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HABITAT COMPLEXITY

Stand structure influences nekton community composition and provides protection from natural disturbance in Micronesian mangroves

Richard A. MacKenzie · Nicole Cormier

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Abstract Structurally complex mangrove roots are thought to provide foraging habitat, predation refugia, and typhoon protection for resident fish, shrimp, and crabs. The spatially compact nature of Micronesian mangroves results in model ecosystems to test these ideas. Tidal creek nekton assemblages were compared among mangrove forests impacted by Typhoon Sudal and differing in stand structure. Structurally complex *Rhizophora* spp. stands were predicted to support higher densities and different communities of nekton and to provide greater protection from typhoons compared to less complex *Sonneratia alba*/*Bruguiera gymnorrhiza* stands. Lift net data revealed that structural complexity did not support greater nekton densities, but did support significantly different nekton assemblages. The cardinalfish *Apogon ceramensis* and goby *Oxyurichthys lonchotus* had significantly higher densities in *S. alba*/*B. gymnorrhiza* mangrove creeks, whereas the silverside *Atherinomorus lacunosus* and diogenid crabs had significantly higher densities in *Rhizophora* spp. creeks. Similar nekton densities 17 and 4 months after the typhoon in *Rhizophora* spp. creeks provided indirect evidence that structural complexity increased protection for resident nekton from disturbances. Findings indicate that studies of structural complexity and nekton densities may be better served when individual species are compared and that diverse mangrove tree assemblages will support diverse nekton assemblages that may be more resilient to disturbance.

Keywords Fish · Shrimp · Crabs · Mangrove tidal creeks · Micronesia · Structural complexity · Typhoon

Introduction

Vascular plants are an important component of habitat complexity in coastal marsh ecosystems (Vince et al., 1976; Rozas & Odum, 1987; MacKenzie & Dionne, 2008). In mangrove forests, tree trunks, prop roots, buttresses, and/or pneumatophores can increase the structural and habitat complexity of the intertidal zone, although the degree of complexity provided varies with stand structure and root type. For example, aerial prop roots that originate from trunks of *Rhizophora* spp. create networks of branching, interwoven roots (Fig. 1) that are often taller and more complex than

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The importance of habitat complexity in waterscapes

R. A. MacKenzie (✉)
USDA Forest Service, Pacific Southwest Research Station, Institute of Pacific Islands Forestry,
60 Nowelo St., Hilo, HI 96720, USA
e-mail: rmackenzie@fs.fed.us

N. Cormier
U.S. Geological Survey, National Wetlands Research Center, 700 Cajundome Blvd., Lafayette, LA 70506, USA

Fig. 1 **A** Mixed stand of *Rhizophora* spp. and *Bruguiera gymnorrhiza* trees. The denser, taller, and branched *Rhizophora* spp. prop roots (foreground and background) create greater habitat complexity than the more open, shorter *Bruguiera gymnorrhiza* knee roots (*center*). **B** Mixed stand of *Sonneratia alba, Bruguiera gymnorrhiza,* and *Rhizophora* spp. The open, shorter pneumatophores create less habitat complexity than the prop roots of *Rhizophora* spp. in the fore and background

stalagmite-like pneumatophores of *Sonneratia* (Fig. 1A) or *Avicennia*, knee roots of *Bruguiera* (Fig. 1B), or ribbon roots of *Xylocarpus* (Tomlinson, 1986; Bosire et al., 2006; Alongi, 2009). Thus, dense thickets of *Rhizophora* prop roots can provide complex habitat throughout most, if not all, of the water column as they are inundated with tidal waters. In contrast, the amount of structural complexity provided by shorter pneumatophores and knee roots is limited by root height, and an open, less complex water column is usually present directly above root tops.

The structural complexity of mangrove roots is thought to provide valuable habitat for resident and transient fish, shrimp, and crabs that utilize these ecosystems (Morton, 1990; Primavera, 1997; Nagelkerken & van der Velde, 2002). This is largely due to root structures: (1) increasing the surface area available for colonization by epiphytic organisms that are important nekton food resources (Alongi & Sasekumar, 1992; Layman, 2007; Demopoulos & Smith, 2010) and (2) providing refuge from predation by larger fish or crabs (Vance et al., 1996; Primavera, 1997; Rönnbäck et al., 1999). Despite the clear evidence of the functional important of mangroves for fish assemblages, studies correlating faunal densities and structural complexity have reported mixed results. An experiment using PVC as artificial mangrove roots reported that three-dimensional complexity and pipe length did not affect fish abundance, number of species, or community composition. Instead, pipe orientation had a stronger influence on fish community variables, with higher fish abundances and numbers of species observed in standing pipes versus hanging ones (Nagelkerken et al., 2010). Another experiment that recreated structural complexity using *Rhizophora mangle* prop root cuttings also revealed that structure did not influence fish densities; shade and water depth were more important (Ellis & Bell, 2004). Similar results were reported for shrimp densities in a northern Australia mangrove. However, when fish densities were compared in this same Australian study, densities were greater in more structurally complex *Rhizophora* prop roots compared to less complex *Ceriops* pneumatophores (Vance et al., 1996). Other studies have also reported that the presence of structural complexity significantly increased fish and shrimp densities (Primavera, 1997; Rönnbäck et al., 1999). It is not clear if the different results reported above are due to differences in mangrove tree species examined, laboratory versus field studies, differences in sampling gear, or geomorphological differences among the different regions studied. Additional studies are needed that compare faunal assemblages across multiple mangrove forests that are geomorphologically similar but that differ in stand structure and thus habitat complexity.

Habitat complexity in mangrove forests may also protect resident fish, shrimp, and crab populations from the impacts of natural disturbances (e.g., hurricanes, typhoons, tsunamis). High winds during hurricanes and typhoons can result in turbulent wave action and tidal surge that can be detrimental to fish and shrimp communities; massive fish kills have been reported from coastal areas following major natural disturbance events (Knott & Martore, 1992; Bouchon et al., 1994; Tilmant et al., 1994; Burkholder et al., 2004). High winds can also uproot trees and severely damage crowns, resulting in high rates of tree mortality and defoliation, leading to degradation of fish habitat (Bouchon et al., 1994; Milbrandt et al., 2006). Whereas vegetation can take several years to fully recover, impacts to fish communities appear to be short-lived. Fish assemblages can recover after several months (Bouchon et al., 1994; Tilmant et al., 1994; Stevens et al., 2006). Although the mechanisms involved in the recovery of mangrove fish populations are unknown, the ability of fish to move to deeper, more protected waters and then recolonize mangrove forests after storms has been suggested (Switzer et al., 2006). Similarly, studies on coral reef ecosystems have shown that larger nekton can avoid storms by swimming out to deeper, more protected waters and then recolonize coastal areas afterwards. However, juvenile fish often exhibit high levels of mortality and low densities following hurricanes (Bouchon et al., 1994; Turpin & Bortone, 2002), which likely affects their recruitment (Turpin & Bortone, 2002). Structural complexity of mangrove forests may also aid in recovery from storms by protecting resident fauna from intensive wave action or storm surge. *Rhizophora* prop roots can significantly reduce the flow of water compared to pneumatophores or knee roots, resulting in increased deposition of sediment (Krauss et al., 2003) and decreased wave energy from storms (Dahdouh-Guebas et al., 2005; Alongi, 2008). Lack of significant changes in fish assemblages after Hurricane Charley in Florida were attributed in part to the protection provided by *Rhizophora* prop roots (Greenwood et al., 2006, 2007).

