Journal of Experimental Marine Biology and Ecology 405 (2011) 53–58

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Predation risks for juvenile fishes in a mangrove estuary: A comparison of vegetated and unvegetated microhabitats by tethering experiments

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ARTICLE INFO

Article history:
Received 26 September 2010
Received in revised form 9 May 2011
Accepted 14 May 2011
Available online 8 June 2011

Keywords:
Juvenile fish
Mangrove estuary
Microhabitat
Predation risk
Structural complexity
Tethering experiment

ABSTRACT

Predation rates for juveniles of three fish species, the resident cardinal fish *Apogon amboinensis*, vagile mojarra *Gerres erythrourus* and benthic resident sand goby *Favonigobius reichei*, were compared in a creek between a mangrove-root area (fringing area with submerged portions of mangrove roots) and a bare sand area (unvegetated central area) in the Urauchi River mangrove estuary, Iriomote island, southern Japan, by daytime tethering experiments. *A. amboinensis*, occurring restrictedly in the mangrove-root area, hovered inactively near mangrove roots during the day. The other two species, on the other hand, inhabited both mangrove-root and bare sand areas, *G. erythrourus* swimming actively and speedily in the water column and *F. reichei* resting immobile on the substratum, its body coloration similar to the later. The predation mortality rate of *A. amboinensis* was significantly lower in the mangrove-root area than the bare sand area, whereas no differences in the rates for *G. erythrourus* and *F. reichei* were found between the two microhabitats. In addition, species and individual densities of piscivorous fishes, determined from a visual census, were significantly higher in the mangrove-root area, suggesting that the potential predation risk was not necessarily lower. The lower mortality rate of *A. amboinensis* in such a predator-rich area may be due to their anti-predator tactic associated with mangrove structural complexity, sheltering behind mangrove roots when disturbed by predators. The similar mortality rates of the other two species between the microhabitats may have resulted from anti-predator tactics independent of mangrove vegetation structure, such as rapid flight and cryptic body coloration.

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1. Introduction

Tropical and subtropical mangrove estuaries often support large numbers of fish species and individuals compared to nearby open-water mud- or sandflats, thereby suggesting that mangroves provide nursery habitats for juveniles of many species (Blaber, 2000; Kathiresan and Bingham, 2001; Nagelkerken, 2009; Nagelkerken et al., 2008; Robertson and Blaber, 1992). Hypotheses that have been proposed to explain the high abundance of small juvenile fishes in mangrove estuaries have been based mainly on the provision by mangroves of effective feeding and refuge areas from predators for juvenile fishes (Laegdsgaard and Johnson, 2001; Manson et al., 2005; Verweij et al., 2006). Among these hypotheses, the refuge value of mangrove habitats has been supported especially by the following: (1) shallow waters exclude large piscivorous fishes (Blaber and Blaber, 1980; Paterson and Whitfield, 2000; Rypel et al., 2007), (2) high turbidity decreases underwater visibility, thereby creating difficulties for visual predators in detecting and catching small prey (Blaber and Blaber, 1980; Cyrus and Blaber, 1987), and (3) the structural complexity of mangrove vegetation provides protection for small fishes in several ways, such as reducing prey visibility, and limiting the searching and catching ability of predators (Laegdsgaard and Johnson, 2001; Rönnbäck et al., 1999).

The potential refuge value of these factors for small fishes, however, has usually been inferred indirectly from habitat use patterns by juveniles and/or piscivores. For example, the sheltering effects of mangrove vegetation structures, such as prop roots, pneumatophores and tree trunks, are mainly supported by results showing higher densities of small fishes and juveniles and/or lower densities of larger carnivores in mangrove habitats than in unvegetated habitats (Blaber, 2000; Robertson and Blaber, 1992; Robertson and Duke, 1987; Shinnaka et al. 2007). Such differential densities, however, do not serve as direct evidence for the sheltering effects of mangrove vegetation structures, because the possibility remains that such patterns may reflect other factors, such as habitat preferences and/or prey availability.

