Fish Assemblage Structures in Intertidal and Subtidal Seagrass Habitats in Trang Province, Southern Thailand

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ABSTRACT

As a first step to clarify the functions of intertidal seagrass habitats in a coastal ecosystem, for which information is still scarce to date, we investigated fish assemblage structures in these habitats during the daytime at Trang, Thailand, in March, June, September 2017 and December 2018, and compared them with those in nearby subtidal seagrass habitats as well as adjacent sand/mud flats. Both intertidal and subtidal seagrass habitats as well as intertidal sand/mud flats, supported fish assemblages with high species diversity, with total species numbers ranging from 36 to 41 in the former, and from 35 to 55 in the the latter. On the other hand, species diversity in subtidal open sand/mud flats was relatively lower, with a total species numbers of 21. Total fish abundances showed similar patterns in both intertidal and subtidal seagrass habitats. Dominant species such as *Siganus canaliculatus, Petroscirtes variabilis* and *Monacanthus chinensis* were common in these habitats. In sand/mud flats, *Acanthosphex leurynnis, Siganus canaliculatus* and *Sillago sihama* were dominant species. The similarity in fish assemblages between subtidal and intertidal seagrass habitats may be due to prey abundance patterns, while other factors could also influence fish assemblage structures in sand/mud flats. These findings suggest that both intertidal seagrass and open sand/mud flats are habitats with high fish diversity and abundances and should be considered in the establishment of management programs for coastal ecosystems.

Keywords: Fish assemblage, Food resources, Intertidal seagrass, Thailand

INTRODUCTION

It is widely acknowledged that seagrass habitats are vital for supporting a large number of fish and providing nursery grounds for the juveniles of various species including those targeted by fisheries (e.g., Dorenbosch *et al*., 2005; Nakamura and Tsuchiya, 2008; Nordlund *et al*., 2018; Unsworth *et al*., 2018). These habitats are crucial for maintaining high biodiversity within coastal ecosystems and are beneficial to local fisheries (e.g., Duffy, 2006; Sano *et al*., 2008; Saenger *et al*., 2013). While such conclusions have predominantly been drawn from studies of subtidal seagrass systems, whether they apply to intertidal seagrass systems remains uncertain. This is due to the paucity of detailed ecological information on intertidal seagrass habitats, although some studies exist (e.g., Polte and Asmus, 2006; Horinouchi *et al*., 2016; Espadero *et al*., 2020). If intertidal seagrass habitats exhibit similar ecological characteristics to their subtidal counterparts, protecting these habitats could enhance

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Received 16 January 2024 / Accepted 23 May 2024

biodiversity and support sustainable fisheries in coastal regions, especially since intertidal seagrass beds are prevalent in the tropical Indo-Pacific (Krumme, 2009).

Intertidal zones, the land-sea interface are highly susceptible to global and local alterations due to human activities (Halpern *et al*., 2008; Jutagate *et al*., 2009). Global seagrass threats, including sediment and nutrient runoff, physical disturbance, invasive species, disease, commercial fishing practices, aquaculture, overgrazing, algal blooms, and global warming, cause seagrass declines at scales of square meters to hundreds of square kilometers (Orth *et al*., 2006). In southern Thailand, many residents enter the intertidal zones to collect fish and macroinvertebrates, including molluscs and crustaceans. Such fishing activities often disturb intertidal substrata, including seagrass habitats severely. For example, fishers dig deep holes in the substrate and put poles in the holes to fix the gill net, with one end being tied to the poles. Such holes sometimes cause severe substrate erosion, leading to the complete removal of seagrasses there (M. Horinouchi per. obs.). In addition, they easily abandon the entangled nets at fishing sites. The abandoned nets often cause ghost fishing, which leads to severe negative impacts on overall coastal ecosystems. Recently, such disturbance has increased with an increase in the local population in coastal areas of Thailand (World Bank, 2006). Therefore, the establishment of conservation policies based on scientific information on the roles/functions of intertidal seagrass habitats (and preferably, also other intertidal habitats) is urgently needed to keep coastal ecosystems healthy. However, as described above, the knowledge of the intertidal seagrass habitats is still scarce to date.

The hypothesis examined in the present study is as follows: intertidal seagrass habitats support fish assemblages with high species diversity and abundances as subtidal seagrass habitats do. To examine this hypothesis, we investigated fish assemblages in intertidal and subtidal seagrass habitats and also nearby open sand/mud flats. Besides, we investigated prey abundances in these habitats to examine whether or not prey abundance patterns were responsible for observed patterns in fish assemblage structures.

MATERIALS AND METHODS

Study site

The study was carried out at Ban Pakmeng (hereafter, abbreviated as PM when needed), Ban Had Yao (HY) and Ban Pakklong (PK), Trang Province, southern Thailand (Figure 1). In PM and HY, the seagrass beds and adjacent open sand/mud flats exist in the intertidal zones. In contrast, in PK, the seagrass bed and adjacent open sand/mud flat exist in the subtidal zone. The habitats in the PM and HY were targeted in this study while those in the PK were regarded as control. All study sites are located near the mouths of mangrove creeks and the *Enhalus acoroides* was the dominant species in seagrass beds. Based on seasonal rainfall patterns, a short dry season (January through March or April) and a long rainy season (April or May through December) were recognized in the study area, the latter being accompanied by strong southwest monsoon winds.

Habitat complexity

During each census, the structural complexity of *Enhalus acoroides* in each seagrass bed was measured. Five 50×50 cm quadrats were randomly established within the seagrass bed, and the number of *E. acoroides* shoots within each quadrat was counted. Shoot density is expressed as the mean number of shoot per 0.25 m^2. Additionally, ten seagrass leaves were randomly selected, and their lengths were measured with a scaled tape. Leaf height is expressed as the mean leaf length.

