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Connectivity of fish assemblages along the mangrove-seagrass-coral reef continuum in Wenchang, China

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Abstract
Understanding the connectivity of fish among different typical habitats is important for conducting ecosystem-based management, particularly when designing marine protected areas (MPA) or setting MPA networks. To clarify of connectivity among mangrove, seagrass beds, and coral reef habitats in Wenchang, Hainan Province, China, the fish community structure was studied in wet and dry seasons of 2018. Gill nets were placed across the three habitat types, and the number of species, individuals, and body size of individual fish were recorded. In total, 3 815 individuals belonging to 154 species of 57 families were collected. The highest number of individuals and species was documented in mangroves (117 species, 2 623 individuals), followed by coral reefs (61 species, 438 individuals) and seagrass beds (46 species, 754 individuals). The similarity tests revealed highly significant differences among the three habitats. Approximately 23.4% species used two habitats and 11.0% species used three habitats. A significant difference ($p<0.05$) in habitat use among eight species (*Mugil cephalus*, *Gerres oblongus*, *Siganus fuscescens*, *Terapon jarbua*, *Sillago maculata*, *Upeneus tragula*, *Lutjanus russellii*, and *Monacanthus chinensis*) was detected, with a clear ontogenetic shift in habitat use from mangrove or seagrass beds to coral reefs. The similarity indices suggested that fish assemblages can be divided into three large groups namely coral, seagrass, and mangrove habitat types. This study demonstrated that connectivity exists between mangrove–seagrass–coral reef continuum in Wenchang area; therefore, we recommend that fish connectivity should be considered when designing MPAs or MPA network where possible.

Key words: connectivity, fish, mangrove, seagrass, coral reef, Wenchang, northern South China Sea

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1 Introduction

Mangroves, seagrass beds, and coral reefs are three typical marine ecosystems, which are often adjacent to one another, forming connections through chemical, biological, and physical interactions (Ogden, 1997). Examples of connections that exist across these habitats include the ontogeny of larval, juvenile, and adult fauna (Lowe and Falter, 2015) and exchange of carbon, nitrogen, and phosphorus among different habitats (Nagelkerken, 2009), leading to connectivity. Several studies have shown that the connectivity of different habitats provides abundant food resources and suitable habitats for the biodiversity of adjacent ecosystems, playing an important role in maintaining population structure and regulating ecological processes (Kindlmann and Burel, 2008; Bauer and Hoye, 2014). However, the above ecosystems are negatively affected by various anthropogenic activities and climate change in recent decades, resulting in habitat loss and fragmentation (Krosby et al., 2010; Brodie et al., 2012). Consequently, the connectivity among these ecosystems is severely reduced (Hughes, 2003), leading to a decrease in the diversity of species and changes in community structures (Pandit et al., 2017). Therefore, it is necessary to increase our understanding about the connectivity across mangroves, seagrass beds, and coral reefs.

Studies on the mechanism of connectivity have mainly focused on the transfer of organisms and nutrients, especially on the fauna migration between ecosystems (Du et al., 2015). Commonly, juvenile and adult fish occupy different habitats to meet their own needs, and undeniably mobile organisms move between and within habitat patches. Furthermore, some species often migrate to nearshore habitats to avoid being preyed (Shulman, 1985; Nakamura et al., 2003) or for food (Nagelkerken et al., 2000a) and as a nursery (Nagelkerken, 2009; Weinstein and Heck, 1979; Dorenbosch et al., 2004; de la Morinière et al., 2002; Nagelkerken et al., 2000b), which increased connectivity among different habitats. On the contrary, the biological connectivity enhances the productivity and biodiversity (Costanza et al., 1997).

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Therefore, it is important to maintain connectivity across different habitats to safeguard the structure and diversity of fish assemblages. However, the ontogenetic shifts and utilization patterns of fish from the typical marine ecosystems remain largely unknown, especially in China.

Wenchang, located on the east coast of Hainan Province, has the largest area of seagrass in China, and it supports one of the few mangrove–seagrass–reef continuums in China. However, the coverage of seagrass and hermatypic corals in this area is sharply declining (Chen et al., 2015; Wu et al., 2017). In this study, we aimed to analyze the fish assemblages and connectivity along mangroves, seagrass beds, and coral reefs in Wenchang. The results of this study are expected to improve our understanding of the connectivity of fish assemblages among habitats in Hainan Province, which could help improve the habitats protection strategies and fisheries management.

2 Materials and methods

2.1 *Study area*

Wenchang has tropical oceanic monsoon climate, sufficient light, high temperature, and abundant rainfall (Yang et al., 2017; Chen et al., 2015; Wu et al., 2011). The fish assemblages in the mangroves, seagrass beds, and coral reefs in Wenchang were studied, during the wet (March) and dry seasons (August) in 2018 (Fig. 1). Three sites passing through mangroves, seagrass beds, and coral reefs were designed. The site in mangrove is situated in the mouth of a lagoon at a depth of 0.5 m; the sediment is mainly silt and sand and the dominant species in mangrove are *Bruguiera gymnorrhiza*, *Kandelia candel*, and *Aegiceras corniculatum*. The site in seagrass is approximately 1 km from the coastline at the depth of 1 m, the most dominant species in seagrass beds is *Enhalus acoroides*, and the sediment is mainly composed of coral chips, shell chips and gravels. In the recent years, the seagrass distribution in this area has become patchy or scattered (average cover 33.55%) (Chen et al., 2015). The site in coral reef fringe is approximately 3 km from the coastline at the depth of 3 m. The dominant species are *Platygyra daedalea* and *Lobophyllia corymbosa* (approximately 65% coverage, but with only 0.33% live coral remaining) (Wu et al., 2011).

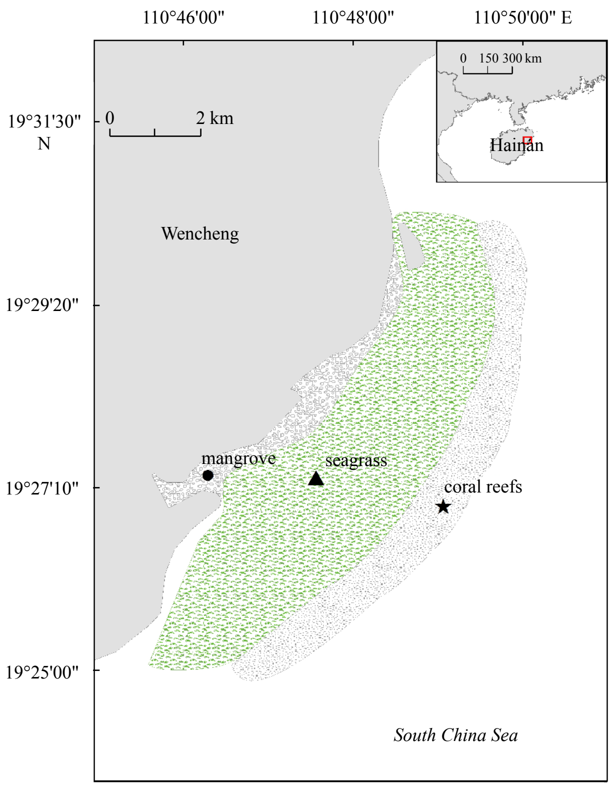

Fig. 1. Three study sites in the mangrove–seagrass–reef continuum in Wenchang, Hainan Province, China. The mangrove area was the closest to land (approximately 360 m) and the seagrass beds were in an intermediate location of mangroves and coral reefs, whereas the coral reefs were located along the edge of the continental shelf.