In addition, the densities of small fishes are not always higher in complex vegetation microhabitats in mangrove estuaries (Smith and Hindell, 2005). Microhabitat use patterns of small fishes differ among species, some fishes occurring mainly in structurally complex areas

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doi:10.1016/j.jembe.2011.05.016

with prop roots and/or pneumatophores while others include bare sand/mud substrata. The sheltering function of mangrove vegetation structures, therefore, may differ among fish species, as already pointed out for a seagrass system (e.g. Horinouchi, 2007a; Horinouchi et al., 2009; Nakamura and Sano, 2004). Accordingly, predation mortality patterns in mangrove systems should be examined in detail.

In the present study, the predation mortality patterns of small juvenile fishes, i.e. the cardinal fish *Apogon amboinensis*, mojarra *Gerres erythrourus* and sand goby *Favonigobius reichei*, which are abundant in the study site, were examined across microhabitats in the mangrove estuary by tethering experiments. The tethering technique, although having some deficiencies (e.g. Curran and Able, 1998; Manderson et al., 2004; Peterson and Black, 1994), is nevertheless an effective tool for quantifying relative predation pressures among habitats and has been employed in many earlier studies (e.g. Baker and Sheaves, 2007; Horinouchi, 2007b; Laegdsgaard and Johnson, 2001; Nakamura and Sano, 2004; Nakane et al., 2009). In this study, the following questions were addressed: (1) Does predation mortality differ between the mangrove-vegetated and unvegetated sand/mud areas? (2) Does the predation mortality pattern differ among the prey species?

2. Materials and methods

2.1. Study site

The study was conducted in a creek in the Urauchi River mangrove estuary (24°24′ N, 123°46′ E), situated on the northern side of Iriomote Island, Ryukyu Islands, Japan, in August and September 2009 (Fig. 1). The mangrove forest comprised dense, undisturbed mature trees, dominated especially by the red mangrove *Rhizophora stylosa*.

Two microhabitats in the study creek were chosen for the tethering experiments: (1) the fringing area with submerged portions of mangrove roots in the creek (hereafter called "mangrove-root area") and (2) the unvegetated central area of the creek (hereafter called "bare sand area"). The mean density of prop roots in the former area was 63.3 ± 3.7 (standard error) m^{-2} ($n = 20$). The tidal range within the creek was approximately 1.5 m, prop roots being inundated at high tide and partially exposed at low tide. Mean water temperature and salinity were 30.1 ± 0.02 °C and 31.3 ± 0.1, respectively, during the study period. Mean water turbidity and clarity at high tide were 7.1 ± 0.7 NTU and 4–6 m, respectively, indicating that the study site could be classified as a "clear water" estuary (Blaber et al. 1997). These environmental factors remained constant between the two microhabitats.