Simultaneously, environmental factors such as water temperature (°C), salinity, and dissolved oxygen ($mg \cdot L^{-1}$) were measured. Sediment grain size was also investigated in each habitat at every site. The values of these factors are shown in the database (https://nrei.rmutsv.ac.th/ruts/en/home/).

Prey abundance

Fish species were assigned to seven trophic groups based on dietary data published in precedent studies conducted near the study area, such as Satapoomin and Satapoomin (2005), Tongnunui *et al*. (2005), Horinouchi *et al*. (2012), Yoknoi *et al*.

(2019) and online sources such as FishBase.org (Froese and Pauly, 2022). These trophic groups include planktonic animal feeders, small benthic/epiphytic crustacean feeders, large benthic/epiphytic crustacean feeders, detritus feeders, polychaete feeders, mollusc feeders and fish feeders. Food abundances can strongly influence fish occurrence patterns (e.g., Horinouchi *et al*., 2012), so the abundances of main food items, excluding fish, such as planktonic animals, small or large benthic/epiphytic crustaceans, polychaetes, molluscs and detritus, were investigated in each habitat as follows:

Planktonic animals were collected using a plankton net equipped with a flow meter (45 cm mouth diameter, 180 cm long, and 315 μm mesh size). Five replicates of nettings were conducted in each habitat at each site on each fish census occasion. The collector held the net just above the sand/mud substratum or seagrass canopy, and walked against the flow from a randomly established starting point within each habitat as fast as possible, checking the flow meter to confirm that the final rounds reached 200. The net content was retrieved and fixed in 5% buffered formalin on the spot. Planktonic copepods and shrimps were counted under a binocular microscope in the laboratory. The densities of these prey items were expressed as the number of individuals per m^3 of seawater.

We measured the ignition loss of the sediment samples as approximate estimates of the detritus content. A cylindrical core sampler (8 cm in diameter) was vertically inserted into the sediment to a depth of 20 cm at a randomly established point in each habitat and then pulled up. The sediment in the core sampler was retrieved and put in a plastic container. This procedure was conducted five times in each habitat at each site on each fish census occasion. In the laboratory, a sub-sample of each sediment sample was first dried at 100 °C for 24 h. The dried sub-sample was weighed and then re-weighed after being combusted at 700 °C for 4 h. The percentage of the lost weight to the original weight of the dried sample was calculated.

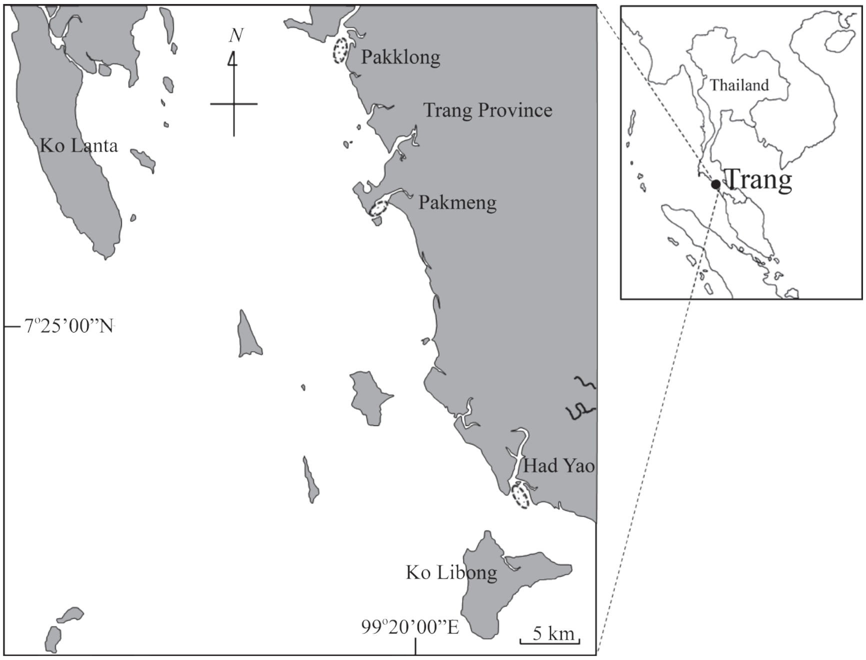

Figure 1. Map depicting study sites of seagrass *Enhalus acoroides* beds and the adjacent open sand/mud areas in the intertidal zones at Pakmeng and HadYao, as well as the subtidal zone at Pakklong (highlighted with broken lines).

Benthic invertebrates in the sediment were also collected using the same core sampler and procedure described above. Each sediment sample was put in a plastic container on the spot within the day and was sieved through a 0.5 mm mesh in the laboratory. The remaining material on the mesh was then preserved in 10% buffered formalin until analysis. Small crustaceans (gammaridean amphipods), large crustaceans (caridean shrimps and crabs), polychaetes and molluscs within each sample were counted under a binocular microscope in the laboratory. The densities of these prey items were expressed as numbers of individuals per m^3 of sediment.

Epiphytic prey animals were collected using a scoop net (30 cm mouth diameter, 40 cm long, and 210 µm mesh size). From above the seagrass canopy at a randomly established point in each habitat, the net was gently sunk to the bottom. The seagrass shoots covered by the net were then cut at the point just above the bottom surface, retrieved, and put in a plastic container in a cooler box with ice on the spot. This procedure was conducted five times in each habitat at each site on each fish census occasion. Within the day, small crustacean (gammaridean amphipods, harpacticoid copepods), large crustacean (caridean shrimps), and polychaetes on seagrass leaves in each sample were counted under a binocular microscope in the laboratory. Densities of these prey items were expressed as numbers of individuals per scoop net operation.