2.2 *Sample collection*

Gill nets (height 1 m, width 150 m, and mesh size 0.5 cm) were used in all the three habitats, and were collected at 2–3 h during the day time (05:00 to 17:00), one net per day for five consecutive days. Gill nets provide a non-destructive method for sampling, and they are an effective method for sampling diurnal near-shore fish assemblages in seagrass and other typical habitats (Unsworth et al., 2007).

All fish were identified to the species level (Chen and Yang, 2013; Liu et al., 2013; http://www.fishbase.org), while it was not possible to identify six species beyond the genus level. The total length (TL) of each specimen was measured to 0.1 cm accuracy. The collection, treatment, and analysis of samples were in accordance with the relevant provisions of the Marine Survey Specifications (General Administration of Quality Supervision, Inspection and Quarantine of the People's Republic of China and Standardization Administration of the People's Republic of China, 2007).

To determine how the fish utilized the habitat, the species were divided into the following seven habitat groups: (1) mangrove species, which were only present in mangrove; (2) seagrass species, which were only present in seagrass beds; (3) reef species, which were only present in coral reefs; (4) mangrove–seagrass species, which were present in both mangrove and seagrass beds; (5) seagrass–reef species, which were present in both seagrass beds and coral reefs; (6) mangrove–reef species, which were present in both mangrove and coral reefs; and (7) mangrove–seagrass–reef species, which occurred in all three habitats (Nakamura and Sano, 2004).

2.3 *Statistical analysis*

All specimens were collected from the three sites. The family composition of species and the number of individuals in each habitat were analyzed. A nonparametric Kruskal–Wallis H-test was used to determine the difference in individual numbers and species in each habitat, because assumptions of homogeneity of variance could not be met by some data, even after transformation (Shibuno et al., 2008). Differences in body length among mangroves, seagrass beds, and coral reefs were analyzed. The numbers of species and individuals were also compared using Mann–Whitney U test in different seasons among the three habitats.

The similarity of fish assemblages in the three habitats was calculated using data obtained from five consecutive days of sampling within each habitat for two seasons. The samples were ordinated based on Bray–Curtis dissimilarity matrices. The fish abundance results were visualized by nonmetric multidimensional scaling (NMDS). Fish community composition difference among habitat types were conducted using a nonparametric multivariate analysis of variance (NPMANOVA; a=0.05). The analysis was performed using the “vegan” package of R ver. 3.5.2 (R development Core Team).

3 Results

3.1 *Community structure*

A total of 3 815 individuals were collected from the three habitats, comprising 154 species belonging to 57 families (Table A1). In the mangrove area, 2 623 individuals of 117 species belonging to 48 families were collected. In contrast, fewer fish were recorded in the seagrass beds (754 individuals belonging to 46 species of 28 families) and coral reefs (438 individuals belonging to 61 species of 35 families). More number of species and individuals were recorded in the mangroves than that in the seagrass beds and coral reef habitats (Table 1). The mean number of individuals in the samples collected for five consecutive days in mangrove area was significantly higher than that in seagrass beds and coral reefs in wet season (p<0.05) (Fig. 2a). The mean number of species in the samples collected for five consecutive days in mangrove was significantly higher than that in coral reefs in wet season and in seagrass in dry season (p<0.05) (Fig. 2b). In addition, there was no significant difference in the mean number of individuals and species between seagrass beds and coral reefs.

The most dominant families in the mangrove were Gobiidae (20 species, 17.1%, represented by *Oxyurichthys ophthalmonema*), followed by Labridae (5 species, 4.3%, represented by *Halichoeres nigrescens*), and Leiognathidae (5 species, 4.3%, represented by *Leiognathus equulus*) (Fig. 3a). In the seagrass beds, Gerreidae (4 species, 8.7%), Leiognathidae (3 species, 6.5%), and Lutjanidae (2 species, 4.3%) were the dominant families, and the representative species included *Gerres oblongus*, *Leiognathus equulus*, and *Lutjanus russellii*. In the coral reef, the most dominant families were Labridae (8 species, 13.1%), Lethrinidae (4 species, 6.6%), and Lutjanidae (4 species, 6.6%), with *Lethrinus haematopterus* being the representative species.

In terms of individual numbers, Gobiidae was the dominant family in the mangrove area, accounting for 21.3% of all species, followed by Mugilidae and Siganidae, which together accounted for 22.4% of the species (Fig. 3b). Mugilidae was the most dominant species in the seagrass beds, representing approximately 47.7%, followed by Terapontidae (101 individuals, 13.4%) and Gerreidae (94 individuals, 12.5%). Siganidae (105 individuals, 24.0%), Mugilidae (89 individuals, 20.3%), and Terapontidae (39 individuals, 8.9%) were the three dominant species in the coral reef.

The similarity indices suggested that fish assemblages can be divided into three groups (coral, seagrass, and mangrove habitat type) (Figs 4a, b). The results of similarity tests using NPMANOVA revealed a highly significant difference among habitats ($F_{2,27}$= 4.01, p=0.003).

3.2 *Fish utilized multiple habitats*

Of the 154 species recorded, 101 species (accounting for approximately 65.6% of all species) occurred in a single habitat, whereas the individuals accounted for 23.7% of all species. However, only 36 species were recorded in two habitats and 17 species were recorded in three habitats; thus, 34.4% of all species were recorded in multiple habitats (Table 1). Specifically, 16 species were recorded in the mangrove–seagrass areas, 17 species were recorded in the mangrove–coral reef areas, 3 species were recorded in the seagrass–coral reef areas, and 17 species were re-

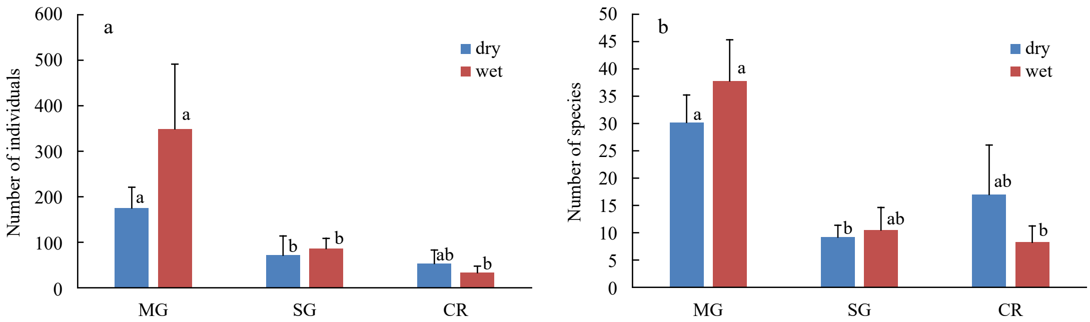

Fig. 2. Mean number of fish species (a) and individuals (b) during sampling months in each habitat. The error bars are standard deviations. MG, SG, and CR represent mangroves, seagrass, and coral reefs, respectively.