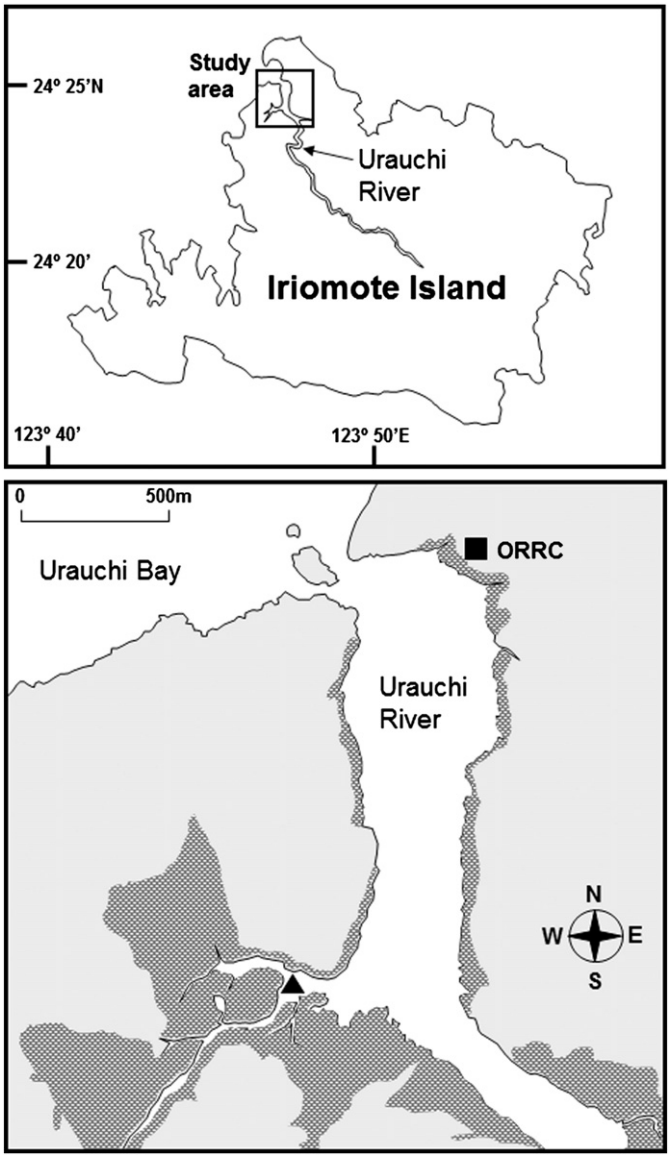

Fig. 1. Map of the Urauchi River mangrove estuary, Iriomote Island, Ryukyu Islands, Japan. Shaded areas indicate mangrove forests. ▲, experimental site; ■, Okinawa Regional Research Center, Tokai University (ORRC).

2.2. Tethering experiment

2.2.1. Experimental prey fish species

Juveniles of three species, the resident cardinal fish *A. amboinensis*, vagile mojarra *G. erythrourus* and benthic resident sand goby *F. reichei*, were employed as representatives of the common prey fish types in the mangrove estuary. They are relatively abundant during the summer season (June–September), being frequently preyed upon by piscivorous fishes (Nanjo et al., 2008). Adults of the former also occurred in the Urauchi River mangrove estuary. The occurrence of *A. amboinensis* was mostly restricted to the mangrove-root area (annual mean density 28.6/20 m^2) (Nanjo, unpublished data), juveniles hovering inactive, although sometimes forming a group, near roots during the day. In contrast, juveniles of *G. erythrourus* and *F. reichei* occurred in both mangrove-root and bare sand areas (annual mean densities 1.6/20 m^2 and 0.2/20 m^2 for *G. erythrourus*; 0.4/20 m^2 and 0.3/20 m^2 for *F. reichei*, respectively) (Nanjo, unpublished data). Juvenile *G. erythrourus*, often forming small aggregations of <10 individuals, swam actively in the water column during the daytime. Solitary *F. reichei* juveniles remained motionless on the substrate surface.

2.2.2. Tethering procedure

To compare relative predation rates for each fish species between the mangrove-root area and bare sand area, tethering experiments were conducted in the mangrove creek (Fig. 1). Tethering experiments can only measure relative predation rates rather than actual predation rates (Peterson and Black, 1994), because of potential artifacts, such as changes in behavior or escape responses of tethered fish, resulting in increased vulnerability to predators (Curran and Able, 1998; Peterson and Black, 1994). The effects of tethering on prey behavior and vulnerability should be assumed as remaining constant across treatments. When the physical nature of the habitats differs between treatments (e.g. vegetated and unvegetated habitats), interactions between experimental artifacts and treatments are most likely to be a problem, especially when tethered prey becomes entangled in vegetation (one treatment) and is less able to avoid predators (Peterson and Black 1994). In addition, it is possible that habitat differences in predator guilds, the predator's ability to detect and capture prey, and prey hiding ability, would interact with experimental artifacts. These inherent limitations must be considered when interpreting results. In order to overcome such deficiencies, we conducted field observations

and preliminary experiments so as to improve the tethering design and obtain more reliable results.