Fish census

We collected fish using a seine net (2 wings of 7.60 m long, 0.80 m height, a 1.40 m long cod-end with 5 mm mesh) between 8:00 and 12:00 on three successive days (spring tide period) in June (early rainy season), September (mid rainy season), December 2017 (late rainy season) and February 2018 (dry season). Nettings were conducted 5 times in each habitat on each census occasion. In each tow, initially, the net was laid out at the randomly established starting point (ca. 0.40–0.60 m depth) so that the net mouth opening was 5.0 m. Twenty-meter-long ropes attached to the tips of the net wings were then pulled by four persons to sweep an area of 100 m^2. Immediately after collection, we injected the concentrated formalin into the body cavity of each specimen, which was then preserved in 10% formalin. In the laboratory, fishes were identified following references (Carpenter and Niem, 2001; Tongnunui *et al*., 2002; Larson and Lim, 2005; Kimura *et al*., 2009; Tran *et al*., 2013) and total lengths (TL) measured to the nearest 0.1 mm.

Statistical analyses

Seagrass shoot density and leaf height were compared between habitats using non-parametric Mann-Whitney test when the assumptions for parametric test were not met. The tests were considered significant at $p<0.05$. The analysis was carried out in IBM SPSS ver. 21.

For the two factors analysis, the sampling design consisted of two factors: “habitat” (two levels for epiphytic animal abundance, four levels for others, fixed), and “sampling season” (month, four levels, fixed). The relative abundance of fish individuals and fish prey is highly skewed and contains many zero counts. Then, the statistical analysis, univariate and multivariate analyses were conducted using Primer v7 software (Clarke and Gorley, 2015) with the PERMANOVA add-on (Anderson *et al*., 2008). Initially, the univariate PERMANOVA was used to test for the variability of the mean total fish species numbers, total fish densities and fish prey such as epiphytic animals, benthic animals, planktonic prey and detritus found in each sampling habitat. The multivariate PERMANOVA was used to explore the variability of the densities of every component species in fish assemblages in each sampling habitat. Permutations (999 under a reduced model) were analyzed based on a Bray-Curtis similarity matrix constructed from log (X+1) transformed abundance data. As mentioned above, the present study is focused on habitat comparison. Where the habitat factor and interaction (Habitat x Season) were significant ($p<0.05$), pairwise tests of each sampling month were conducted using t statistics calculated by PERMANOVA analysis for comparing between habitats separately. In case the interaction between the two factors was not significant, all data were pooled and pairwise tests were conducted based on combining all sampling months.

The similarity percentage (SIMPER) test was conducted for each pair of habitat assemblages to identify the key species that contribute significantly to each habitat. To visualize the prey density and the abundance of key species across habitats, the Canonical Analysis of Principal Coordinates (CAP) was performed. Permutations (999 under a reduced model) were analyzed, based on a Euclidean distance matrix constructed from a log (x+1) transformed abundance data of key fish species. Vectors were overlaid onto the CAP plots to display the strength of Pearson's correlation between prey gradient and the CAP axes. These vectors were also used to illustrate the strength of multi-correlation between the abundance of each key fish species and the CAP axes.

RESULTS

Habitat complexity

The seagrass leaf height and shoot density in each seagrass bed on every sampling occasion are shown in the database (https://nrei.rmutsv.ac.th/th). Generally, leaf heights and shoot densities did not differ between intertidal and subtidal seagrass beds throughout the study period, except in June when the leaf heights in the former were higher than in the latter (Figure 2).

Prey abundance

In general, the densities of epiphytic prey, both small and large crustaceans, in intertidal seagrass beds tended to be nearly equal to or higher than those in subtidal seagrass beds. An exception was observed for large crustaceans in June, when their densities were lower in intertidal seagrass beds (Table 1, Figure 3). The densities of epiphytic polychaetes did not significantly differ between intertidal and subtidal seagrass beds.

The densities of benthic prey, including small and large crustaceans, in intertidal seagrass beds or on open sand/mud flats tended to be higher than or nearly equal to those in subtidal habitats. Moreover, densities in seagrass beds did not significantly differ from those on sand/mud flats, with the exception of large crustaceans in February, when their densities on intertidal sand/mud flats were higher than in other habitats (Table 2, Figure 4). On the contrary, densities of benthic prey polychaetes tended to be higher in subtidal seagrass beds or sand/mud flats than in intertidal habitats, with no significant differences observed between the paired intertidal and subtidal habitats. Densities of benthic molluscs tended to be higher in intertidal seagrass beds than in subtidal seagrass beds although not significantly differed from each other. Conversely, their densities in subtidal sand/mud flats tended to be higher than those in intertidal sand/mud flats, with the exception of September, when densities were higher in the latter. Occasionally, densities in seagrass beds were higher than those in both intertidal and subtidal sand/mud flats.

The abundance of planktonic copepods and planktonic shrimp exhibited a significant interaction between habitat and sampling month (Table 2). Planktonic copepods in the intertidal seagrass habitats displayed fluctuating abundances, with no consistent pattern across habitats but peaking on some occasions (Figure 5). Planktonic

Table 1. Univariate PERMANOVA analysis results for the epiphytic animal on seagrass canopy, the total number of small crustaceans, the total number of large crustaceans and polychaetes in studied intertidal/subtidal seagrass beds, Trang Province, Thailand.

Source	Df	Small crustaceans			Large crustaceans			Polychaetes		
		MS	**Pseudo-F**	**p**	**MS**	**Pseudo-F**	**p**	**MS**	**Pseudo-F**	**p**
Habitat	1	785.62	17.592	0.001	0.023712	0.033244	0.863	0.41365	1.9405	0.174
Season	3	665.39	14.899	0.001	0.87837	1.2314	0.308	1.2618	5.9193	0.004
Habitat×Season	3	430.53	9.6404	0.001	6.0809	8.5251	0.001	0.4313	2.0233	0.129
Residual	52	44.659			0.71329			0.21316		

Table 2. Univariate PERMANOVA analysis results for the abundance of benthic animals, planktonic animals and organic matter (in terms of ignition loss percentage) in studied intertidal or subtidal seagrass beds and open sand/mud flats, Trang Province, Thailand.