Mangrove forests on the island of Yap, Federated States of Micronesia provided us with model ecosystems for examining: (1) relationships between structural complexity and the resident fauna that access mangrove forests during high tide and (2) the potential role structural complexity plays in protecting resident faunal assemblages from typhoons. Advantages of these ecosystems included the fact that they are spatially compact compared to larger mangrove forests found in Australia, Indonesia, or South America (Ewel et al., 1998; Ewel et al., 2003); entire mangrove forest stands range from 10 to 50 ha (Falanruw et al., 1987). Replicate mangrove forests are also present that vary in tree species assemblages and thus habitat complexity. Finally, the island of Yap was devastated by a category 3 typhoon in April of 2004. Thus, tidal creek assemblages of fish, shrimp, and crabs could be easily sampled and compared across geomorphologically similar mangrove forests that differed in stand structure, habitat complexity, and that had been impacted by a major tropical storm.

We compared resident small-bodied fish, shrimp, and crab assemblages (<80-mm total length) among tidal creeks from six different mangrove forests that varied in basal area of *Rhizophora* spp., *Sonneratia alba* (Smith 1819), and *Bruguiera gymnorrhiza* (Lamarck, 1798). Mangroves with higher basal areas of *Rhizophora* spp. were considered to provide greater habitat complexity due to abundance of structurally complex prop roots; mangroves with higher basal areas of *S. alba*/*B. gymnorrhiza* were considered to provide lower habitat complexity due to less complex pneumatophores and knee roots (Rönnbäck et al., 1999). We hypothesized that more structurally complex mangrove forests would: (1) support higher densities of fish, shrimp, and crabs, (2) support different fish, shrimp, and crab communities, and (3) provide greater protection to fish, shrimp, and crab communities from the impacts of typhoons.

Materials and methods

Study site description

Yap is the westernmost state in the Federated States of Micronesia and consists of 134 islands and atolls that are part of the Caroline Archipelago and are spread out over 500,000 km^2 of the ocean (Merlin et al., 1996). Most of Yap (>75%) is represented by Yap proper (Wa'ab; hereafter referred to as Yap), four main islands formed by tectonic uplift and volcanic activity 10–28 MYA (Merlin et al., 1996; Hasurmai et al., 2005). Yap is ~10,000 ha, with an extensive coastal plain where most of the island's 15,000 inhabitants reside (Prior & Guard, 2005).

Mangrove forests account for nearly 12% of the island area of Yap (Falanruw, 1994) and are largely represented by narrow bands (<100 m wide) of fringing, coastal mangrove forests (Ewel et al., 1998; Kauffman & Cole, 2010). West coast mangrove forests are dominated by mixed stands of *S. alba* and *B. gymnorrhiza* assemblages, whereas east coast mangrove forests are dominated by mixed stands of *Rhizophora* spp. assemblages that include *R. apiculata*, *R. mucronata*, and *R. stylosa* (Falanruw, 1994; Kauffman & Cole, 2010). Differences in west versus east coast assemblages of mangrove forests have been attributed to impacts of previous tropical storms (Kauffman & Cole, 2010), especially since all three of these trees can coexist in similar hydrological and geomorphological settings (Ewel et al., 1998; Krauss et al., 2003). Tropical storms originate east of the islands (Gray, 1968) and first reach the windward, eastern coast, where high winds tend to inflict more damage than on the more protected, leeward western coast (Schneider, 1967). As a result, *S. alba* trees that are sensitive to high winds tend to occur at higher densities and basal areas in the more protected mangrove forests on the leeward side of the island compared to the windward side (Allen et al., 2000; Kauffman & Cole, 2010).

The average annual rainfall on Yap is 3,000 mm (Merlin et al., 1996). Most rainfall occurs from June to October, while November to May tend to be relatively dry months with strong east to northeast trade winds. Peak typhoon season occurs during the months that transition between the wet and dry seasons (e.g., May–June), although typhoons can occur throughout the year (Merlin et al., 1996). An average of three typhoons per year enter Yapese waters, but few pass over Yap (Schneider, 1967). The last major, destructive typhoon to hit Yap was in 1920 (Merlin et al., 1996).

Habitat complexity

Rhizophora spp. produce dense assemblages of tall, branching aerial prop roots that originate from their trunks and are inter-woven amongst prop roots from other trees. The resulting tall, dense thickets of prop roots provide structurally complex habitat (Fig. 1) throughout the water column at high tide. These dense thickets of prop roots are often impenetrable by larger organisms. In contrast, *S. alba* and *B. gymnorrhiza* produce much shorter pneumatophores and knee roots, respectively, that emerge from the sediments (Ellison, 1998; Krauss et al., 2003). While these roots can also have high densities, their tertiary structure is much less complex compared to *Rhizophora* spp. prop roots and can result in a more open forest floor (Fig. 1). In addition, their lower stature results in less habitat at high tide, and there is typically an open water column directly above them that larger fish can access. Thus, habitat complexity was considered to be greater in forest stands with greater basal areas of *Rhizophora* spp. than in forest stands with greater basal areas of *S. alba* and *B. gymnorrhiza*.

Tree basal area was used as a proxy for habitat complexity (Gallina et al., 1996; Bosire et al., 2006) for two reasons. First, basal area was positively correlated to tree density (*Rhizophora* spp. $r^2 = 0.68$, $P < 0.05$; *B. gymnorrhiza* $r^2 = 0.60$, $P < 0.05$; *S. alba* $r^2 = 0.44$, $P = 0.2$). Thus, increasing basal area represent increased densities of trees and thus numbers of roots that provide habitat complexity. Secondly, basal area also takes into account the size of the tree, and larger trees, especially *Rhizophora* spp., can produce significantly more prop roots than smaller trees (Tomlinson, 1986). For a detailed description of how basal area was measured, see Kauffman & Cole (2010). Basal area was only measured in 2004.

Typhoon Sudal

On 9 April 2004, Typhoon Sudal, a category 3 typhoon passed directly over Yap (Boyle, 2004). Although the entire island was impacted by the storm, the center of the storm stalled over the southeastern portion of the island and, as a result, higher winds were reported along the southeastern shore (155–210 km/h) compared to the northern shore (120-150 km/h) (Prior & Guard, 2005). The typhoon hit Yap during a spring tide and, as a result, many of the lowland areas were submerged under 2–4 m of water or damaged by wave action. Nearshore waves as high as 12 m (FSM, 2004) washed ashore thousands of dead reef fish (e.g., parrot fish, small groupers; M. Lander, University of Guam, personal communication).