Juveniles of *A. amboinensis*, *G. erythrourus* and *F. reichei* were collected in the creek near the experimental site using a 6 m pocket seine net or small hand nets and maintained in water tanks for one day. After transportation to the tethering site, each experimental juvenile was immobilized in a tray of cool brackish water with crushed ice, measured (total length-TL) and then tethered. Similarly-sized juveniles were used so as to minimize the effects of prey size on predation (mean ± standard error = 43.5 ± 0.3 mm TL for *A. amboinensis*, 42.2 ± 0.3 mm TL for *G. erythrourus* and 35.1 ± 0.3 mm TL for *F. reichei*). Each tether comprised a thin transparent monofilament line (1.0 m long, 0.13 mm in diameter), one end being attached to a small fishing hook (5 mm long, 0.22 mm in diameter) and the other end to a small lead weight (0.5 kg). In the case of *G. erythrourus*, the hook was sewn through the nostrils, although in the membrane behind the lower jaw in the other species. In field observations prior to the experiment, we confirmed that such treatment did not severely influence tethered fish behavior; fish rarely became entangled in mangrove roots and remained able to exhibit anti-predator maneuvers, such as hiding behind mangrove roots, remaining stationary on the sediment or fleeing. Preliminary tethering experiments were also conducted in a predator free area (surrounded by a mesh net) in the estuary, employing ten individuals of each species for a single trial (six replicates). Tethered individuals neither weakened, nor died or broke free from the tether during the 30 minute duration of each trial.

Tethering experiments were conducted in both mangrove-root and bare sand areas at depths of 0.8–1.0 m at flood tide (between 9:00 and 17:00). Each trial employed ten individuals of a single species (six replicates for each species). Immediately after being tethered, each individual was set on the substrate using the anchor weight attached to the tether, and its presence/absence noted after 30 min. In the mangrove-root area, the anchors were placed on the substratum near the border of the area, and on the substratum near the creek center in the bare sand area. Each prey individual was separated from each other by at least 10 m. At this separation, it was assumed that a predator consuming a tethered individual would not be able to detect the one next closest. Accordingly, each predation event could be considered independent. The proportion of missing individuals was regarded as the predation mortality rate of the species in the area. We checked each tether very carefully at the end of the trials, ascertaining whether or not it had become entangled. Because two individuals of *G. erythrourus* became entangled in mangrove roots, two additional trials were conducted for that species. Entanglement never occurred for the other two species.

In addition, some predatory fishes which preyed upon the tethered juveniles became hooked themselves. Such predators were captured at the completion of the tether trials, identified, measured (TL) and then released.

A *t*-test was used to examine differences in mortality rates for each species between the mangrove-root and bare sand areas. Prior to the analysis, the homogeneity of variances was improved by arcsine transformation.

2.3. Visual censuses

In order to clarify the species composition and densities of predatory fishes, a visual census was conducted in the mangrove-root area near the border of the mangrove forest and the bare sand area, at depths of 0.8–1.0 m between 9:00 and 17:00. In each microhabitat, six belt transects (1 × 20 m), parallel to the creek and separated from each other by at least 20 m, were established randomly using a scaled measure. All fishes within the transect area were counted and their TLs estimated by the observer (K. Nanjo). Following Horinouchi et al. (2005), the observer attempted to maintain a swimming speed of about 1.0 m min^{-1} in order to sight and record all fishes correctly and reduce the possibility of counting the same fish twice. The classification of fish species as piscivores was based upon published dietary data from a preliminary study conducted at the mangrove estuary (Nanjo et al., 2008). Piscivorous fishes >60 mm in TL were counted as predators, because such are known to feed upon small fishes, including juveniles employed in the present tethering experiments (Nanjo et al., 2008). Species richness and abundance of piscivores in each microhabitat were expressed as the mean numbers of species and individuals per transect (20 m^2), respectively. Fish identifications followed Nakabo (2002).

To determine whether or not the species and individual densities of piscivorous fishes differed between the two microhabitats, a *t*-test was conducted. Before the analysis, data were log transformed to standardize variances.