Source	Df	MS	Pseudo-F	p
Benthic animals				
Small crustacean				
Habitat	3	56.451	5.116	0.002
Season	3	51.658	4.6817	0.004
Habitat×Season	9	12.833	1.163	0.331
Residual	104	11.034		
Large crustacean				
Habitat	3	34.866	4.0461	0.009
Season	3	43.143	5.0065	0.005
Habitat×Season	9	11.972	1.3893	0.214
Residual	104	8.6173		
Polychaetes				
Habitat	3	65.067	14.332	0.001
Season	3	73.891	16.275	0.001
Habitat×Season	9	9.5362	2.1004	0.039
Residual	104	4.5401		
Molluscs				
Habitat	3	60.936	6.3111	0.001
Season	3	32.979	3.4156	0.035
Habitat×Season	9	24.573	2.545	0.013
Residual	104	9.6552		
Planktonic animals				
Planktonic copepods				
Habitat	3	0.063413	1.8435	0.16
Season	3	1.1154	32.426	0.001
Habitat×Season	9	0.23838	6.9298	0.001
Residual	104	0.034399		
Planktonic shrimps				
Habitat	3	0.20863	8.378	0.001
Season	3	0.07846	3.1508	0.022
Habitat×Season	9	0.43354	17.41	0.001
Residual	104	0.024902		
Ignition loss (%)				
Habitat	3	0.002543	0.91437	0.456
Season	3	0.0055458	1.9941	0.125
Habitat×Season	9	0.006774	2.4357	0.015
Residual	104	0.0027811		

shrimp were found in relatively low abundance, occasionally equal with levels in other habitats, but only in September and December. The ignition loss percentages (i.e., indicators that roughly represent the amount of detritus) showed no significant differences among habitats or sampling months (Table 2, Figure 6).

Fish assemblage structure

A total of 8,390 individuals, representing 39 fish families and 90 fish species, were recorded during the study period (Table 3). In terms of individual numbers, *Siganus canaliculatus* (5,057 individuals), *Letrinus lentjan* (462), *Pelates quadrilineatus* (411), *Halichoeres bicolor* (368), *Petroscirtes variabilis* (334), *Monacanthus chinensis* (302), *Acanthosphex leurynnis* (148), *Syngnathoides biaculeatus* (146), *Upeneus tragula* (139) and *Nuchequula gerreoides* (135) were dominant, accounting for 89.6% of the total. Most of the individuals collected were small-sized fishes such as juveniles, although some species reached adult size while still small (Table 3). The species diversity of fish showed a significant difference among habitats (Table 4). A higher number of fish species was found in the intertidal seagrass and sand/mud areas (Figure 7). Fish densities in the intertidal seagrass were occasionally high in comparison with other habitats throughout the sampling seasons (Figure 7).

The present study assessed differences in the fish assemblage structures among habitats, with sampling month (Table 4). The SIMPER analysis showed that the species contributed a high percentage to the average similarity of each group (habitat) (Table 5). Overlapping of typical species was found in some sampling months. For example, *Siganus canaliculatus, Petroscirtes variabilis* and

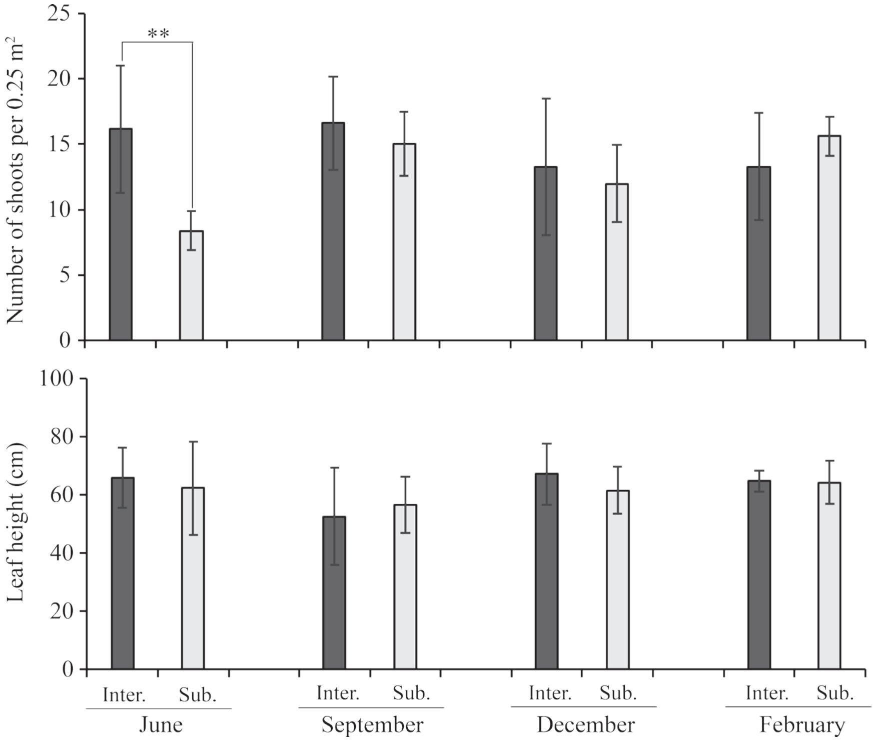

Figure 2. Mean seagrass shoot density and leaf height of each seagrass bed. Habitats named Intertidal seagrass and Subtidal seagrass beds abbreviated to Inter. and Sub. respectively. Error bars indicate standard deviations. ** = highly significant difference ($p<0.01$) based on a pair-wise comparison in the Mann-Whitney test.