Canopy cover

Aerial photographs from each forest (except Runuuw) were taken 3 months after Typhoon Sudal (July 2004) to estimate percent canopy cover. A grid

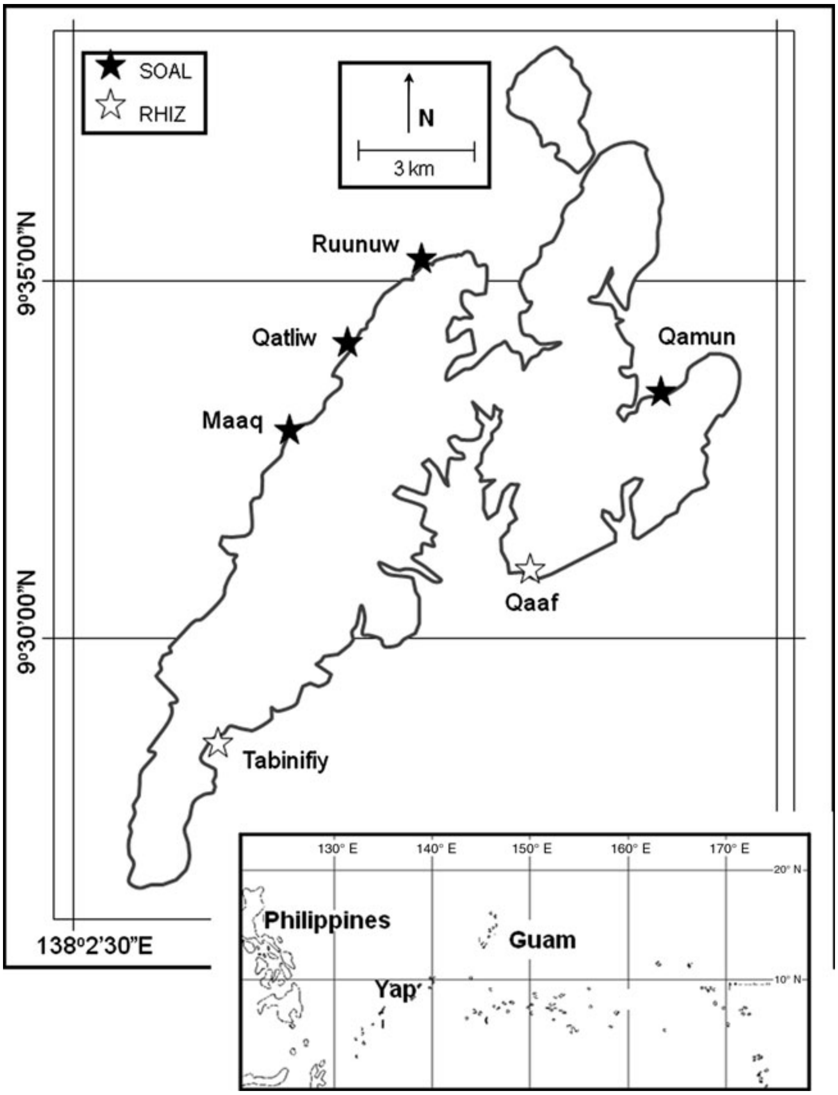

Fig. 2 Mangrove forests sampled on Yap Proper, Federated States of Micronesia. *Black stars* represent *S. alba*/*B. gymnorrhiza*-dominated mangrove forests (SOAL), while *white stars* represent *Rhizophora* spp. dominated forests (RHIZ). Maaq, Qatliw, Runuuw, Qamun, Qaaf, and Tabinifiy are villages where the mangroves were sampled

of 1 × 1 cm^2 squares was laid over each mangrove forest photo and six squares were randomly chosen. Squares that included tidal creeks were not included for analyses. Images were converted to 8-bit images and analyzed for percent canopy cover using Image J Analysis software (v. 1.39u 2005). Values were then averaged for each of the five forests.

Sampling methods

Resident small-bodied fish, shrimp, and crab assemblages (<80-mm total length) were sampled from the mouths of three replicate tidal creeks within each of the six different mangrove forests on Yap (Fig. 2) that ranged in *Rhizophora* spp., *S. alba* and *B. gymnorrhiza* abundance (Table 1) and thus habitat complexity. Nekton sampled from tidal creeks at low tide were considered to be resident species, as they spend most if not all of their lives in the subtidal habitat of tidal creeks and the flooded intertidal zone of mangroves or marshes (Weisberg & Lotrich, 1982; MacKenzie & Dionne, 2008). Samples collected from tidal creeks are also a good proxy for fish, shrimp, and crab assemblages found on the flooded marsh surface (Vance et al., 1996; Dionne et al., 1999; Eberhardt, 2004).

Tidal creeks were randomly selected from field surveys, with sampling stations located at the mangrove forest edge (i.e., mangrove-ocean interface).

Table 1 Average values (± 1 SE) for site characteristics from the six mangrove forests sampled. Forest characteristics are based upon measurements made in August, 2004

	SOAL				RHIZ	
	Maaq	Qatliw	Runuuw	Qamun	Qaaf	Tabinifiy
Mangrove area (ha)	27.9	31.5	25.1	12.9	23.1	19.0
Canopy cover (%)	96.6 (0.4)	95.1 (0.9)	–	90.8 (1.1)	82.8 (2.2)	69.8 (4.4)
B. gymnorrhiza (m^2/ha)	28.23	13.68	35.34	0.05	6.41	0.01
Rhizophora spp. (m^2/ha)	1.19	8.78	0.00	15.99	27.62	20.69
S. alba (m^2/ha)	53.25	28.17	57.34	21.89	8.57	0.00
2004						
DO (mg/l)	4.65 (0.25)	3.32 (0.50)	4.02 (0.14)	4.25 (0.13)	3.49 (1.08)	7.34 (0.11)
Temp. (°C)	26.93 (0.20)	28.93 (0.09)	27.43 (0.55)	28.73 (0.09)	27.43 (0.07)	32.40 (0.35)
Salinity (‰)	14.4 (3.5)	28.5 (0.09)	25.07 (0.55)	29.5 (0.3)	14.8 (4.4)	29.4 (1.15)
2005						
DO (mg/l)	5.34 (0.29)	2.78 (0.59)	2.01 (0.77)	5.91 (na)	7.92 (0.07)	7.19 (0.28)
Temp	28.40 (0.17)	30.33 (0.12)	30.60 (0.15)	27.60 (na)	32.63 (0.06)	32.60 (0.06)
Salinity	30.3 (0.3)	30.5 (0.3)	28.5 (0.5)	28.0 (na)	31.0 (0.4)	30.7 (1.4)

Mangrove area (ha) is from Falanruw et al. (1987); basal densities of mangroves (m^2/ha) are from Kauffman & Cole (2010)

SOAL represents mangroves dominated by *S. alba*/*B. gymnorrhiza*, RHIZ represents mangroves dominated by *Rhizophora* spp. Maaq, Qatliw, Runuuw, Qamun, Qaaf, and Tabinifiy are villages where the mangroves were sampled