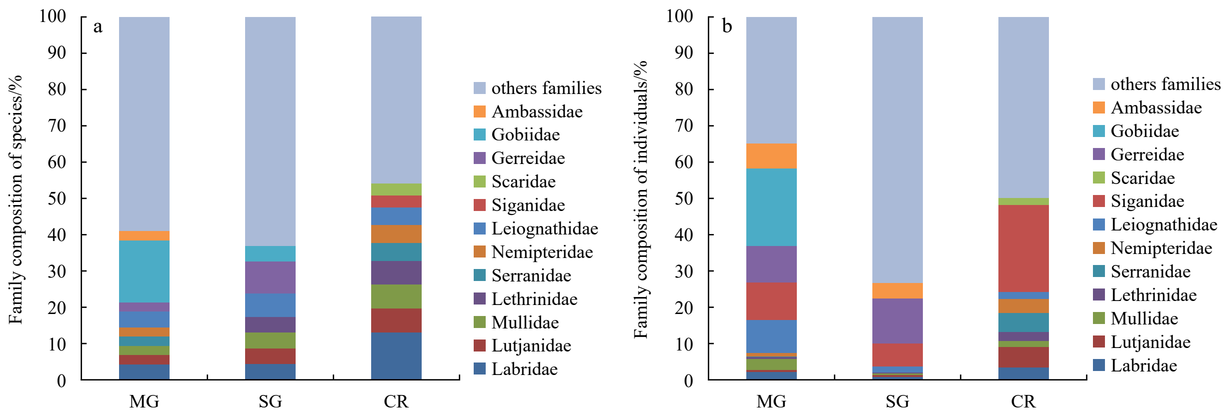

Fig. 3. Relative family composition of fish species (a) and the number of individuals (b) in the three habitats.

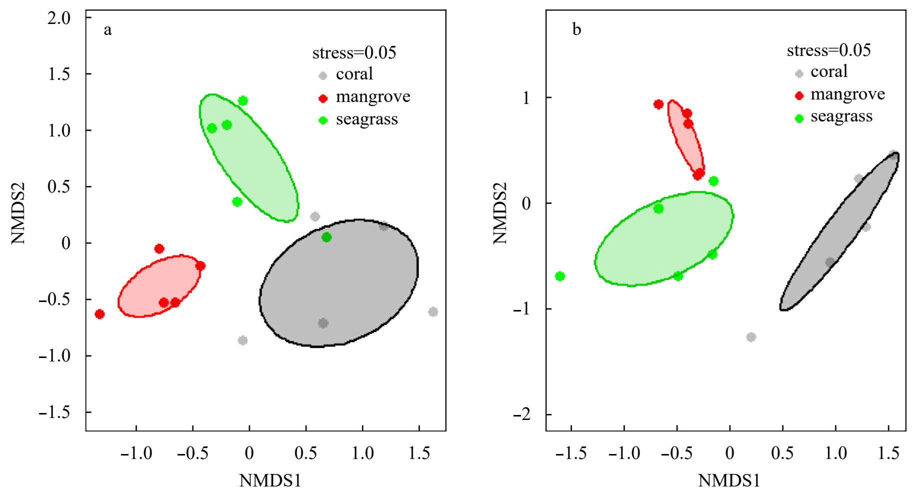

Fig. 4. Nonmetric multidimensional scaling (NMDS) of data from all five days in each habitat in March (a) and August (b).

Table 1. Percentage contribution by species and individuals for each habitat group

Habitat/habitat group	All species/% (n)	Individuals/%
Mangrove		
Mangrove species	57.3 (67)	31.3
Mangrove–seagrass species	13.7 (16)	17.9
Mangrove–reef species	14.5 (17)	2.9
Mangrove–seagrass–reef species	14.5 (17)	48.0
Seagrass bed		
Seagrass species	21.7 (10)	2.8
Mangrove–seagrass species	34.8 (16)	19.9
Seagrass–reef species	6.5 (3)	0.4
Mangrove–seagrass–reef species	37.0 (17)	76.9
Coral reef		
Reef species	39.3 (24)	16.1
Seagrass–reef species	4.9 (3)	3.0
Mangrove–reef species	27.9 (17)	10.1
Mangrove–seagrass–reef species	27.9 (17)	70.8

Note: Number of fish species is shown in parentheses.

corded in the mangrove–seagrass–coral reef areas. In the mangrove and coral reef areas, the local species represented more than 35% of the total species. In comparison, in the seagrass area, species that used multiple habitats accounted for 78.3% of all species. In terms of individuals, more than 60% of all individuals used two or three habitats, especially seagrass and coral reef areas. The mangrove–seagrass–coral reef species contributed to approximately 70% of all individuals in seagrass and coral reef areas, although seagrass–coral reef species only represented 0.4% of individuals in the seagrass beds. Minimal differences were found in both fish species and individuals using the mangrove–seagrass–coral reef continuum (Table 1).

The length of eight species (*Mugil cephalus*, *G. oblongus*, *Siganus fuscescens*, *Terapon jarbua*, *Sillago maculata*, *Upeneus tragula*, *L. russellii*, and *Monacanthus chinensis*) was higher in coral reef than that in seagrass and mangrove areas, showing possible ontogenetic habitat shifts from mangrove or seagrass beds to coral reef (Fig. 5). This shift might explain the trend towards changing habitats by individuals and species. On the whole, in their early stages of development, these fish mainly inhabited the mangrove and seagrass beds, which is consistent with the fact that mangrove and seagrass habitats serve as nurseries for fish (Beck et al., 2001).