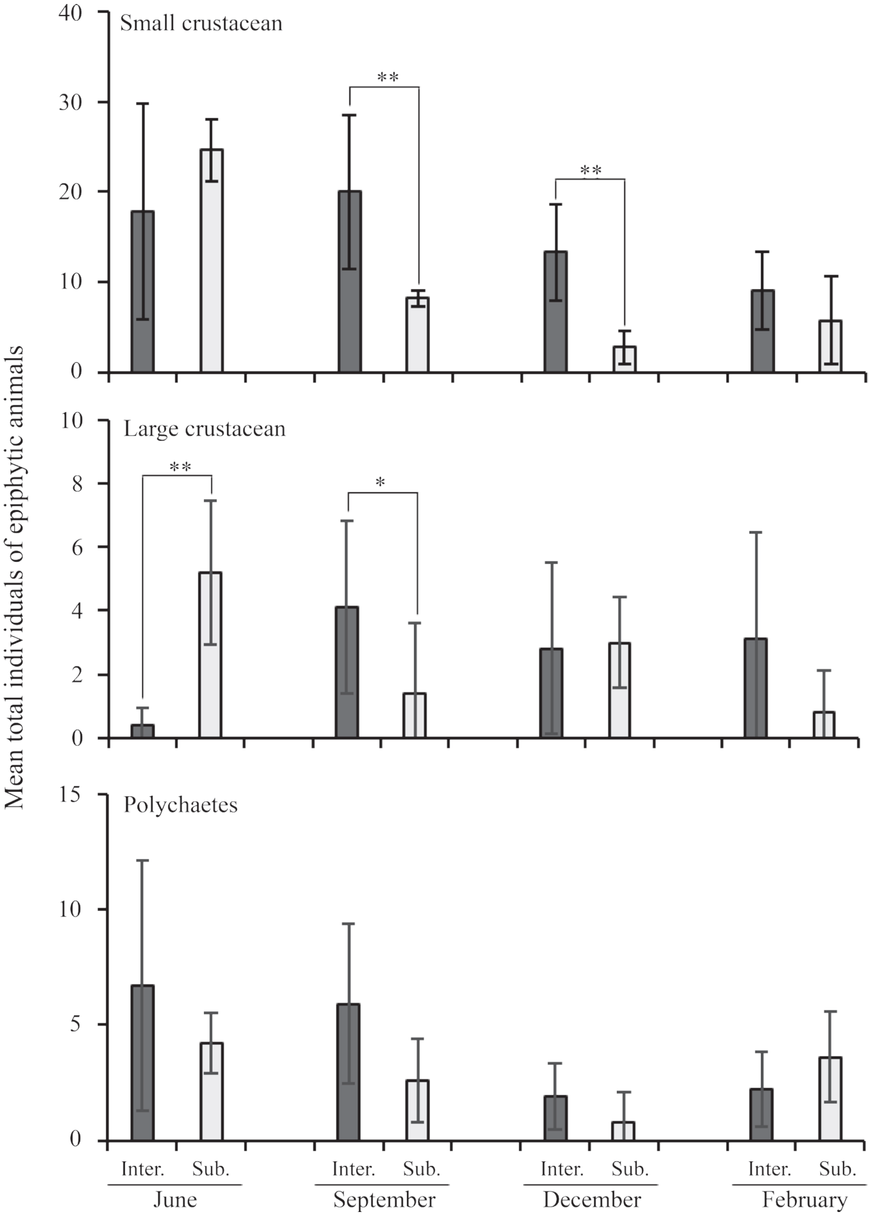

Figure 3. Mean total epiphytic individuals recorded in the *Enhalus acoroides* seagrass beds at intertidal (Inter.) and subtidal (Sub.) sites from June 2017 through February 2018. Error bars indicate standard deviations. * = significant difference ($p<0.05$), ** = highly significant difference ($p<0.01$) based on pair-wise comparison in PERMANOVA analysis.