Creeks originated near the mangrove interior-upland interface and drained the entire width of the mangrove forest. Tidal input occurred twice a day, with maximum tidal height of 1 to 2 m. Mangrove trees along the edge of the creeks represented the dominant species found within the mangrove forest. Thus, tidal creeks draining forests on the west coast were lined by *S. alba* and *B. gymnorrhiza* and had low habitat complexity, whereas creeks draining forests on the east coast were lined by *Rhizophora* spp. and had high habitat complexity due to the presence of dense, tall prop root assemblages. Samples were collected once at the end of August of 2004 and then again at the beginning of September of 2005. Tidal creeks were 2–3 m wide with water depths of 10–20 cm at slack low tide and creek lengths <100 m. Lift nets, which have been shown to effectively document community structure of small-bodied fish, shrimp, and crab assemblages from subtidal and intertidal habitats (Dionne, 2000; Eberhardt, 2004; MacKenzie & Dionne, 2008) were used to sample each of the tidal creeks. Each site was sampled on consecutive days by laying one 3-mm, 2 m^2 mesh lift net on the bottom of each creek ~1 h after slack low tide. All sites were sampled during the same lunar phase in 2004 and 2005, four (August 2004) and 17 months after (September 2005) Typhoon Sudal. After nets had been deployed for 30–45 min, they were quietly approached by two people in the water until they were 3–4 m away (i.e., not directly over the net). After an additional 2 min, nets were quickly lifted out of the water using lines that extended 3–4 m from each side of the net. Three lift net samples were collected from each mangrove forest. Immediately after samples were collected, dissolved oxygen, temperature, and salinity were measured at the water surface in an undisturbed area of water adjacent to the sampling area with a YSI™ 85 multimeter (Table 2).

Total lengths of fish and shrimps (rostrum to telson) as well as carapace width of crabs were measured to the nearest mm in the field or in the lab. Specimens were then identified to the lowest practical taxon (Myers, 1991; Carpenter & Niem, 2001). Densities (no/m^2) were calculated by dividing the total catches by the areas of the nets used to sample the nekton.

Statistical analyses

Average dissolved oxygen, salinity, and temperature values were compared between years (2004 vs. 2005) as well as between sites (RHIZ vs. SOAL) using a two-way analysis of variance (ANOVA). Site designations were based upon dominant basal densities of

Table 2 Average nekton densities (no/m^2 ± 1 SE) sampled with a lift net from tidal creeks in six different mangrove forests in Yap, Federated States of Micronesia

Taxa	SOAL								RHIZ			
	Maaq		Qatliw		Runuuw		Qamun		Qaaf		Tabinifiy	
	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005
Apogonidae												
Apogon ceramensis	–	11.6 (4.9)	0.1 (0.1)	–	0.3 (0.3)	3.7 (2.7)	3.4 (2.9)	4.5 (3.3)	–	0.1 (0.1)	–	0.5 (0.5)
Rhabdamia sp.	0.3 (0.3)	–	–	–	–	–	–	–	–	–	–	–
Atherinidae												
Atherinomorus lacunosus	0.1 (0.1)	–	–	–	–	–	–	0.1 (0.1)	–	4.2 (4.2)	2.5 (1.3)	–
Bothidae												
Bothus pantherinus	0.1 (0.1)	–	–	–	–	–	–	–	–	–	–	–
Callionymidae												
Callionymus sp.	–	–	–	–	–	–	–	–	–	–	–	0.1 (0.1)
Carangidae												
Caranx sexfasciatus	–	–	–	0.4 (0.4)	–	–	–	–	–	–	–	–
Gobiidae	–	–	0.1 (0.1)	–	–	–	–	–	–	–	–	–
Acentrogobius suluensis	–	0.1 (0.1)	–	–	0.3 (0.3)	3.1 (2.4)	–	0.4 (0.4)	–	–	–	–
Amblygobius buanensis	–	–	–	–	–	–	–	–	–	0.4 (0.4)	–	–
Asterropteryx semipunctatus	–	0.5 (0.5)	–	–	–	–	–	–	–	–	–	–
Cryptocentroides sp.	–	–	–	–	–	–	–	–	–	–	–	0.1 (0.1)
Drombus hulei	0.1 (0.1)	–	–	–	–	–	–	–	–	–	–	0.1 (0.1)
Eviota sp.	–	–	–	–	–	–	0.6 (0.6)	–	–	–	–	–
Exyrias puntang	–	–	–	–	–	–	–	–	0.1 (0.1)	–	–	–
Favonigobius reichei	–	–	–	–	0.1 (0.1)	0.1 (0.1)	–	–	–	–	–	–
Oxyurichthys lonchotus	0.3 (0.3)	0.1 (0.1)	1.9 (0.5)	1.7 (1.7)	1.5 (0.7)	0.1 (0.1)	1.2 (0.7)	0.5 (0.3)	–	–	–	–
Pandaka rouxi	–	–	–	–	–	–	–	–	1.8 (1.2)	–	–	–
Redigobius sp.	–	–	–	–	–	–	–	–	0.9 (0.7)	–	–	–
Sphyraenidae												
Sphyraena sp.	–	–	–	–	–	–	–	–	–	–	0.1 (0.1)	–
Hemiramphidae												
Zenarchopterus sp.	–	–	0.4 (0.4)	–	–	–	–	–	0.1 (0.1)		–	–
Alpheidae												
Alpheus sp.	–	–	–	–	0.3 (0.3)	–	–	–	–	–	–	–
Synalpheus sp.	–	–	0.1 (0.1)	0.2 (0.2)	–	–	–	–	–	–	–	–

Table 2 continued

Taxa	SOAL								RHIZ			
	Maaq		Qatliw		Runuuw		Qamun		Qaaf		Tabinifiy	
	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005
Palaemonidae	–	–	–	–	–	–	–	1.9 (1.7)	–	–	–	–
Kemponia sp.	0.4 (0.4)	–	–	–	–	–	–	–	–	–	–	–
Leandrites sp. nov.	0.1 (0.1)	–	0.4 (0.3)	2.4 (2.2)	0.1 (0.1)	0.3 (0.3)	6.9 (1.5)	1.5 (1.5)	5.7 (3.1)	0.9 (0.9)	–	–
Periclimenella sp.	–	–	–	–	–	–	1.3 (0.2)	–	0.1 (0.1)	0.3 (0.2)	–	–
Diogenidae	–	–	–	–	–	–	0.4 (0.3)	0.2 (0.2)	1.9 (1.5)	–	1.6 (0.8)	2.1 (1.4)
Grapsidae	–	–	–	0.1 (0.1)	–	–	–	–	–	–	–	–
Leucosiidae	0.3 (0.1)	–	–	0.1 (0.1)	–	–	–	0.3 (0.3)	–	–	–	–
Majiidae	0.1 (0.1)	–	–	–	–	–	0.3 (0.3)	–	–	–	–	–
Ocypodidae	–	–	–	–	–	–	0.4 (0.4)	–	–	–	–	–
Portunidae												
Charybdis truncate	–	–	–	–	–	0.1 (0.1)	–	–	–	–	–	–
Thalamita sp.	–	–	0.6 (0.6)	–	–	–	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)	–	0.1 (0.1)	–
Jelly Fish	–	–	–	–	–	–	–	–	0.1 (0.1)	–	–	–
Sepiidae	–	–	0.1 (0.1)	–	–	–	–	–	–	–	–	–

Samples were collected once in August of 2004, four months after Typhoon Sudal, and again in September of 2005, 17 months after the typhoon. Eighteen samples were collected each year, for a total of 36 samples collected during the study. SOAL represents *S.alba*/*B. gymnorrhiza*-dominated mangroves; RHIZ represents *Rhizophora* spp. dominated mangroves. Maaq, Qatliw, Runuuw, Qamun, Qaaf, and Tabinifiy are villages where the mangroves were sampled mangrove species (Kauffman & Cole, 2010), where RHIZ represented mangrove forests dominated by *Rhizophora* spp. and SOAL represented mangrove forests dominated by mixed assemblages of *S. alba* and *B. gymnorrhiza.* Percent canopy covered was only measured in 2004. Thus, comparisons of percent canopy could only be made between sites. Because aerial photos were not included for the Runuuw site, it was not included in the percent canopy analysis.

