Habitat function of intertidal seagrass beds for fishes in the Philippines
(魚類の生息場所としてのフィリピンの 潮間帯海草藻場の機能)

Anabelle Dece A. Espadero

Seagrasses are marine flowering plants with underground roots and rhizome systems, which form extensive monospecific or mixed species beds or meadows (Green and Short, 2003; Short et al., 2007). Seagrass beds are widely distributed along the protected coastlines of temperate and tropical regions (Short et al., 2007). A total of 72 seagrass species have been identified worldwide (Short et al., 2011). Of these, 25 are found in the tropical Indo-Pacific, which supports the highest seagrass biodiversity (Short et al., 2011), and 18 species of those have been recorded in the Philippines (Fortes, 2013).

Seagrass beds are among the most productive coastal habitats, and they serve as important nursery and foraging grounds for a diverse array of marine organisms, including commercially important species (Krumme, 2009; Nagelkerken, 2009). In the Indo-Pacific region, seagrass beds harbor high densities of juvenile Lethrinidae, Lutjanidae, and Scaridae, which seek food and the refuge provided by the complex structure of seagrass leaves, where the predation risk is low and foraging is optimized, before these fish move to coral reefs via ontogenetic migration (Dorenbosch et al., 2005; Nakamura et al., 2012). Moreover, large predatory fishes, such as *Hemiramphus far* and *Caranx melampygus*, are thought to migrate from nearby coral reefs to seagrass beds to feed on the high abundance of these small fishes (Unsworth et al., 2007). In the Caribbean, *Haemulon parrai*, *Lutjanus apodus*, and *Ocyurus chrysurus* depend highly on seagrass beds compared to coral reefs as nursery habitat (Nagelkerken et al., 2001; Verweij et al., 2008). The use of tropical seagrass beds as a foraging ground has been studied extensively in the Caribbean seas, where Lutjanidae and Haemulidae emerge from their daytime resting sites, such as mangroves and coral reefs, and migrate at night to seagrass beds to feed on the high abundance of prey items, including small crustaceans and shellfish (Ogden and Ehrlich, 1977; Nagelkerken et al., 2000), which are sustained by the high growth rates of epiphytes.

Most studies highlighting the importance of tropical seagrass beds as nursery and foraging grounds have been conducted on subtidal beds in the Caribbean (Nagelkerken et al., 2002; Verweij et al., 2008), where small tidal amplitudes result in continual non-exposure of the beds (Krumme, 2009). In contrast, tropical Indo-Pacific seagrass beds are typically subjected to much wider tidal ranges (Krumme, 2009), and can be classified as intertidal or subtidal depending on the length of time they are exposed at low tide (Unsworth et al., 2007). Since intertidal seagrass beds occur at the land-sea interface, they are directly affected by many human-related activities, such as agricultural runoff, coastal development, and intensive fishing activities (Waycott et al., 2009; Unsworth and Cullen, 2010). As resilient seagrasses are to disturbances, the current rate of environmental changes is much faster than in previous decades and is possibly too fast for seagrasses to adapt (Orth et al., 2006). Moreover, intertidal seagrass habitats are often neglected having disappeared without noticed as a consequence (Green and Short, 2003). Although the importance of subtidal seagrass beds for fishes is widely recognized, only a few studies have focused on tropical intertidal seagrass beds. Consequently, their habitat function is still largely unknown. Hence, it is critical to address this research gap for the conservation and management of these habitats.

This thesis tried to investigate the important habitat function of tropical intertidal seagrass for fishes in the Indo-Pacific region, particularly in the Philippines, which is a hotspot of reef fish biodiversity (Carpenter and Springer, 2005). The first chapter aimed to determine the occurrence and foraging activities of fishes in intertidal seagrass beds on a rising tide. The second chapter further investigated the possible drivers of fish migration to intertidal seagrass beds, including what type of fishes occur in the beds and if do they differ from those in subtidal seagrass beds. Overall, this thesis provides confirmation that intertidal seagrass beds is an essential habitat for coastal fishes and has significant implications for coastal management policies, as their conservation will assist in sustaining coastal fish biodiversity and fishery resources.

Chapter 1: Tropical intertidal seagrass beds: An overlooked foraging habitat for fishes revealed by underwater videos

Intertidal seagrass beds occur throughout the Indo-Pacific region. Some studies suspect that small fishes and their piscivorous predators moved to intertidal seagrass beds for foraging when inundated. For example, Unsworth et al. (2007) identified transient fish species in intertidal seagrass beds relative to various tide heights at Hoga Island, Indonesia, believing that the fishes had migrated from nearby subtidal seagrass and coral habitats to forage. Davis et al. (2017) reported that some coral reef fishes in southeast Queensland, Australia, utilized subtidal and intertidal seagrass beds as corridors when migrating from offshore coral reefs to coastal mangroves during flood tides, and Polte and Asmus (2006) found that temperate intertidal seagrass beds were visited by many juvenile fish species, probably due to high prey abundance providing greater foraging opportunities. However, direct qualitative and quantitative evidence showing fishes engaged in foraging activities in tropical intertidal seagrass is lacking.