4 Discussion

This study demonstrated that the structure of fish assemblages across mangroves, seagrass beds, and coral reefs differed with respect to the number of individuals and species (Fig. 3, Table 1). More number of individuals and species were present in mangroves than that in seagrass and coral reef areas. This result is different from that reported in Mindoro and Mindanao Islands in Philippines, where the fish species in coral reef (265) was much higher than that in mangroves (47) and seagrass beds (38) (Honda et al., 2013). This might be because the gill net was used to collect samples in this study, while the diving visual censuses was used in Philippines, which might miss several small fish, such as goby. Moreover, the fish diversity in mangrove is also high in other areas in China; for example, 115 species in Dongzhaigang National Nature Reserve for Mangroves (Shi, 2005) and 127 species in the Leizhou Peninsula (He et al., 2003). In addition, fewer individuals were present in coral reefs than those in seagrass; however, the diversity of species in coral reefs was higher than that in seagrass. The 117 fish species recorded in mangrove accounted for approximately 76.0% of all fish species recorded, whereas only 16 and 17 species exclusively utilized seagrass and coral reef habitats, respectively (Table 1). The fact that 67 species were found only in mangrove habitats emphasizes the need to protect multiple habitats even without considering connectivity.

In this study, 53 of the 154 species were detected in two to three of the surveyed habitats. The distribution of the eight species based on the body length was significantly different among the three habitats (p<0.05; Fig. 5), which might reflect ontogenetic changes in habitat use among the three habitats. In recent years, several studies have focused on the ontogenetic changes in fish using the gut content and stable isotope (δ^{13}C and δ^{15}N) analyses (de la Morinière et al., 2003; Berkström et al., 2013). *Monacanthus chinensis* is omnivorous and seagrass is its minor food item (Bell et al., 1975). Most individuals of this species were detected in the mangrove area of this study and were in the early stage of development. Some adult individuals were also recorded in the seagrass beds. However, there was no record of this species in seagrass beds at Had Khanom Mu Ko Thale Tai Na-

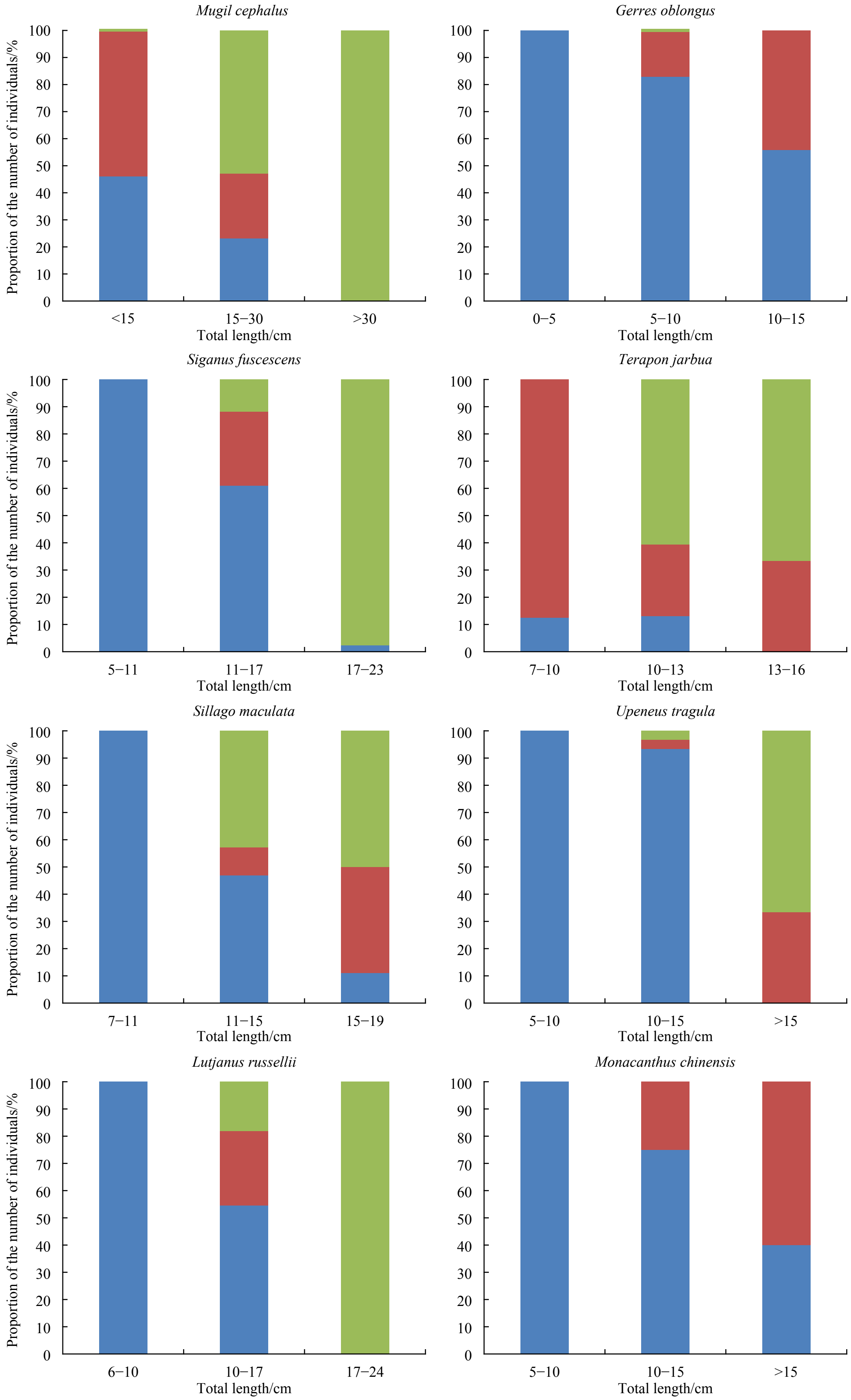

Fig. 5. Relative abundance of the eight fish species in the mangrove (blue), seagrass (red), and coral reefs (green) habitats according to the class size using pooled date.

tional Park of Thailand (Sichum et al., 2003).

Most individuals of the species *L. russellii* were detected in the mangroves and coral reefs, and this multiple habitat use reflects a relaxed day–night shift, with individuals feeding in seagrass beds at night and shifting to sheltered areas (mangrove/coral reefs) by daytime (Nagelkerken et al., 2000a; Bond et al., 2018). *Upeneus tragula* and *Sillago maculata* utilized almost all habitats. *Gerres oblongus* is a common species in coastal areas, and it spawns from February to June in the Jaffna Lagoon, Sri Lanka (Sivashanthini and Abeyrami, 2003). Thus, the samples collected from the mangrove and seagrass beds were juveniles, which preferentially use mangroves as a nursery over seagrass beds. Most juveniles and a group of adults of *T. jarbua* were found occupying the seagrass beds. Other adult fish of this species were found in coral reefs. On the contrary, 77% of *Triacanthus biaculeatus* individuals were recorded in seagrass beds, and only a few in mangroves. Overall, there was an abundance of fish in the early stages of development in the mangrove and seagrass beds, with more number of individuals in the later stages of development in the coral reefs. This finding was similar to that detected for fish assemblages in the Indo–Pacific (Unsworth et al., 2009) and Caribbean islands (Nagelkerken et al., 2002).