Pearson's correlation was used to examine relationships between 2004 and 2005 densities of total fauna, fish, shrimp, crab and basal areas of *Rhizophora* spp., *S. alba*, and *B. gymnorrhiza* across individual sites. Total fauna represents all fish, shrimp, and crabs that were sampled.

Community composition of lift net fauna was compared at the species level among sites (RHIZ vs. SOAL) and between years using a two-way analysis of similarities (ANOSIM). ANOSIM estimates community similarity using species composition and species abundances in a non-parametric permutation procedure applied to a Bray-Curtis similarity matrix (Clarke & Warwick, 1994). Contributions of individual species to differences in community structure were determined using similarity percentages (SIMPER). Pair-wise comparisons of species densities between sites (RHIZ vs. SOAL) generated an overall measure of dissimilarity, which was then used to rank species in order of their relative percent contribution to that dissimilarity. Densities of the top four species contributing to dissimilarity were compared between sites and years using a two-way ANOVA.

Due to the unpredictable and rare nature of typhoons on Yap Island, we lacked pre-typhoon data on fish, shrimp, and crab assemblages. Furthermore, we were unable to sample immediately after the typhoon. Fish assemblages can recover from typhoons within several months, although small-bodied adults and juveniles require longer recovery times (Bouchon et al., 1994; Turpin & Bortone, 2002). Thus, the small-bodied faunal assemblages that were sampled four months after the typhoon in August of 2004 were assumed to represent resident communities still recovering from the typhoon. Samples collected 17 months after the typhoon in September of 2005 were assumed to represent faunal communities that had fully recovered. Although these were broad assumptions to make, we felt our data set could provide indirect evidence on the potential role habitat structure plays in the recovery of resident faunal assemblages in mangrove forests.

In order to assess the relationship between habitat structure and protection from natural disturbance, we used ratios from 2005 and 2004 densities of total fauna, fish, shrimp, or crabs as a proxy for faunal response to the typhoon under the assumptions stated above. Ratios represent a more robust comparison among mangroves as they standardize the magnitude of densities across sites. For example, fish densities may have been lower in one mangrove forest, but higher in another in both 2004 and 2005. Direct comparisons made each year would simply confirm differences, whereas comparison of ratios would reveal potential responses. For example, if ratios were the same, then we could assume that there was no change to the fish community between years and those sites provided fauna with greater protection from the typhoon. If the ratio from one site was higher than that from the other site, then it would provide indirect evidence that the site with the higher ratio provided fauna with less protection from the typhoon, because higher ratios would have resulted from faunal densities being much lower during the impacted year (2004) compared to the recovered year (2005).

In order to account for the structural complexity in each of the six mangrove forests, an index of structural complexity was developed using principal component analysis (PCA) on basal area data of the three dominant mangrove tree species. Eigenvalues for each of the six sites were obtained from the first principle component (PC1) and plotted against ratios of total fauna, fish, shrimp, or crab densities. More positive eigenvalues represented higher levels of structural complexity from increased basal area of *Rhizophora* spp., whereas more negative values represented lower levels of structural complexity from increased basal areas of *S. alba* and *B. gymnorrhiza*.

Densities and ratios of total fauna, fish, shrimp, and crab densities did not meet assumptions of normality and equal variance and were (log + 1) transformed prior to analyses; percent canopy values were arcsine transformed. All similarity analyses were performed on (log + 1) transformed abundances in the PRIMER statistical package (v. 6.1.9 2007) (Clarke & Warwick, 1994; Carr, 1997). Because the treatment factor was unbalanced (two RHIZ vs. four SOAL), all ANOVAs were performed in PROC GLM in SAS 9.1 (SAS Institute, Cary, North Carolina) using Type III sums of squares set at an alpha level of 0.05 to get the appropriate F statistics for an unbalanced design (Shaw & Mitchell-Olds, 1993). Pearson's correlations were performed using SYSTAT v. 10.0 (SPSS, Chicago, Illinois) and linear regressions were performed in Sigma Plot v. 11.0 (SPSS, Chicago, Illinois).

Results

Tidal creek characteristics

Dissolved oxygen concentrations were significantly higher in tidal creeks in *Rhizophora* spp. mangrove forests (6.49 ± 1.01 mg/l) than in tidal creeks in *S. alba*/*B. gymnorrhiza* mangrove forests (4.04 ± 0.46 mg/l) (ANOVA, $P < 0.05$, $F = 6.60$, df = 1), but were similar between years as well as between sites in 2004 and 2005 (Table 1). Water temperatures were also significantly higher in tidal creeks in *Rhizophora* spp. mangrove forests (31.3 ± 3.9°C) than in tidal creeks in *S. alba*/*B. gymnorrhiza* mangrove forests (28.6 ± 1.9°C) (ANOVA, $P < 0.05$, $F = 6.90$, df = 1), but were similar between years. No significant differences were observed when salinities were compared between sites or years, although sites exhibited a greater range in salinity values in 2004 (14.4–29.5 ‰) than in 2005 (28.0–31.0 ‰). Comparison of individual sites revealed that Tabinifiy had the highest dissolved oxygen concentrations and temperatures than the other 5 sites, which was most apparent in 2004.

Percent canopy was nearly 20% greater in *S. alba*/*B. gymnorrhiza*-dominated forests (94.2 ± 1.7%) compared to Rhizophora spp. dominated forests (76.3 ± 6.5%), and this difference was significant (ANOVA, $P < 0.05$, $F = 13.1$, df = 1).

Fish, shrimp, and crab assemblages in tidal creeks

Tidal creek samples were dominated by fish, whose abundances represented 56.0 ± 8.6 and 67.8 ± 11.3% of the total catch in 2004 and 2005, respectively. In 2004, fish were dominated by gobies (53.3 ± 14.6%), largely *Oxyurichthys lonchotus* (Jenkins, 1903), followed by the *Atherinomorus lacunosus* (Forster, 1801) silverside (17.3 ± 14.6%) and the *Apogon ceramensis* (Bleeker, 1952) cardinalfish (16.9 ± 8.7%). In 2005, *A. ceramensis* were the dominant fish collected (46.7 ± 15.7%), followed by gobies (30.9 ± 12.2%) and then *A. lacunosus* (16.5 ± 16.0%). Shrimp were largely represented by the newly discovered *Leandrites* sp. nov. (Bruce, 2004) and comprised 27.2 ± − 8.6 and 18.6 ± 8.7% of the total catch in 2004 and 2005, respectively. Crabs only comprised 16.8 ± 5.3 and 13.6 ± 11.1% of the total catch in 2004 and 2005, respectively.