This chapter aimed to assess the feeding behavior of juvenile fish communities during an incoming tide at two intertidal seagrass bed sites in northern Mindanao, Philippines (i.e., Plaridel and Laguindingan), during both wet (December 2017 to January 2018) and dry seasons (April to May 2018), by deploying remote underwater video cameras. Three or four video deployments were conducted simultaneously in the intertidal seagrass beds over two consecutive census days at each site. The cameras (GoPro Hero3 with BacPac batteries) were deployed randomly in different areas each day, being positioned at least 50 m apart. Seven replicate deployments were made in the wet season and six in the dry season at each site, a total of 26 deployments for both sites. All video equipment was set up during lowest low tide and began recording simultaneously when the tide height reached 0.3 m (fully submerging the camera).

Results of the study showed 59 fish species (23 families) were recorded in all 26 video deployments (53 species in 23 families at Plaridel, 37 species in 17 families at Laguindingan). Video footage (3 h) revealed nearly half of the recorded fish species arrived within 30 min from the start of recording, and that species richness gradually increased with the rising tide, reaching 80% of recorded species within 120 min at both sites in both seasons. Three main fish behaviors were observed and categorized, i.e. feeding, swimming, and unidentified (motionless or very slowly swimming but not seen in the act of capturing prey and picking behavior). Most fish species recorded showed feeding behaviors as early as tide started to inundate the beds, particularly, small juveniles (< 10 cm total length) of labrids, lethrinids, lutjanids, and siganids were most abundant in all video recordings. Large juveniles (> 10 cm total length) of the latter three families were first to invade intertidal seagrass beds with incoming tides, whereas those of Labridae were more abundant in later stages of the tidal cycle (120 min from the start of recording). However, the timing of feeding behaviors exhibited by those large juveniles also differ, i.e. labrids, lethrinids, and lutjanids tend to feed at later tides, while siganids fed on the onset of recording. Furthermore, the timing of feeding for benthic-invertebrate feeders such as *Choerodon anchorago*, *Halichoeres argus, Lethrinus harak*, and *Lutjanus fulviflamma* were species-specific, while that of herbivorous species *Siganus fuscescens* and *S. guttatus* fed throughout the incoming tide. In addition, piscivorous *Cheilio inermis* were also observed feeding throughout the tide cycle, while *Sphyraena barracuda* did not exhibit any direct feeding behavior but changing body color patterns were recorded whilst remaining motionless close to seagrass leaves, possibly preparing for an ambush attack.

In this chapter, the occurrence and foraging behavior exhibited by those identified fishes in intertidal seagrass beds demonstrated one of the critical habitat functions of intertidal seagrass beds for fishes which is a foraging ground for a diverse array of fish species in juvenile stage, including some fishery target families (Lethrinidae, Lutjanidae and Siganidae). This chapter is the first to provide detailed quantitative and qualitative dataset examining behaviors of fishes in tropical intertidal seagrass beds during an incoming tide.

Chapter 2: Tropical intertidal seagrass beds as fish habitat: Similarity of fish assemblages between intertidal and subtidal seagrass beds in the Philippines

A number of fish species utilize temperate or tropical seagrass bed habitats. Pollard's (1984) worldwide review of studies of such, most having been conducted in temperate regions, found that seagrass bed fish assemblages commonly comprised permanent residents (remaining in seagrass beds throughout their life cycle), seasonal residents (utilizing seagrass beds as a nursery), transients (visiting seagrass beds during foraging over a variety of habitats), and occasional migrants (appearing only occasionally in seagrass beds). Although these habitat use patterns by fishes have been recognized most often in temperate subtidal seagrass beds, some permanent residents (e.g. gobiids and syngnathids) and transient fishes (e.g. mugilids), are also known to occur in temperate intertidal beds (Jenkins et al., 1997; Polte and Asmus, 2006). Over the past 20 years, several studies of fishes in tropical subtidal seagrass beds have found similar patterns of habitat use. In the Indo-Pacific, seagrass beds function as a permanent habitat for *Leptoscarus vaigiensis* and *Calotomus spinidens* (Nakamura and Tsuchiya, 2008; Lee et al., 2016), as well as foraging grounds for mullids (Nakamura and Tsuchiya, 2008).