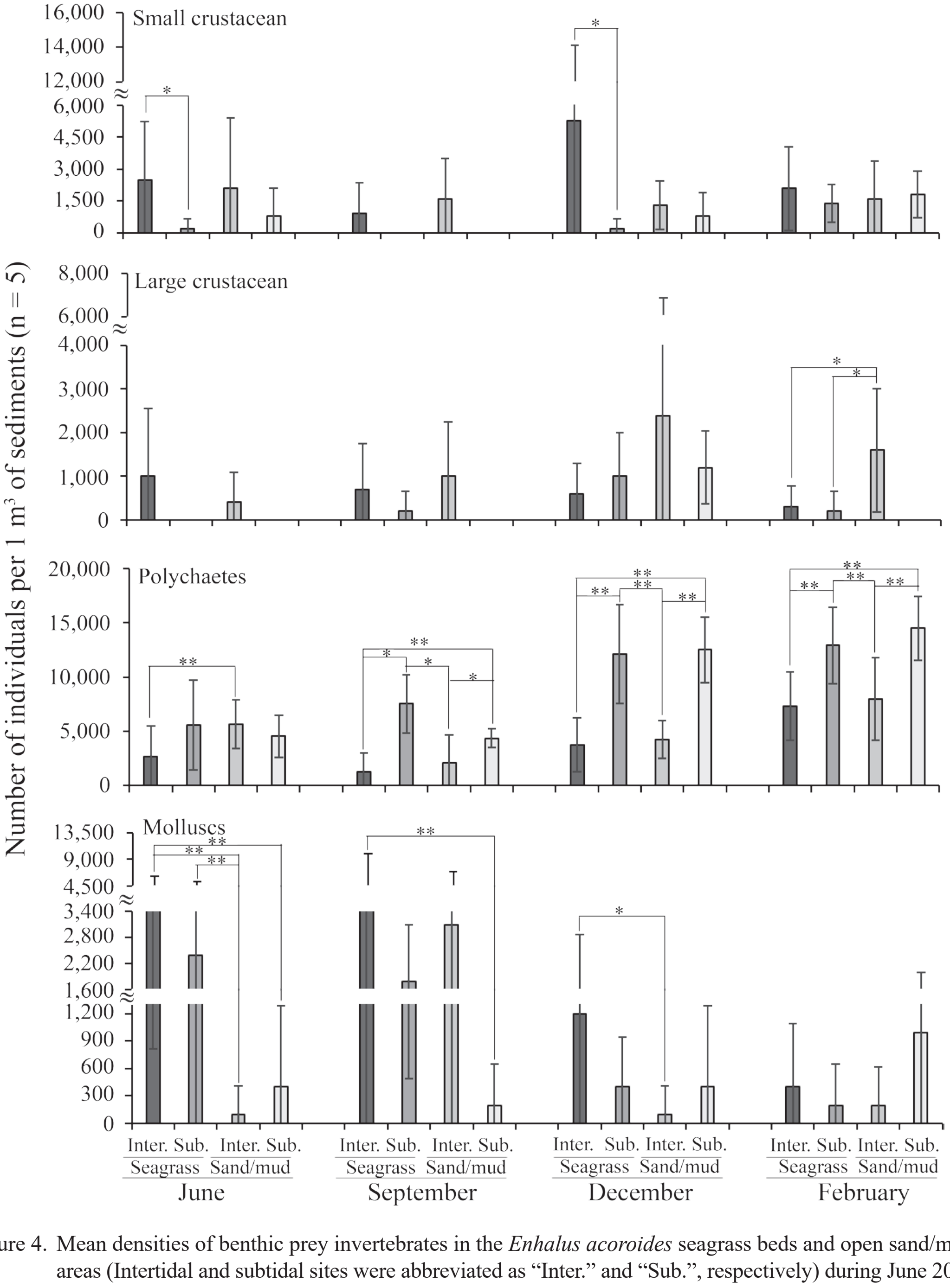

Figure 4. Mean densities of benthic prey invertebrates in the *Enhalus acoroides* seagrass beds and open sand/mud areas (Intertidal and subtidal sites were abbreviated as "Inter." and "Sub.", respectively) during June 2017 through February 2018. Error bars indicate standard deviations. * = significant difference ($p<0.05$), ** = highly significant difference ($p<0.01$) based on pair-wise comparison in PERMANOVA analysis.

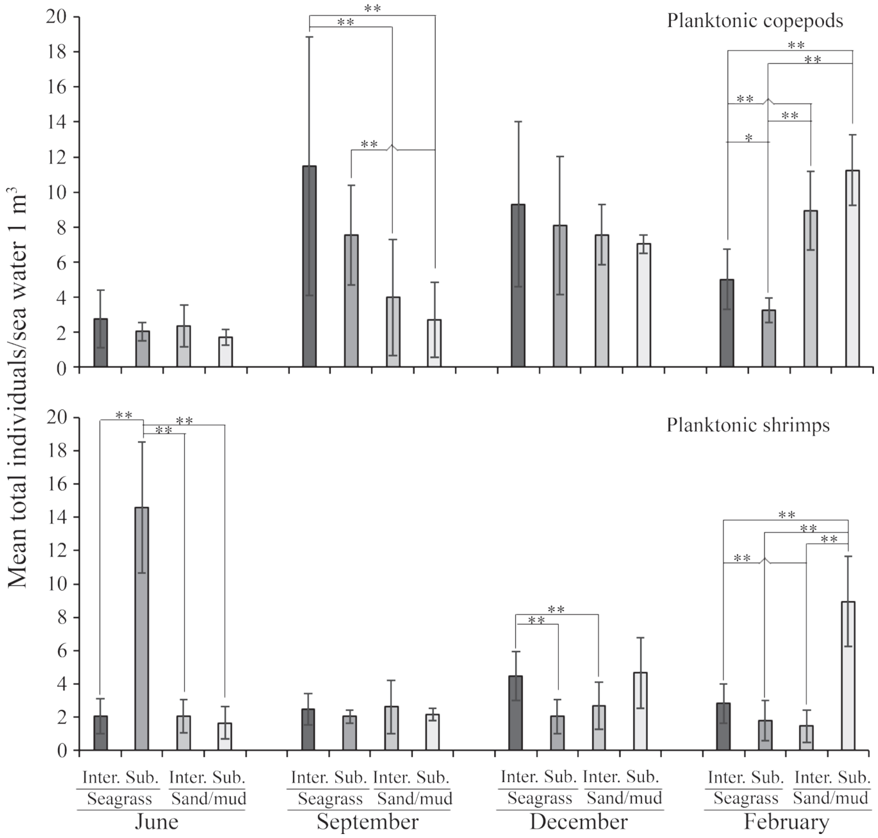

Figure 5. Mean total planktonic copepods and planktonic shrimp recorded in the *Enhalus acoroides* seagrass beds and open sand/mud areas at intertidal (Inter.) sites and the subtidal (Sub.) sites during June 2017 through February 2018. Error bars indicate standard deviations. * = significant difference ($p<0.05$), ** = highly significant difference ($p<0.01$) based on pair-wise comparison in PERMANOVA analysis.

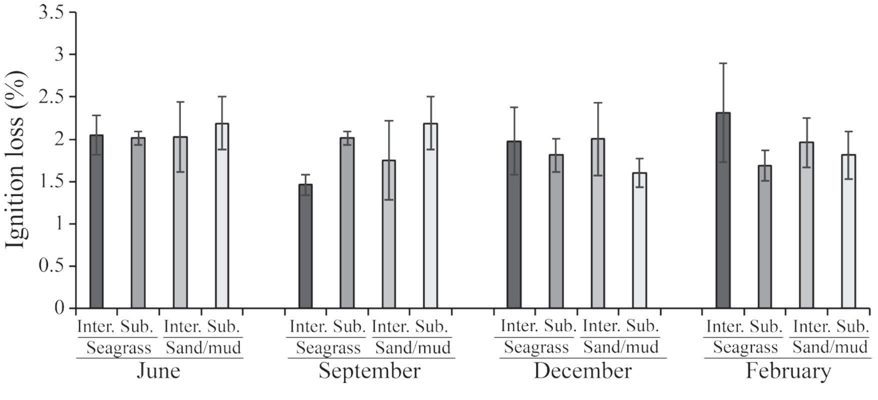

Figure 6. Mean total Ignition loss (%) recorded in the *Enhalus acoroides* seagrass beds and open sand/mud areas at intertidal (Inter.) sites and the subtidal (Sub.) sites during June 2017 through February 2018. Error bars indicate standard deviations.