Relationships between habitat complexity and tidal creek fauna

In 2004, total catch, shrimp, and crab densities in tidal creeks were positively correlated to basal densities of *Rhizophora* spp. ($r = 0.58$, $P < 0.01$; $r = 0.46$, $P < 0.05$; $r = 0.59$, $P < 0.01$, respectively), but were negatively correlated to *B. gymnorrhiza* ($r = -0.59$, $P < 0.01$; $r = -0.46$, $P < 0.05$; $r = -0.51$, $P < 0.05$, respectively) and *S. alba* ($r = -0.45$, $P = 0.06$; $r = -0.29$, $P = 0.2$; $r = -0.56$, $P < 0.01$, respectively). These correlations were not apparent in 2005 nor were there any significant correlations between fish densities and basal areas in 2004 or 2005.

ANOSIM revealed that the community composition of total catches from tidal creeks was significantly different between more complex mangroves dominated by *Rhizophora* spp. and less complex mangroves dominated by *S. alba*/*B. gymnorrhiza* (ANOSIM, $r = 0.54$, $P < 0.05$). Community composition was similar between years (ANOSIM, $r = -0.04$, $P = 0.5$). SIMPER analyses revealed that differences between *Rhizophora*- and *S.alba*/*B. gymnorrhiza*-dominated habitats were driven by four main species that contributed to a total of 53% of community dissimilarity between forest types. These four species included *A. ceramensis*, *A. lacunosus*, a diogenid hermit crab, and the goby, *O. lonchotus*, each of which contributed to 15, 14, 14, and 10% of community dissimilarity, respectively. Specifically, *A. ceramensis* and *O. lonchotus* had significantly higher densities in tidal creeks in *S. alba*/*B. gymnorrhiza* mangroves than in tidal creeks in *Rhizophora* spp. mangroves (3.0 ± 1.4 vs. 0.2 ± 0.1 no/m^2; $P < 0.05$, $F = 5.52$, df = 1 and 1.0± 0.3 no/m^2 vs. 0 no/m^2; $P < 0.01$, $F = 9.62$, $df = 1$, respectively). *A. lacunosus* and diogenid crabs had significantly higher densities in tidal creeks in *Rhizophora* spp. mangroves than in tidal creeks in *S. alba*/*B. gymnorrhiza* mangroves (1.7 ± 1.0 vs. 0.1 ± 0.1 no/m^2; $P < 0.05$, $F = 5.60$,

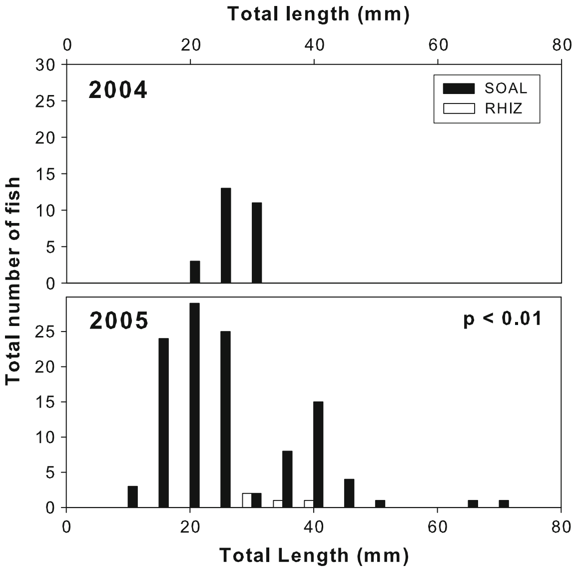

Fig. 3 Size class distribution of *Apogon ceramensis* in *S. alba*/*B. gymnorrhiza*-dominated mangrove forests (SOAL) (*black bars*) and *Rhizophora* spp. dominated forests (RHIZ) (*white bars*) from August, 2004 samples and September, 2005 samples. Eighteen samples were collected each year, for a total of 36 samples over the duration of the study

df = 1 and 1.4 ± 0.5 vs. 0.1 ± 0.1 no/m^2; $P < 0.001$, $F = 13.82$, df = 1, respectively).

Since *A. ceramensis* was the dominant fish species present in all six mangrove forests sampled, its size classes were compared between mangrove forest types. Only one cohort of *A. ceramensis* was sampled in 2004 from *S. alba*/*B. gymnorrhiza* mangroves; no *A. ceramensis* were collected from *Rhizophora* spp. mangroves (Fig. 3). In 2005, three cohorts were observed in *S. alba*/*B. gymnorrhiza* mangroves, while only one cohort was observed in *Rhizophora* spp. mangroves. As a result, size classes of *A. ceramensis* could only be compared between *S. alba*/*B. gymnorrhiza* and *Rhizophora* spp. mangroves in 2005. In 2005, significantly smaller *A. ceramensis* were present in tidal creeks in *S. alba*/*B. gymnorrhiza* mangroves (23.7 ± 1.0 mm) than in *Rhizophora* spp. mangroves (32.3 ± 2.52 mm; ANOVA, $P < 0.01$, $F = 6.58$, $df = 1$).

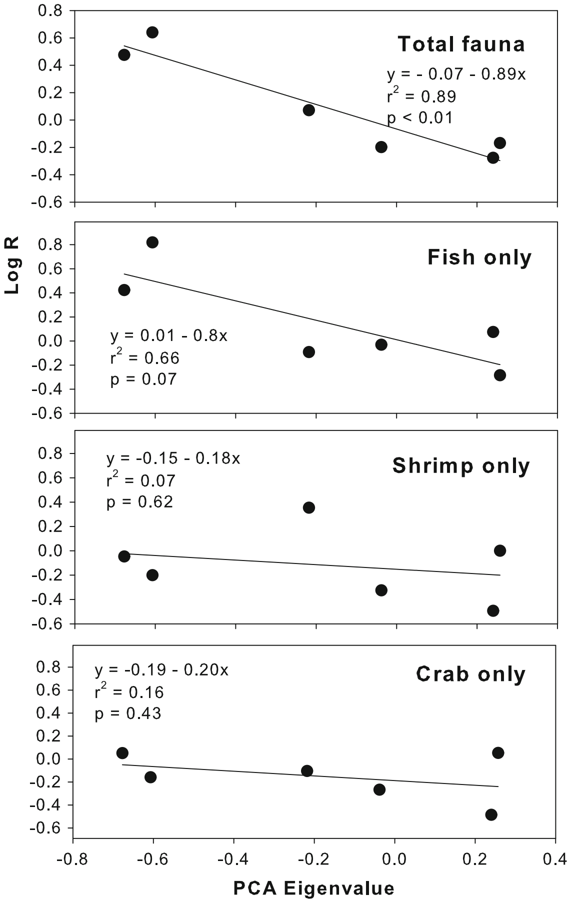

Fig. 4 Linear regressions of the ratios of total nekton, fish, shrimp, and crab densities from 2004 and 2005 and PCA eigen values. Eigen values were determined from relationships among basal densities of *S. alba*, *B. gymnorrhiza*, and *Rhizophora* spp. More positive numbers indicate greater basal densities of *Rhizophora* and thus more structural complexity. More negative numbers indicate greater basal densities of *S. alba* and *B. gymnorrhiza* and thus less structural complexity. Higher ratios represent nekton communities more impacted from the typhoon and result from greater densities 17 months after the typhoon (recovered) than four months after (impacted). Lower ratios represent nekton communities that were less impacted from the typhoon and result from similar densities 17 and 4 months after the typhoon

Relationship between habitat complexity and protection from natural disturbances

Principal component analysis conducted on basal areas of mangrove trees yielded two principal components with eigenvalues >1, which accounted for 90.1 and 9.9% of total variation. Basal areas of *Rhizophora* spp. (45.3) and *S. alba* (-39.5) loaded more heavily on PC1 than *B. gymnorrhiza* (−5.89). Basal areas were more evenly distributed across PC2, with basal areas of *Rhizophora* spp., *S. alba*, and *B. gymnorrhiza* having principal scores of −6.41, 9.79, and 16.2, respectively.