Studies on connectivity among coastal habitats have mainly focused on the Indo–Pacific (Unsworth et al., 2007, 2008, 2009) and Caribbean (Weinstein and Heck, 1979; Nagelkerken et al., 2002; Kopp et al., 2007), particularly with respect to fish structure among different habitats. It is widely accepted that mangroves and seagrass beds serve as nurseries for reef fish species; however, empirical studies supporting this assumption remain limited. The structure, food resources, and shade provided by mangrove–seagrass beds strongly attract juvenile fish (Verweij et al., 2006). In addition, some studies have emphasized the importance of mangrove and seagrass beds for maintaining fish density in coral reefs (Nagelkerken et al., 2002). Furthermore, overlapping use of seagrass beds with adjacent coral by fish has been documented (Nakamura and Sano, 2004). Consequently, habitat degradation or loss in coastal areas could have significant negative effects on other fauna occupying these habitats.

The rich fishery resources and numerous fishing gears in the South China Sea have promoted the rapid development of the marine fishery. According to the characteristics of fish and the environment, the choice of suitable gear is an issue worth considering. Trawling is the most important fishing tool in the South China Sea, but it is also the most damaging to fisheries and the marine environment (Yang, 1997). More numbers of young fish can be caught using stow net than by trawling (Zhang, 2014). Diving or snorkeling represent a good approach to study fish assemblages (Honda et al., 2013); however, this method depends on the water visibility is good enough. Gill nets were used in this study considering the complex habitats and low visibility in March and August. In the future, different methods may be used to study the connectivity, such as underwater visual census in appropriate months (Verweij et al., 2006; Hylkema et al., 2015). If possible, combining with the skill of otolith (Lueders-Dumont et al., 2018) would be another choice.

Coverage of coastal habitats and fish diversity is declining, with multiple ecological habitats requiring protection for the comprehensive management of marine biodiversity. Relevant research is required for rapid recovery of population structures. This study contributes towards advancing our understanding of fish ecology and connectivity among habitats. In particular, the connectivity of coastal habitats should be incorporated into management plans, as these habitats are already severely degraded. For example, there is *Eucheuma* Nature Reserve of Hainan Province in Wenchang area, however, the key protected objects in this reserve is *Eucheuma*, but not the habitats (Wu et al., 2017). Moreover, there are also other MPAs, such as Qinglangang Provincial Mangrove Nature Reserve and Tongguling National Nature Reserve in Wenchang area, while the former focuses on mangrove and the latter focuses on coral reef; both do not consider the connectivity between these habitats. Therefore, it is recommended that fish connectivity should be considered when designing MPAs or MPA network where possible.

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References

Bauer S, Hoye B J. 2014. Migratory animals couple biodiversity and ecosystem functioning worldwide. Science, 344(6179): 1242552, doi: 10.1126/science.1242552

Beck M W, Heck K L, Able K W, et al. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. Bioscience, 51(8): 633–641, doi: 10.1641/0006-3568(2001)051[0633:TICAMO]2.0.CO;2

Bell J D, Burchmore J J, Pollard D A. 1975. Feeding ecology of three sympatric species of leatherjackets (Pisces: Monacanthidae) from a *Posidonia* Seagrass Habitat in New South Wales. Australian Journal of Marine and Freshwater Research, 29(5): 631–643

Berkström C, Jörgensen T, Hellström M. 2013. Ecological connectivity and niche differentiation between two closely related fish species in the mangrove-seagrass-coral reef continuum. Marine Ecology Progress Series, 477: 201–215, doi: 10.3354/meps10171

Bond T, Langlois T J, Partridge J C, et al. 2018. Diel shifts and habitat associations of fish assemblages on a subsea pipeline. Fisheries Research, 206: 220–234, doi: 10.1016/j.fishres.2018.05.011

Brodie J E, Kroon F J, Schaffelke B, et al. 2012. Terrestrial pollutant runoff to the Great Barrier Reef: an update of issues, priorities and management responses. Marine Pollution Bulletin, 65(4–9): 81–100, doi: 10.1016/j.marpolbul.2011.12.012

Chen Mingru, Yang Shengyun. 2013. Fish Illustration of Taiwan Strait and Its Adjacent Waters (in Chinese). Beijing: China Science and Technology Press

Chen Shiquan, Wang Daoru, Wu Zhongjie, et al. 2015. Discussion of the change trend of the seagrass beds in the east coast of Hainan Island in nearly a decade. Marine Environmental Science, 34(1): 48–53

Costanza R, d'Arge R, de Groot R, et al. 1997. The value of the world's ecosystem services and natural capital. Nature, 387(6630): 253–260, doi: 10.1038/387253a0

de la Morinière E C, Pollux B J A, Nagelkerken I, et al. 2002. Post-settlement life cycle migration patterns and habitat preference of coral reef fish that use Seagrass and mangrove habitats as nurseries. Estuarine, Coastal and Shelf Science, 55(2): 309–321, doi: 10.1006/ecss.2001.0907

de la Morinière E C, Pollux B J A, Nagelkerken I, et al. 2003. Ontogenetic dietary changes of coral reef fishes in the mangrove-seagrass-reef continuum: stable isotopes and gut-content analysis. Marine Ecology Progress Series, 246: 279–289, doi: 10.3354/meps246279

Dorenbosch M, van Riel M C, Nagelkerken I, et al. 2004. The relationship of reef fish densities to the proximity of mangrove and seagrass nurseries. Estuarine, Coastal and Shelf Science, 60(1): 37–48, doi: 10.1016/j.ecss.2003.11.018

Du Jianguo, Ye Guanqiong, Zhou Qiulin, et al. 2015. Progress and prospects of coastal ecological connectivity studies. Acta Ecologica Sinica, 35(21): 6923–6933

General Administration of Quality Supervision, Inspection and Quarantine of the People's Republic of China, Standardization Administration of the People's Republic of China. 2007. GB/T 12763.6-2007 Specifications for oceanographic survey—Part 6: marine biological survey (in Chinese). Beijing: China Standards Press

He Xiuling, Ye Ning, Xuan Liqiang. 2003. Investigation of fishes in mangrove areas of Leizhou Peninsula. Journal of Zhanjiang Ocean University, 23(3): 3–10

Honda K, Nakamura Y, Nakaoka M, et al. 2013. Habitat use by fishes in coral reefs, seagrass beds and mangrove habitats in the Philippines. PLoS One, 8(8): e65735, doi: 10.1371/journal.pone.0065735

Hughes T P, Baird A H, Bellwood D R, et al. 2003. Climate change, human impacts, and the resilience of coral reefs. Science, 301(5625): 929–933