Table 3. Species collected in the seagrass *Enhalus acoroides* beds and sand/mud areas in the intertidal zones at Pakmeng and HadYao and the subtidal zone at Pakklong from June 2017 through February 2018, including overall density (per 100 m^2) and size range (mm TL), code and trophic category of key species.

Family	**Species**	**Code**	**TC**	**Seagrass bed**		**Sand/mud area**	
				Intertidal Pakmeng/HadYao	**Subtidal Pakklong**	**Intertidal Pakmeng/HadYao**	**Subtidal Pakklong**
Dasyatidae	*Himantura walga*				0.05 (183.0)	0.05/0.15 (134.5–192.2)	
Ophichthidae	*Pisodonophis cancrivorus*			0/0.05 (400.5)		0/0.05 (355.9)	
Engraulidae	***Stolephurus indicus***	1	Pa/Sc/Lc	0.35/0 (37.4–89.4)	0.60 (35.0–63.8)	0/0.20 (42.2–98.30)	0.20 (31.4–63.3)
Clupeidae	*Escualosa thoracata*			0.05/0 (30.2)		0/0.05 (47.7)	
	Spratelloides sp.				0.05 (46.0)		
Synodontidae	*Saurida nebulosa*			0/0.05 (140.2)	0.15 (106.2–-114.8)	0/0.10 (97.6–120.0)	
	Trachinocephalus myops			0/0.05 (118.9)		0.20/0 (50.8–75.0)	
Mugilidae	Mugilidae sp.				0.25 (30.0–32.2)	0.40/0.05 (27.9–34.2)	
Atherinidae	*Hypoatherinna valenciennesi*			0/0.05 (38.9)			
	Atherinomorus lineatus			0/0.10 (38.3–51.8)			
	Atherinomorus duodecimalis			0/0.05 (54.4)			
Syngnathidae	*Hippichthys cyanospilus*			0.35/0.55 (99.2–153.5)	0.55 (106.1–144.8)	0/4.30 (91.4–144.5)	
	Syngnathoides biaculeatus	2	Sc/Lc/Fi	2.35/2.25 (51.6–208.2)	2.35 (97.6–211.0)	0/0.35 (165.0–205.0)	
	Hippocampus kuda					0/0.10 (43.3–43.4)	0.05 (42.2)
Centriscidae	*Aeoliscus strigatus*			0.95/1.40 (75.5–169.6)	0.05 (84.2)		
Aploactinidae	***Acanthosphex leurynnis***	3	Sc			0.60/5.75 (18.7–30.1)	1.05 (19.3–39.5)
Platycephalidae	*Platycephalus indicus*					0/0.10 (62.4–132.1)	
	Inegocia japonica	4	Lc	0/0.15 (46.3–191.1)	0.10 (118.8–136.1)	0/1.45 (39.4–141.5)	0.30 (26.1–144.5)
	Thysanophrys chiltonae				0.05 (153.3)		
	Sunagocia otaitensis			0/0.10 (109.6–113.5)	0.05 (92.5)		
	Grammoplites scaber				0.05 (138.6)		
Ambassidae	*Ambassis vachellii*					0/0.05 (54.9)	

Note: Code = assigned for key species which used in Figure 8; TC = trophic category of the key species; Pa = Planktonic animal feeders; Sc = Small benthic/epiphytic crustacean feeder; Lc = Large benthic/epiphytic crustacean feeder; Pol = Polychaete feeders; De = detritus feeder; Fi = fish feeders; Mo = Molluscs feeder

Table 3. Continued.

Family	Species	Code	TC	Seagrass bed		Sand/mud area	
				Intertidal Pakmeng/HadYao	Subtidal Pakklong	Intertidal Pakmeng/HadYao	Subtidal Pakklong
Serranidae	*Epinephelus sexfasciatus*			0.05/0 (24.2)	0.05 (25.1)	0/0.05 (25.2)	
	Epinephelus bleekeri			0.30/0 (80.2–207.0)			
	Epinephelus coioides			0.05/0 (157.9)			
	Epinephelus quoyanus			0.20/0 (127.5–137.2)			
	Epinephelus malabaricus					0/0.10 (68.7–75.9)	
Apogonidae	*Fowleria variegata*			0.45/0 (33.5–58.2)		0/0.05 (43.3)	
Sillaginidae	*Sillago intermedius*					0.05/0 (64.4)	
	Sillago sihama	5	Pa/Sc/Lc/Pol		0.05 (36.1)		1.00 (35.1–70.0)
Carangidae	*Scomberoides tol*				0.05 (77.9)		
	Scomberoides sp.					0.05/0.05 (21.2–30.2)	
	Selaroides leptolepis			0.05/0 (117.5)			
Leiognathidae	*Gazza achlamys*				0.05 (63.7)	0/0.05 (29.2)	
	Gazza sp.			0/0.05 (24.4)	0.25 (13.9–32.7)	0/0.15 (30.2–35.2)	
	Karalla daura					0.40/0 (22–35)	
	Nuchequula blochii					0.85/0.15 (14–31.1)	
	Nuchequula gerreoides	6	Pa/Sc/De/Lc/Mo		5.35 (13.3–51.4)	1.10/0.25 (14.5–82.9)	0.05 (16.5)
	Equulites stercorarius	7	De/Sc/Pol	1.60/0 (62.6–81.5)		0.45/1.30 (23.5–90.0)	0.35 (57.4–84.5)
	Leiognathus longgipinis					0.05/0.10 (12.8–71.5)	
	Leiognathus equulus					0.05/0 (72.5)	
	Eubleekeria jonesi			0.05/0 (90.0)		0.05/0 (53.2)	
	Secutor hanedai			0/0.10 (14.9–15.7)	0.05 (16.2)	0.95/0.20 (12.9–39.9)	0.25 (16.1–20.1)
	Secutor megalolepis					0.05/0 (68.3)	
Lutjanidae	*Lutjanus russelli*			0.75/0.25 (22.1–114.2)	0.10 (76.1–97.8)	1.10/0.10 (19.1–24.9)	0.05 (120.6)
	Lutjanus mandras			0.55/0.10 (29.4–86.7)	0.10 (31.6–37.5)	0.25/0.40 (30.5–69.8)	