Ratios of total faunal densities were linearly correlated to PC1 eigenvalues determined from basal areas of *S. alba*, *B. gymnorrhiza*, and *Rhizophora* spp. ($r^2 = 0.85$, $P < 0.01$) (Fig. 4). Ratios of fish densities were also negatively correlated to PC1 eigenvalues, but this was only significant for a one-tailed comparison at an alpha level of 0.1 ($r^2 = 0.59$, $P = 0.07$). Higher total faunal and fish ratios were observed in less complex mangrove forests than in more complex ones. Post- to pre-disturbance ratios of neither shrimp nor crabs were significantly correlated with PC1 eigenvalues ($r^2 = 0.07$, $P = 0.62$ and $r^2 = 0.16$, $P = 0.43$, respectively).

Discussion

Community structure of tidal creek assemblages in Yapese mangroves

Fish, shrimp, and crab assemblages sampled from tidal creeks in Yap mangroves were considered to be representative of the resident fauna commonly found in mangrove forests in this region of the world. The cardinal fish *A. ceramensis* was the most abundant fish species collected and has been previously described as a mangrove resident species (Robertson & Duke, 1990; Unsworth et al., 2009). Gobies were another dominant fish collected, and many of the genera collected are also mangrove residents (Kuo et al., 1999; Ikejima et al., 2003). Congenerics of diogenid hermit crabs and palaemonid shrimp are also commonly found in tidal creeks and flooded forest floors of mangrove forests (R. MacKenzie, unpublished data; Rönnbäck et al., 1999; Rahayu & Koma, 2000). The silverside, *A. lacunosus* is considered a reef-associated species, but is commonly found in tidal creeks of mangroves (Conand, 1993).

Does habitat complexity influence densities of mangrove fauna?

Comparison of faunal densities across sites that differed in structural complexity did not fully support our first hypothesis that structurally complex mangrove forests would harbor higher densities of fish, shrimp, and crabs. Positive correlations to structurally complex *Rhizophora* spp. trees were only observed for densities of total fauna, shrimp, and crabs, and only in 2004. These patterns were not apparent in 2005 or for fish densities in either year. Significant correlations in 2004 may have been a result of Typhoon Sudal, because samples collected that year were assumed to represent faunal communities still recovering from the typhoon. Thus, significant positive correlations between densities of shrimp and crabs in *Rhizophora* spp. mangroves in 2004, but not in 2005, may have resulted from greater habitat complexity providing greater protection to benthic fauna then the less complex *S. alba*/*B. gymnorrhiza* forests. Alternatively, higher shrimp and crab densities in *Rhizophora* spp. mangroves in 2004 may have been due to higher levels of dissolved oxygen in *Rhizophora* spp. tidal creeks or greater inputs of litterfall. Significantly lower canopy cover in *Rhizophora* spp. mangroves compared to *S. alba*/*B. gymnorrhiza* mangroves following the typhoon was likely due to greater levels of defoliation that also occurred in these stands (N. Duke, personal communication). Shrimp densities commonly increase following hurricanes (Knott & Martore, 1992; Crowl et al., 2001; Stevens et al., 2006), which has been attributed to additional food and shelter provided by increased litterfall (Crowl et al., 2001; Stevens et al., 2006).

Lack of correlations between 2005 faunal densities, which were assumed to represent fully recovered, pre-typhoon assemblages, and basal areas of mangrove trees suggests that structural complexity may not be the primary factor influencing faunal densities in tidal creeks. Similar results were reported from tidal creeks in northern Australia, where banana prawn densities from tidal creeks did not significantly differ between more complex *R. stylosa* and less complex *Ceriops tagal* mangroves (Vance et al., 1996). Similarly, shrimp densities sampled using stake nets from the flooded forest floor of a Philippines mangrove, were not significantly different between *R. stylosa* stands and less complex *Avicennia officinalis* (Rönnbäck et al., 1999). However, when individual species were compared, differences were observed, with banana prawn having higher densities in *R. stylosa* prop roots (Rönnbäck et al., 1999). Studies assessing fish densities on the flooded mangrove forest floor have also reported mixed results. Fish densities were lower in more complex *R. stylosa* forests than less complex *Avicennia* forests in one Australian mangrove (Morton, 1990; Halliday & Young, 1996), but were higher in *R. stylosa* than less complex *Ceriops* stands in another Australian study (Vance et al., 1996).

Increased food availability and protection from predation in structurally complex mangrove roots (Alongi & Sasekumar, 1992; Primavera 1997; Rönnbäck et al., 1999; Layman, 2007; Demopoulos & Smith, 2010) was expected to result in strong positive correlations between habitat complexity and overall faunal densities in mangrove lined tidal creeks. Lack of correlation may have been due to several potential reasons. First, habitat complexity may have a stronger influence on individual species as opposed to total nekton assemblages as discussed below. Second, the resident fauna we sampled may have utilized other mechanisms to avoid predation, independent of mangrove-related habitat structure. For example, some species of shrimp or gobies can burrow into sediments or utilize crab burrows (Primavera & Lebata, 1993; Berti et al., 2008). Other species may have moved further into mangrove forests to use shallower water depths to avoid predation (Vance et al., 1996; Ellis & Bell, 2004). Third, the small-bodied fauna that we sampled may have been able to hide in the smaller spaces provided by lower knee roots and pneumatophores compared to the larger spaces present under taller prop roots (Primavera, 1997). Fourth, complexity of *Rhizophora* spp. prop roots may not have offered substantial refugia from predation compared to *S. alba* or *B. gymnorrihiza*. Kon et al. (2009) demonstrated that the presence of mangrove root structures did not reduce benthic invertebrate or crab predation in the laboratory or in the field. However, their results contradict other studies that have demonstrated that predation rates of fish are much lower within mangrove roots than in open intertidal areas (Sheridan & Hays, 2003; Ellis & Bell, 2004). Finally, food resources may have been abundant in mangrove forests regardless of root type. The presence of mangrove roots can significantly increase the amount epiphytic algae and animals growing in a mangrove forest compared to areas with no structure (Laegdsgaard & Johnson, 2001; MacDonald et al., 2008; Demopoulos & Smith, 2010). However, few studies have compared benthic and/or epiphytic organisms, and thus food sources, across different root structures. A preliminary comparison of benthic infauna among our six mangrove forests revealed no differences in invertebrate abundances among root types (A. Demopolous, unpublished data). This suggests that there were abundant food sources available for nekton regardless of root type.