Hylkema A, Vogelaar W, Meesters H W G, et al. 2015. Fish species utilization of contrasting sub-habitats distributed along an ocean-to-land environmental gradient in a tropical mangrove and Seagrass Lagoon. Estuaries and Coasts, 38(5): 1448–1465, doi: 10.1007/s12237-014-9907-1

Kindlmann P, Burel F. 2008. Connectivity measures: a review. Landscape Ecology, 23(8): 879–890

Kopp D, Bouchon-Navaro Y, Louis M, et al. 2007. Diel differences in the seagrass fish assemblages of a Caribbean island in relation to adjacent habitat types. Aquatic Botany, 87(1): 31–37, doi: 10.1016/j.aquabot.2007.01.008

Krosby M, Tewksbury J, Haddad N M, et al. 2010. Ecological connectivity for a changing climate. Conservation Biology, 24(6): 1686–1689, doi: 10.1111/j.1523-1739.2010.01585.x

Liu Min, Chen Xiao, Yang Shengyun. 2013. Marine fishes of Southern Fujian, China: Volume 1 (in Chinese). Beijing: China Ocean Press

Lowe R J, Falter J L. 2015. Oceanic forcing of coral reefs. Annual Review of Marine Science, 7: 43–66, doi: 10.1146/annurev-marine-010814-015834

Lueders-Dumont J A, Wang X T, Jensen O P, et al. 2018. Nitrogen isotopic analysis of carbonate-bound organic matter in modern and fossil fish otoliths. Geochimica et Cosmochimica Acta, 224: 200–222, doi: 10.1016/j.gca.2018.01.001

Nagelkerken I. 2009. Evaluation of nursery function of mangroves and Seagrass beds for tropical decapods and reef fishes: patterns and underlying mechanisms. In: Nagelkerken I, ed. Ecological Connectivity Among Tropical Coastal Ecosystems. Dordrecht: Springer, 357–399

Nagelkerken I, Dorenbosch M, Verberk W C E P, et al. 2000a. Day-night shifts of fishes between shallow-water biotopes of a Caribbean bay, with emphasis on the nocturnal feeding of Haemulidae and Lutjanidae. Marine Ecology Progress Series, 194: 55–64, doi: 10.3354/meps194055

Nagelkerken I, Roberts C M, van der Velde G, et al. 2002. How important are mangroves and seagrass beds for coral-reef fish? The nursery hypothesis tested on an island scale. Marine Ecology Progress Series, 244: 299–305, doi: 10.3354/meps244299

Nagelkerken I, van der Velde G, Gorissen M W, et al. 2000b. Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. Estuarine, Coastal and Shelf Science, 51(1): 31–44, doi: 10.1006/ecss.2000.0617

Nakamura Y, Horinouchi M, Nakai T, et al. 2003. Food habits of fishes in a seagrass bed on a fringing coral reef at Iriomote Island, southern Japan. Ichthyological Research, 50(1): 15–22, doi: 10.1007/s102280300002

Nakamura Y, Sano M. 2004. Overlaps in habitat use of fishes between a seagrass bed and adjacent coral and sand areas at Amitori Bay, Iriomote Island, Japan: Importance of the seagrass bed as juvenile habitat. Fisheries Science, 70(5): 788–803, doi: 10.1111/j.1444-2906.2004.00872.x

Ogden J C. 1997. Ecosystem interactions in the tropical coastal seascape. In: Birkeland C, ed. Life and Death of Coral Reefs. New York: Chapman & Hall, 288–297

Pandit S N, Maitland B M, Pandit L K, et al. 2017. Climate change risks, extinction debt, and conservation implications for a threatened freshwater fish: carmine shiner (*Notropis percobromus*). Science of the Total Environment, 598: 1–11, doi: 10.1016/j.scitotenv.2017.03.228

Shi Fushan. 2005. The ecological studies on fishes in Dongzhaigang National Nature Reserve for Mangroves, Hainan (in Chinese) [dissertation]. Xiamen: Xiamen University

Shibuno T, Nakamura Y, Horinouchi M, et al. 2008. Habitat use patterns of fishes across the mangrove-seagrass-coral reef seascape at Ishigaki Island, southern Japan. Ichthyological Research, 55(3): 218–237, doi: 10.1007/s10228-007-0022-1

Shulman M J. 1985. Recruitment of coral reef fishes: effects of distribution of predators and shelter. Ecology, 66(3): 1056–1066, doi: 10.2307/1940565

Sichum S, Tantichodok P, Jutagate T. 2003. Diversity and assemblage patterns of juvenile and small sized fishes in the Nearshore habitats of the Gulf of Thailand. Raffles Bulletin of Zoology, 61(2): 795–809

Sivashanthini K, Abeyrami B. 2003. Length-weight relationship and relative condition of a silver biddy Gerres oblongus (Pisces: Perciformes) from the Jaffna lagoon, Sri Lanka. Indian Journal of Geo-Marine Sciences, 32(3): 252–254

Unsworth R K F, de Leon P S, Garrard S L, et al. 2008. High connectivity of Indo-Pacific seagrass fish assemblages with mangrove and coral reef habitats. Marine Ecology Progress Series, 353: 213–224, doi: 10.3354/meps07199

Unsworth R K F, Garrard S L, de León P S, et al. 2009. Structuring of Indo-Pacific fish assemblages along the mangrove-seagrass continuum. Aquatic Biology, 5: 85–95, doi: 10.3354/ab00139

Unsworth R K F, Wylie E, Smith D J, et al. 2007. Diel trophic structuring of seagrass bed fish assemblages in the Wakatobi Marine National Park, Indonesia. Estuarine, Coastal and Shelf Science, 72(1–2): 81–88, doi: 10.1016/j.ecss.2006.10.006

Verweij M C, Nagelkerken I, de Graaff D, et al. 2006. Structure, food and shade attract juvenile coral reef fish to mangrove and seagrass habitats: a field experiment. Marine Ecology Progress Series, 306: 257–268, doi: 10.3354/meps306257

Weinstein M P, Heck K L Jr. 1979. Ichthyofauna of seagrass meadows along the Caribbean coast of Panamá and in the Gulf of Mexico: composition, structure and community ecology. Marine Biology, 50(2): 97–107, doi: 10.1007/BF00397814

Wu Zhongjie, Chen Shiquan, Zhang Guangxing, et al. 2017. Distribution of resources, existing problems and protection countermeasures of Eucheuma nature reserve of Hainan Province. Wetland Science & Management, 13(2): 38–41

Wu Zhongjie, Wu Rui, Wang Daoru, et al. 2011. A preminary study on the status of coral reef health in the southeast coastal regions of Hainan Island. Chinese Journal of Tropical Crops, 32(1): 122–130

Yang Lin. 1997. The influence of the trawl and stow net fishing gear on fishery resources in the South China sea. Fisheries Science & Technology, (3): 4–6