3. Results

3.1. Mortality rates of tethered fishes and hooked predatory fishes

The mortality rates of tethered fishes varied between the mangrove-root and bare sand areas, and among the three fish species (Fig. 2). For *A. amboinensis*, a significantly lower mortality rate was obtained for the mangrove-root area compared with the bare sand area (*t*-test; t = −4.13, df = 10, p = 0.002). In contrast, no significant differences in the mortality rates of *G. erythrourus* (*t*-test; t = −1.53, df = 10, p = 0.16)

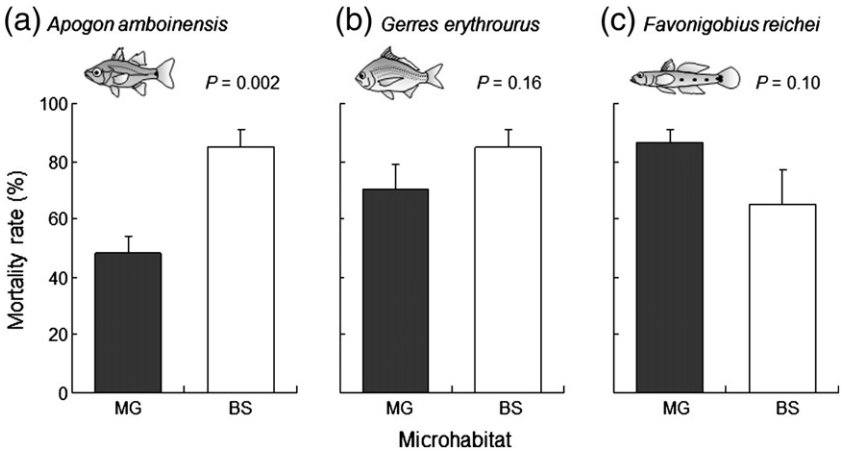

Fig. 2. Mortality rates of tethered fish species, (a) *Apogon amboinensis*, (b) *Gerres erythrourus* and (c) *Favonigobius reichei* per replicate (n = 6) in each microhabitat. Black columns = mangrove-root area (MG), white columns = bare sand area (BS). Error bar indicates standard error.

Table 1
Total lengths (TL) of tethered fishes and hooked predatory fishes in tethering experiments in each microhabitat.

Mangrove-root area						Bare sand area					
Prey			Predator			Prey			Predator		
Species	n	TL (mm)	Species	n	TL (mm)	Species	n	TL (mm)	Species	n	TL (mm)
Gerres erythrourus	2	42, 43	*Lutjanus fulvus*	1	128	*Gerres erythrourus*	5	42–45	*Caranx papuensis*	2	108, 115
			Terapon jarbua	1	142				*Terapon jarbua*	3	121–145
Apogon amboinensis	4	40–47	*Lutjanus fulvus*	2	77, 103	*Apogon amboinensis*	3	42–50	*Terapon jarbua*	3	201–247
			Lutjanus fulviflamma	1	99						
			Terapon jarbua	1	217						
Favonigobius reichei	10	33–36	*Caranx papuensis*	1	115	*Favonigobius reichei*	2	33, 37	*Terapon jarbua*	2	121, 206
			Lutjanus fulvus	7	77–96						
			Lutjanus fulviflamma	2	99, 110						
Mean ± standard error		37.4 ± 1.2			105.1 ± 8.8			42.4 ± 1.5			162.7 ± 16.2

and *F. reichei* (*t*-test; t = 1.84, df = 10, p = 0.10) were found between the microhabitats.

The species compositions of hooked predatory fishes which preyed upon tethered juveniles differed between the mangrove-root and bare sand areas, a total of 26 individuals representing four species being captured (Table 1). *Lutjanus fulviflamma* and *Lutjanus fulvus* preyed upon tethered fish only in the mangrove-root area, whereas *Caranx papuensis* and *Terapon jarbua* captured prey fish in both microhabitats. The mean predator size was less in the mangrove-root area (105.1 ± 8.8 mm TL) than in the bare sand area (162.7 ± 16.3 mm TL).

3.2. Predator densities

A total of 140 piscivorous fish individuals, representing eight species, were observed in the mangrove-root and bare sand areas during the study period (Table 2). Both species and individual densities of piscivores were significantly higher in the mangrove-root area (*t*-test; species density, t = 5.81, df = 10, p < 0.001; individual density, t = 6.41, df = 10, p < 0.001). Eight piscivorous fish species, including carangids (*Caranx melampygus*, *C. papuensis* and *Caranx sexfasciatus*), lutjanids (*Lutjanus argentimaculatus*, *L. fulviflamma* and *L. fulvus*), *T. jarbua* and *Sphyraena barracuda*, were observed in the mangrove-root area, whereas only two piscivores, *C. papuensis* and *T. jarbua*, occurred in the bare sand area.