Structural complexity influences tidal creek community composition

Significant differences in tidal creek community structure fully supported our second expectation that community structure would differ with habitat complexity. Over 50% of differences in community structure reported from ANOSIM were driven by four main species. Resident *A. ceramensis* cardinalfish and *O. lonchotus* gobies had significantly greater densities in the structurally less complex *S. alba/B. gymnorrhiza* mangroves. In contrast, *A. lacunosus* silversides and diogenid hermit crabs had significantly greater densities in the structurally more complex *Rhizophora* spp. mangroves. The dominant shrimp, *Leandrites* sp.nov. had similar densities between mangrove types.

Greater densities of adult, juvenile, and young-of-year *A. ceramensis* cardinalfish in structurally less complex mangrove stands may have been due to their foraging habit. *A. ceramensis* are visual predators of small fish and crustaceans (Unsworth et al., 2009), and the less complex root structures of *S. alba/B. gymnorrhiza*, with the open water column above roots and the more open forest floor in these root types, may have provided optimal foraging habitat for them. Furthermore, their small size, especially true for the abundant young-of-year, may have enabled them to utilize the limited vertical structure provided by the shorter knee roots of *B. gymnorrhiza*. Thus, *S. alba/B. gymnorrhiza* may provide better foraging and nursery habitat for this common mangrove inhabitant. Higher densities of gobies, especially *O. lonchotus*, in *S. alba/B. gymnorrhiza* forests could be explained by the more open forest floor, as the lower density of roots would provide more open muddy substrate for these demersal fish to burrow into or forage (Ikejima et al., 2003).

Although differences in densities of individual species, community composition and size class distributions of *A. ceramensis* were attributed to differences in structural complexity, these patterns may have also been due to other factors. Tidal creeks in *Rhizophora* spp. mangroves had significantly higher levels of dissolved oxygen and temperatures compared to tidal creeks in *S. alba/B. gymnorrhiza* mangroves. These were both attributed to lower canopy cover in *Rhizophora* spp. mangroves than in *S. alba/B. gymnorrhiza* mangroves. Canopy cover was not measured in 2005, but gaps in the canopy present in the second year suggest that canopy cover was still lower in *Rhizophora* spp. mangroves in 2005. Other potential reasons for observed patterns include differences in the soil properties associated with the different mangrove tree species described above. For example, redox potential and extractable phosphorous have been shown to be significantly higher in *Rhizophora* plots compared to *B. gymnorrhiza* plots in a similar mangrove forests on the island of Kosrae, Federated States of Micronesia (Gleason et al., 2003).

Relationships between habitat complexity and natural disturbance

The unpredictable and rare nature of typhoons on the island of Yap made it difficult for us to collect pre-typhoon data on tidal creek assemblages. However, if we assume that 2005 data represented fully recovered faunal assemblages and that 2004 data represented impacted assemblages, then our results can provide initial insight into the relationship between habitat complexity and protection from natural disturbance.

Ratios of densities of total fauna from 2005 (recovered) and 2004 (impacted) significantly decreased with increasing PC1 eigenvalues, a proxy for habitat complexity. Lower ratios, indicative of nekton densities that were more similar between years, suggest that fauna were not severely impacted by the typhoon as the mangrove forests they resided in afforded them greater protection from the typhoon. Alternatively, higher ratios that resulted from lower densities four months and higher densities 17 months after the typhoon suggests that these fauna were negatively impacted by the storm as the mangrove forests that they resided in did not afford them much protection. These results suggest that the greater habitat complexity of *Rhizophora* spp. stands provided better protection from the typhoon compared to the lower habitat complexity of *S. alba*/*B. gymnorrhiza* stands. Comparison of fish, shrimp, and crab ratios to PCA eigenvalues revealed that this trend was largely due to changes in fish densities; whereas shrimp and crab densities were similar 4 and 17 months after the typhoon. Thus, our data only partially supported or third hypothesis, that more structurally complex mangrove would provide greater protection to tidal creek fauna than less structurally complex mangroves.

Our data also suggest that pelagic organisms in Yap mangroves were more susceptible to impacts from the typhoon than benthic shrimp and crabs. The dense, branching, thickets of *Rhizophora* spp. prop roots can significantly reduce the flow of water compared to pneumatophores or knee roots, which is one reason why they are so effective at trapping sediments (Krauss et al., 2003) and protecting shorelines from storm damage (Dahdouh-Guebas et al., 2005; Alongi, 2008). This ability to reduce the flow of water moving through them may have also provided protection to resident small-bodied fish assemblages present in the mangroves at high tide when the typhoon struck. Small-bodied fish in *S. alba*/*B. gymnorrhiza* were likely killed by the storm (Bouchon et al., 1994), although the larger size classes may have avoided the storm by swimming out to deeper, more protected waters (Switzer et al., 2006). Shrimp and crabs likely burrowed into muddy substrate to avoid the storm.

Summary

Mangrove forests on the main island of Yap provided us with multiple spatially compact, geomorphologically similar ecosystems that differed in structural complexity to examine how habitat complexity influences densities and community composition of tidal creek fauna. These forests also provided initial insight on the relationship between habitat complexity and natural disturbances, such as hurricanes and typhoons. Structural complexity appeared to only be important for crab and shrimp densities immediately after Typhoon Sudal, although these patterns may have also been influenced by litter input. No patterns were apparent 17 months after the typhoon or for fish assemblages in either year. Structural complexity had a stronger influence on individual species than on total abundance, which was evident from significant differences in nekton community structure between *Rhizophora* spp. and *S. alba*/*B. gymnorrhiza*-dominated forests. The most abundant resident fish collected, *A. ceramensis*, preferred the less complex *S. alba*/*B. gymnorrhiza* habitat, as evident from the presence of significantly higher densities of adults, juveniles, and young-of-year in this habitat. Thus, our data only partially supported our first hypothesis, that structural complexity would harbor/shelter higher densities of fish, shrimp, and crabs, but fully supported our second hypothesis, that structural complexity would affect fish, shrimp, and crab communities. Finally, the correlation between ratios of fish densities and structural complexity only partially supported our third hypotheses. Increasing structural complexity appeared to provide increased protection from natural disturbance to small-bodied fish assemblages, but did not affect benthic shrimp or crab. Additional studies are needed to verify relationships between habitat complexity and protection from natural disturbances in a more deterministic way.

Our data revealed that the interaction between stand structure and tidal creek faunal assemblages is complex. Future studies examining relationships between habitat complexity of mangroves and fish, shrimp, and crab assemblages may be better served when community structure of abundance of individual species are compared. Use of pooled species (i.e., total fish, total shrimp, total crabs) may mask any influence habitat complexity has on faunal assemblages (i.e., Rönnbäck et al., 1999). Although none of the species we collected were of economic or cultural importance in Yap, they are an important food source linking mangrove production to nearshore production of larger species that are an important food source for human populations (e.g., snappers, emperor fish) (R. MacKenzie, unpublished data). Thus, relationships between stand structure and tidal creek nekton assemblages should be considered when mangrove restoration or preservation actions are taken. Mangroves that consist of diverse assemblages of trees will support diverse assemblages of ecologically, economically, and culturally important nekton species. This is particularly important now as island governments have been challenged by the Micronesian Conservation Trust, a local NGO, to set aside 30% of their coastal areas for conservation.

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