Yang Zhongyang, Xue Yang, Su Shaofeng, et al. 2017. The survey on plant community characteristics of Bamenwan mangroves in Wenchang City. Chinese Journal of Tropical Agriculture, 37(1): 48–52, 59

Zhang Min. 2014. The investigation of stow net in Yellow and Bohai sea and the stow net operation performance evaluation (in Chinese) [dissertation]. Qingdao: Ocean University of China

Appendix:

Table A1. The number of individuals of fish in mangrove, seagrass bed and coral reef in Wenchang, China

Species	Common name	Family	Number of individuals		
			Mangrove	Seagrass bed	Coral reef
Cynoglossus macrolepidotus	Tonguesole	Cynoglossidae	0	0	1
Cynoglossus joyneri	Red tonguesole	Cynoglossidae	2	0	0
Brachirus orientalis	Oriental sole	Soleidae	9	1	0
Pardachirus pavoninus	Peacock sole	Soleidae	1	0	0
Sardinella zunasi	Japanese sardinella	Clupeidae	5	9	1
Konosirus punctatus	Dotted gizzard shad	Clupeidae	0	4	0
Thrissa setirostris	Longjaw thryssa	Engraulidae	0	1	0
Dasyatis akajei	Whip stingray	Dasyatidae	1	0	1
Siganus fuscescens	Mottled spinefoot	Siganidae	260	48	104
Siganus guttatus	Orange-spotted spinefoot	Siganidae	14	0	1
Leiognathus brevirostris	Shortnose ponyfish	Leiognathidae	5	1	4
Leiognathus equulus	Common ponyfish	Leiognathidae	202	11	1
Leiognathus berbis	Berber ponyfish	Leiognathidae	1	0	0
Nuchequula nuchalis	Spotnape ponyfish	Leiognathidae	14	1	3
Gazza minuta	Toothpony	Leiognathidae	15	0	0
Gerres oblongus	Slender silver-biddy	Gerreidae	200	53	1
Gerres filamentosus	Whipfin silver-biddy	Gerreidae	48	34	0
Gerres erythrourus	Deep-bodied mojarra	Gerreidae	0	5	0
Gerres limbatus	Saddleback silver-biddy	Gerreidae	0	1	0
Gerres macracanthus	Longspine silverbiddy	Gerreidae	15	0	0
Upeneus tragula	Freckled goatfish	Mullidae	74	2	3
Upeneus sulphureus	Sulphur goatfish	Mullidae	1	0	0
Parupeneus ciliatus	Whitesaddle goatfish	Mullidae	2	0	1
Parupeneus indicus	Indian goatfish	Mullidae	0	1	2
Parupeneus multifasciatus	Manybar goatfish	Mullidae	0	0	1
Terapon jarbua	Jarbua terapon	Terapontidae	15	66	39
Therapon oxyrhynchus	Sharpbeak terapon	Terapontidae	2	0	0
Terapon theraps	Largescaled terapon	Terapontidae	2	0	0
Pelates quadrilineatus	Fourlined terapon	Terapontidae	218	35	0
Scarus frenatus	Bridled parrotfish	Scaridae	0	0	4
Scarus ghobban	Blue-barred parrotfish	Scaridae	6	0	5
Leptoscarus vaigiensis	Marbled parrotfish	Scaridae	1	0	0
Sillago maculata	Trumpeter whiting	Sillaginidae	98	12	30
Sillago japonica	Japanese sillago	Sillaginidae	38	1	0
Lutjanus malabaricus	Malabar blood snapper	Lutjanidae	0	0	1
Lutjanus russellii	Russell's snapper	Lutjanidae	12	3	6
Lutjanus fulviflamma	Dory snapper	Lutjanidae	2	1	17
Lutjanus argentimaculatus	Mangrove red snapper	Lutjanidae	1	0	1
Lethrinus haematopterus	Chinese emperor	Lethrinidae	0	1	8
Lethrinus ornatus	Ornate emperor	Lethrinidae	3	0	1
Lethrinus nebulosus	Spangled emperor	Lethrinidae	10	1	1
Lethrinus harak	Thumbprint emperor	Lethrinidae	0	0	1
Scolopsis monogramma	Monogrammed monocle bream	Nemipteridae	17	0	10
Scolopsis vosmeri	Whitecheek monocle bream	Nemipteridae	2	0	4
Scolopsis lineata	Striped monocle bream	Nemipteridae	0	0	3
Scolopsis taenioptera	Lattice monocle bream	Nemipteridae	3	0	0
Pentapodus setosus	Butterfly whiptail	Sparidae	1	0	0
Acanthopagrus schlegelii	Blackhead seabream	Sparidae	0	0	7
Acanthopagrus chinshira	Okinawan yellow-fin seabream	Sparidae	1	0	0
Rhabdosargus sarba	Goldlined seabream	Sparidae	0	1	0
Labracinus cyclophthalmus	Fire-tail devil	Pseudochromidae	0	0	1