4. Discussion

The present study revealed that the predation mortality rates of some prey types (strong-swimming species, such as *G. erythrourus*, and benthic species, such as *F. reichei*) did not differ between the complex mangrove-root and unvegetated sand areas, thereby contrasting with the generally-held notion of lower predation mortality in a more structurally complex, mangrove dominated microhabitat (e.g. Laegdsgaard and Johnson, 2001). However, the result obtained for the mangrove-root area specialist *A. amboinensis* was consistent with the latter. Caution was clearly required when interpreting the results of the tethering experiments, because of the inherent limitations of the study (i.e. possible occurrence of artifacts). Nevertheless, the present results and subsequent conclusions should be reasonable, reflecting predation rate patterns among the fishes examined and between the two microhabitats, because of the experimental manipulation and efforts made to overcome potential artifacts. In addition, the mangrove-root structured area harbored significantly greater numbers of resident piscivorous fishes, suggesting that in such a microhabitat, the potential predation risk is not necessarily low, as generally believed, but in fact rather high, as recently indicated by Hammerschlag et al. (2010a).

Several explanations can be advanced for the lack of any significant difference in the predation mortality rates of *G. erythrourus* and *F. reichei* between the complex vegetated and open bare microhabitats. The fishes may have anti-predator tactics independent of mangrove vegetation structure, making them less vulnerable and able to reside in open habitats. For example, benthic fishes such as *F. reichei* have body coloration similar to the sand/mud substratum. Such coloration of benthic fishes may significantly decrease predation risk, even on an unstructured sand/mud substratum (Horinouchi, 2007b; Sogard, 1992). In addition, *F. reichei* was sometimes observed burying themselves in the sediment using their fins, together with undulatory body movements. Such tactics may also enable them to avoid predation on a substratum lacking above-ground structures (Horinouchi, 2009). Fleeing speedily in response to the presence or approach of predators

Table 2
Mean number of individuals (± standard error) in each size class (total length) of each piscivorous fish species per transect (20 m^2, n = 6) observed at each microhabitat.

Family	Species	Mangrove-root area					Bare sand area				
		Size class (mm)				Total	Size class (mm)				Total
		60–100	110–150	160–200	210–250		60–100	110–150	160–200	210–250	
Carangidae	*Caranx melampygus*	0.7 ± 0.7	–	–	–	0.7 ± 0.7	–	–	–	–	–
	Caranx papuensis	1.2 ± 0.8	1.2 ± 0.7	0.3 ± 0.3	–	2.7 ± 1.3	–	–	0.2 ± 0.2	–	0.2 ± 0.2
	Caranx sexfasciatus	–	0.8 ± 0.8	1.3 ± 1.0	–	2.2 ± 1.8	–	–	–	–	–
Lutjanidae	*Lutjanus argentimaculatus*	–	–	1.8 ± 1.5	0.8 ± 0.7	2.7 ± 2.1	–	–	–	–	–
	Lutjanus fulviflamma	–	–	0.2 ± 0.2	0.2 ± 0.2	0.3 ± 0.2	–	–	–	–	–
	Lutjanus fulvus	5.3 ± 2.3	3.3 ± 1.6	4.2 ± 3.0	0.2 ± 0.2	13.0 ± 6.4	–	–	–	–	–
Teraponidae	*Terapon jarbua*	–	0.7 ± 0.4	1.0 ± 0.4	0.3 ± 0.3	1.7 ± 0.7	–	0.2 ± 0.2	0.8 ± 0.3	0.2 ± 0.2	1.2 ± 0.3
Sphyraenidae	*Sphyraena barracuda*	–	–	0.2 ± 0.2	–	0.2 ± 0.2	–	–	–	–	–
Mean number of species						3.8 ± 0.3					1.0 ± 0.3
Mean number of individuals						22.0 ± 6.8					1.3 ± 0.3

–, not observed.

also enables fishes to reduce predation risks in unstructured areas, such anti-predator tactics being often employed by fishes with strong swimming ability, such as *G. erythrourus*.