Although Chapter 1 confirmed the vital habitat function of tropical intertidal seagrass beds, as a foraging habitat for some fishes, two critical questions were left unanswered: (1)

What fishes occur in intertidal seagrass beds and do they differ from those in subtidal seagrass beds? (2) What are the possible drivers of fish migration to intertidal seagrass beds?

This study was conducted at the same study sites in Chapter 1. Fish samples were collected from four habitat types, using a 7.5 × 1 m beach seine net (mesh size 5 mm, mouth opening 3 m): intertidal seagrass beds, subtidal seagrass beds, intertidal bare-sand areas, and subtidal bare-sand areas. Sampling was conducted during the wet (December and January) and dry seasons (April and May) for two consecutive years, 2018 and 2019. Ten replicate tows (each 20 m, covering a total area of 60 m^2 per tow) separated from each other by at least 10 m were conducted between 0600 h and 1600 h in each seagrass bed and bare-sand area at each site on three consecutive days during each season in both years. Since fish assemblage structures may change with tide level (Unsworth et al., 2007), all tows in the four habitats were conducted at a similar tide level (ca. 60 cm). At this level in the subtidal habitats, intertidal seagrass beds were already inundated, allowing fish movement from subtidal habitats, thereby avoiding aggregations of fishes in subtidal habitats. In fact, many fishes occurred in the intertidal seagrass beds when the tide reached ca. 60 cm at the study sites (Chapter 1) (Espadero et al., 2020). After each tow, collected fishes were placed immediately into labeled plastic bags and stored in a cooler box with crushed ice. In the laboratory, the fish samples were sorted, counted, and identified to the lowest possible taxon, following Nakabo (2002).

Since several benthivorous fish species have been previously recorded foraging in intertidal seagrass beds at the study sites (Chapter 1) (Espadero et al., 2020), four of them, *Halichoeres argus, H. papilionaceous, Lethrinus harak,* and *Parupeneus barberinus*, which were common at both sites and all collected in the intertidal seagrass beds at each site, were subjected to gut content analysis (up to 30 individuals for each species in each site). To investigate whether the densities of potentially important food items for these benthivorous fishes (e.g., crustaceans, molluscs, and polychaetes) were sufficiently high in the intertidal seagrass beds, compared with adjacent subtidal seagrass beds, and intertidal and subtidal bare-sand areas, epifauna (invertebrates living on seagrass leaves) were collected from four randomly selected points located at least 10 m apart in the intertidal and subtidal beds in January 2018, using a 15 × 15 cm hand-closing net (mesh size 0.4 mm, length 35 cm). In the laboratory, each invertebrate sample was sorted, counted, and identified to the lowest taxon, following Nakamura and Sano (2005), using a binocular microscope.

Results of the study showed a total of 5559 individuals belonging to 135 species in 39 families were collected across all four habitats at Plaridel and Laguindingan. Of these, 109 species (33 families) were recorded from the intertidal and subtidal seagrass beds, 81 species (29 families) from the intertidal beds, and 80 species (25 families) from the subtidal beds. Fifty-two species (18 families) or about 65% overlapped between the intertidal and subtidal seagrass beds. The species richness and abundance of both residents and visitors between the two seagrass habitats not differing substantially (although significantly higher than in intertidal and subtidal bare-sand areas), as many site-attached residents appeared to remain in the intertidal beds during low tide. Benthic-invertebrate feeders, including juveniles of commercially important species, dominated intertidal seagrass beds, comprising >70% of species richness and abundance. Four of them (*Halichoeres argus, H. papilionaceous, Lethrinus harak,* and *Parupeneus barberinus*) fed primarily on small benthic crustaceans (i.e., harpacticoid copepods and amphipods) and polychaetes. Furthermore, the densities of collected epifauna such as small and large benthic crustaceans, molluscs, and polychaetes were significantly higher in the intertidal and subtidal seagrass beds than in the surrounding bare-sand areas.

This chapter demonstrated that in addition to intertidal seagrass beds functioning as a foraging grounds for many visiting fishes because of its high prey abundance, the beds also provide a permanent habitat for resident species. Moreover, this chapter provides a comprehensive quantitative dataset investigating the fish assemblage structure in tropical intertidal seagrass beds with a detailed comparison to subtidal seagrass beds and the surrounding bare-sand areas.

Appendices

Appendices comprised of schematic illustrations of video setup and fish species occurrence in intertidal seagrass beds during flood tides (Chapter 1), fish species occurrence in intertidal and subtidal seagrass beds during low and high tide phase (Chapter 2), and photographs of the 143 identified fish species, including species that have only been identified to genus level, following the photo-documentation methods of Motomura and Ishikawa (2013).

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