to be continued

Continued from Table A1

Species	Common name	Family	Number of individuals		
			Mangrove	Seagrass bed	Coral reef
Epinephelus quoyanus	Longfin grouper	Serranidae	3	0	21
Epinephelus fasciatomaculosus	Rock grouper	Serranidae	2	0	1
Epinephelus trimaculatus	Threespot grouper	Serranidae	3	0	1
Rachycentron canadum	Cobia	Rachycentridae	0	0	2
Sphyraena flavicauda	Yellowtail barracuda	Sphyraenidae	1	0	3
Sphyraena jello	Pickhandle barracuda	Sphyraenidae	4	2	0
Sphyraena barracuda	Great barracuda	Sphyraenidae	17	1	0
Monodactylus argenteus	Silver moony	Monodactylidae	3	0	1
Drepane punctata	Spotted sicklefish	Drepaneidae	0	0	1
Pennahia argentata	Silver croaker	Sciaenidae	1	0	1
Nibea albiflora	Yellow drum	Sciaenidae	1	4	0
Dendrophysa russelii	Goatee croaker	Sciaenidae	0	2	0
Trachinotus blochii	Snubnose pompano	Carangidae	0	0	1
Trachinotus baillonii	Pompano	Carangidae	1	0	0
Scomberoides commersonnianus	Talang queenfish	Carangidae	0	0	1
Scomberoides lysan	Doublespotted queenfish	Carangidae	2	0	0
Caranx papuensis	Brassy trevally	Carangidae	0	0	1
Caranx sexfasciatus	Bigeye trevally	Carangidae	3	0	0
Alectis ciliaris	African pompano	Carangidae	1	0	0
Selaroides leptolepis	Yellowstripe scad	Carangidae	1	0	0
Trachurus japonicus	Japanese jack mackerel	Carangidae	0	2	0
Eleutheronema tetradactylum	Fourfinger threadfin	Polynemidae	0	0	2
Halichoeres nigrescens	Bubblefin wrasse	Labridae	34	5	3
Halichoeres marginatus	Dusky wrasse	Labridae	0	0	1
Choerodon schoenleinii	Blackspot tuskfish	Labridae	2	1	2
Stethojulis strigiventer	Three-ribbon wrasse	Labridae	14	0	1
Stethojulis interrupta	Cutribbon wrasse	Labridae	8	0	0
Bodianus sp. 1	hogfish	Labridae	0	0	1
Bodianus sp. 2	hogfish	Labridae	1	0	0
Hemigymnus fasciatus	Barred thicklip	Labridae	0	0	1
Hemigymnus melapterus	Blackeye thicklip	Labridae	0	0	3
Cheilinus chlorourus	Floral wrasse	Labridae	0	0	3
Pempheris schwenkii	Silver sweeper	Pempheridae	0	0	16
Oreochromis sp. 1	tilapia	Cichlidae	1	2	0
Oreochromis sp. 2	tilapia	Cichlidae	0	3	0
Oreochromis sp. 3	tilapia	Cichlidae	1	0	0
Ambassis kopsii	Singapore glassy perchlet	Ambassidae	8	33	0
Ambassis urotaenia	Banded-tail glassy perchlet	Ambassidae	173	0	0
Ambassis interrupta	Long-spined glass perchlet	Ambassidae	2	0	0
Scatophagus argus	Spotted scat	Scatophagidae	2	0	0
Selenotoca multifasciata	Spotbanded scat	Scatophagidae	3	0	0
Glossogobius bicirrhosus	Bearded flathead goby	Gobiidae	11	0	0
Psammogobius biocellatus	Sleepy goby	Gobiidae	44	0	0
Glossogobius giuris	Tank goby	Gobiidae	5	0	0
Acentrogobius caninus	Tropical sand goby	Gobiidae	9	0	0
Oligolepis fasciatus	Platband goby	Gobiidae	2	0	0
Oligolepis acutipennis	Sharptail goby	Gobiidae	14	0	0
Amblygobius albimaculatus	Butterfly goby	Gobiidae	1	0	0
Amblygobius phalaena	Whitebarred goby	Gobiidae	1	0	0
Yongeichthys criniger	Horny goby	Gobiidae	77	1	0
Acentrogobius viridipunctatus	Spotted green goby	Gobiidae	2	0	0
Acentrogobius caninus	Tropical sand goby	Gobiidae	3	0	0
Synechogobius ommaturus	Asian freshwater goby	Gobiidae	48	0	0
Rhinogobius davidi	Stream goby	Gobiidae	1	0	0

to be continued

Continued from Table A1

Species	Common name	Family	Number of individuals		
			Mangrove	Seagrass bed	Coral reef
Chaenogobius annularis	Forktongue goby	Gobiidae	3	0	0
Exyrias puntang	Puntang goby	Gobiidae	6	0	0
Favonigobius reichei	Indo-Pacific tropical sand goby	Gobiidae	15	0	0
Oxyurichthys ophthalmonema	Eyebrow goby	Gobiidae	200	0	0
Oxyurichthys tentacularis	Tentacle goby	Gobiidae	108	0	0
Oxyurichthys cornutus	Horned tentacle goby	Gobiidae	8	0	0
Cryptocentroides insignis	Insignia prawn-goby	Gobiidae	0	1	0
Amblychaeturichthys hexanema	Pinkgray goby	Gobiidae	2	0	0
Taeniamia fucata	Orangelined cardinalfish	Apogonidae	1	0	0
Taeniamia lineolata	Shimmering cardinal	Apogonidae	8	0	0
Ostorhinchus cookii	Cook's cardinalfish	Apogonidae	23	0	0
Salarias fasciatus	Jewelled blenny	Blenniidae	3	0	0
Chaetodon auriga	Threadfin butterflyfish	Chaetodontidae	1	0	0
Chaetodon auripes	Oriental butterflyfish	Chaetodontidae	0	0	6
Eleotris fusca	Dusky sleeper	Eleotridae	2	0	0
Eleotris melanosoma	Broadhead sleeper	Eleotridae	3	0	0
Valenciennea sp. 1	Sleeper	Eleotridae	1	0	0
Ophiocara porocephala	Northern mud gudgeon	Eleotridae	1	0	0
Butis melanostigma	Black-spotted gudgeon	Eleotridae	1	0	0
Stegastes fasciolatus	Pacific gregory	Pomacentridae	17	0	0
Neoglyphidodon melas	Bowtie damselfish	Pomacentridae	13	0	0
Abudefduf vaigiensis	Indo-Pacific sergeant	Pomacentridae	1	0	0
Pomadasys maculatus	Saddle grunt	Haemulidae	1	1	0
Pomadasys kaakan	Javelin grunter	Haemulidae	3	1	0
Platax orbicularis	Orbicular batfish	Ephippidae	1	0	0
Rastrelliger kanagurta	Indian mackerel	Scombridae	0	1	0
Gymnothorax isingteena	Spotted moray	Muraenidae	2	0	0
Pisodonophis boro	Rice-paddy eel	Ophichthidae	3	0	0
Ophichthus macrochir	Bigfin snake eel	Ophichthidae	1	0	0
Muraenichthys gymnopterus	Snake eel	Ophichthidae	1	0	0
Plotosus lineatus	Striped eel catfish	Plotosidae	4	5	1
Diodon holocanthus	Longspined porcupinefish	Diodontidae	0	0	1
Monacanthus chinensis	Fan-bellied leatherjacket	Monacanthidae	17	5	0
Stephanolepis cirrhifer	Threadsail filefish	Monacanthidae	0	1	2
Triacanthus biaculeatus	Short-nosed tripodfish	Triacanthidae	19	24	0
Lactoria cornuta	Longhorn cowfish	Ostraciidae	1	0	0
Takifugu alboplumbeus	Pufferfish	Tetraodontidae	3	0	0
Synodus variegatus	Variegated lizardfish	Synodontidae	2	0	1
Trachinocephalus myops	Snakefish	Synodontidae	2	0	0
Minous trachycephalus	Striped stingfish	Synanceiidae	1	0	3
Onigocia macrolepis	Notched flathead	Platycephalidae	1	0	0
Scorpaenopsis neglecta	Yellowfin scorpionfish	Scorpaenidae	1	0	0
Scorpaenodes guamensis	Guam scorpionfish	Scorpaenidae	0	0	3
Mugil cephalus	Flathead grey mullet	Mugilidae	314	360	89
Megalops cyprinoides	Indo-Pacific tarpon	Megalopidae	3	0	0
Elops machnata	Tenpounder	Elopidae	7	1	1
Hyporhamphus dussumieri	Dussumier's halfbeak	Hemiramphidae	6	1	0
Hypoatherina tsurugae	Silverside	Atherinidae	2	4	0
Fistularia commersonii	Bluespotted cornetfish	Fistulariidae	0	0	1