Of these tactics, camouflaging body coloration similar to the sand substratum should remain effective even in the complex mangrove-root area with a higher density of piscivores, thereby being responsible for the lack of any significant differences in survival of *F. reichei* between the vegetated and bare areas. Rapid flight tactics may also be effective in the mangrove-root area. Because spaces among mangrove roots are relatively large, fish of small body size, such as *Gerres* juveniles may swim rapidly without much disturbance and exhibit flight behavior effectively to some degree. However, this tactic is less effective in a complex microhabitat having only narrow spaces among vegetation, such as seagrass systems (Horinouchi, 2007a, 2009).

In addition, prey fishes may change their anti-predator tactics according to habitat structure, resulting in a lack of any significant difference in the predation mortality rates between complex vegetated and open bare microhabitats. Laurel and Brown (2006) found that prey fishes adjusted their position and behavior in response to habitat types, resulting in similar levels of prey mortality between seagrass and bare habitats. Similar behavioral shifts of prey have also been observed in a freshwater vegetation system (Savino and Stein, 1989). In addition to the above-mentioned anti-predator tactics, prey fishes might also employ alternative tactics associated with mangrove structures (e.g. hiding behind mangrove roots). If such flexibility occurs when necessary, it may be possible to reduce potentially high predation risks in predator-rich mangrove-root areas, again resulting in similar mortality rates to those over bare substrate. Data supporting for such flexibility, however, were not obtained during the present study.

Contrary to the findings for *G. erythrourus* and *F. reichei*, the mortality rate of *A. amboinensis* was significantly lower in the complex mangrove-root area than in the unvegetated bare sand area, suggesting that the anti-predator tactics of the latter were restricted to the former microhabitat where they were highly effective. In fact, when disturbed by predators, juvenile *A. amboinensis* hid behind mangrove roots or retreated into a denser root area, thus often successfully avoiding predators (K. Nanjo, personal observation). Clearly, *A. amboinensis*, could co-exist with numerous piscivorous fishes within the mangrove-root area. In the open unstructured area, however, this species was unable to employ similar or alternative tactics to avoid predators, resulting in a significantly lower survival rate.

In conclusion, although the mangrove-root area should have high potential predation risks due to the abundance of resident piscivorous fishes, some prey species can co-occur with such predators in such a microhabitat. Anti-predator tactics associated with mangrove-root structure may be responsible for such co-existence involving mangrove-root area specialists, such as *A. amboinensis*. The occurrence patterns of other prey types may also be due (at least partly) to anti-predator tactics and/or possible behavioral flexibility. In addition, a trade-off between food availability and predation risk sometimes influences habitat use patterns of small fishes (e.g. Dahlgren and Eggleston, 2000; Hammerschlag et al. 2010b). In fact, in the present mangrove estuary, food densities were much higher in the mangrove-root areas than in the open sand/mud areas (e.g., mean densities of crabs, 10.8/m^2 and 0.2/m^2, respectively) (Nanjo, unpublished data). Such relatively higher food availability may compensate for relatively higher potential predation risks and thus prey fish may utilize the mangrove-root area. However, supporting data, especially for the latter, are still insufficient. In addition, prey–predator interaction patterns in the night-time have yet to be clarified. Further studies need to examine not only the sheltering functions of mangrove vegetation structure but also detailed prey–predator interactions in both day- and night-time and the effects of other possible factors, such as a trade-off between food gain and predation risk, in order to clarify mechanisms enabling small fishes to co-exist with their predators within a mangrove system.

Acknowledgments

We are grateful to Ken Sakihara, Akira Mizutani and the Okinawa Regional Research Center, Tokai University, for assistance in the fieldwork. Constructive comments on the manuscript from Graham Hardy and two anonymous reviewers were much appreciated. This study was funded by a Grant-in-Aid for Scientific Research (B) from the Japan Society for the Promotion of Science (No. 21380121) and the Global COE Program (Center of Excellence for Asian Conservation Ecology as a Basis of Human-Nature Mutualism, representative: T. Yahara), Japan. **[ST]**

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