species of sponges and tunicates common on mangrove roots near reefs was low when they were transplanted into Placencia Lagoon.

Salinities measured during this study were generally within published ranges for both sites. Laguna La Mancha is an estuarine coastal lagoon with salinities averaging 19.7 ppt and ranging from 11.5-25 ppt (Contreras-Espinoza and Warner 2004). This lagoon is also very turbid with low chlorophyll *a* values and net productivity relative to most other estuaries on the Mexican Gulf Coast. Laguna La Mancha and Laguna Tamiahua share similar hydrologic characteristics as well as similar mangrove root faunas. Salinities in the northern portion of the lagoon system in the Sian Ka'an Biosphere Reserve averaged 4.5-17.8 ppt during October and February, and 4.5-24.8 ppt during May and August (Sanvicente-Añorve et al. 2002). The ichthyoplankton assemblage in the northern half of the lagoon system (Campechén, Boca Paila, San Miguel) was dominated by estuarine components, unlike the assemblage in the southern portion lagoon system which was described as oceanic. The mangrove root fauna in the northern portion of the lagoon system could similarly be described as estuarine. The macrofaunal communities of ungrounded mangrove prop roots in Laguna La Mancha and Laguna Boca Paila described in this study reflect the estuarine conditions of the lagoons from which they were collected. Although both lagoons are isolated to varying degrees from potential sources of reef associated fauna, salinities that average less than marine are likely a major force determining community composition.

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