Note: Code = assigned for key species which used in Figure 8; TC = trophic category of the key species; Pa = Planktonic animal feeders; Sc = Small benthic/epiphytic crustacean feeder; Lc = Large benthic/epiphytic crustacean feeder; Pol = Polychaete feeders; De = detritus feeder; Fi = fish feeders; Mo = Molluscs feeder

Table 3. Continued.

Family	**Species**	**Code**	**TC**	**Seagrass bed**		**Sand/mud area**	
				Intertidal Pakmeng/HadYao	**Subtidal Pakklong**	**Intertidal Pakmeng/HadYao**	**Subtidal Pakklong**
Gerreidae	*Gerres erythrourus*					0.20/0.10 (66.7–85.4)	
	Gerres macracanthus	8	Pa/Sc/Lc/Mo	0.05/0.25 (19.8–29.9)	0.30 (22.9–57.9)	0.85/0.80 (20.5–72.2)	0.10 (30.3–61.2)
	Gerres limbatus				0.05 (77.5)		
Nemipteridae	*Scolopsis monogramma*			0.20/0.05 (57.6–134.7)			
	Scolopsis taenioptera				0.05 (127.5)		
Lethrinidae	***Lethrinus lentjan***	9	Sc/De	13.05/6.50 (10.9–148.6)	0.15 (17.9–50.3)	0.20/3.20 (17.7–75.8)	
	Lethrinus ornatus			0.05/0.10 (67.7–80.4)			
Mullidae	***Upeneus tragula***	10	Pa/Sc/Lc/Mo	0.75/2.15 (32.4–119.7)	0.45 (31.5–117.20)	0.45/3.10 (29.4–117.8)	0.05 (38.3)
	Upeneus sulphureus			0/0.20 (31.1–138.40)		0.40/0.05 (25.9–81.8)	0.05 (50.1)
	Upeneus guttatus			0.05/0 (43.6)	0.05 (32.2)	0/0.10 (77.8–109.8)	
	Upeneus sundaicus	11	Lc	0/0.35 (48.7–59.9)	0.15 (36.2–84.9)	0.35/1.50 (29.5–103.5)	0.15 (58.3–113.3)
Chaetodontidae	*Parachaetodon ocellatus*			0/0.10 (17.5–19.8)	0.10 (48.4–62.1)	0/0.10 (19.8–20.5)	
Terapontidae	***Pelates quadrilineatus***	12	Pa/Sc/ Po/Mo	16.35/3.75 (20.0–102.5)		0/0.45 (22.2–52.3)	
Labridae	***Halichoeres bicolor***	13	Sc/Mo/Lc	13.40/1.85 (27.4–103.0)	0.50 (36.7–79.9)	0.80/1.70 (29.9–110.0)	0.15 (56.1–106.4)
	Halichoeres argus			0.05/0.20 (34.9–72.8)		0/0.05 (40.0)	
	Halichoeres chloropterus			0.05/0.25 (31.5–80.7)			
	Halichoeres nigrescens			0.25/0.05 (35.9–64.2)			
Scaridae	*Scarus ghobban*			0.10/0 (101.8–117.5)			
Blenniidae	***Petroscirtes variabilis***	14	Pa/Sc/De	2.85/8.65 (31.6–110.5)	3.20 (32.2–109.4)	0.05/1.70 (35.0–86.7)	0.25 (79.8–98.2)
Callionymidae	***Repomucenus schaapii***	15	Sc/Mo			0.10/0.40 (23.7–55.5)	0.35 (35.3–100.5)
	Paradiplogrammus enneactis			0.05/0.15 (22.4–43.3)		0/0.20 (27.2–37.6)	
Gobiidae	*Favonogobius reichei*					0/0.30 (25.4–32.5)	
	Mahidolia mystacina					0/0.05 (44.8)	
	Psammogobius biocellatus			0.05/0 (30.0)		0.10/0.20 (71.1–79.7)	0.05 (61.2)

Note: Code = assigned for key species which used in Figure 8; TC = trophic category of the key species; Pa = Planktonic animal feeders; Sc = Small benthic/epiphytic crustacean feeder; Lc = Large benthic/epiphytic crustacean feeder; Pol = Polychaete feeders; De = detritus feeder; Fi = fish feeders; Mo = Molluscs feeder

Table 3. Continued.

Family	Species	Code	TC	Seagrass bed		Sand/mud area	
				Intertidal Pakmeng/HadYao	Subtidal Pakklong	Intertidal Pakmeng/HadYao	Subtidal Pakklong
	Acentrogobius nebulosus	16	De/Sc/Po			0.50/0.05 (44.4–73.4)	
	Aulopareia cyanomos					0.05/0.05 (33.4–62.8)	
Siganidae	***Siganus canaliculatus***	17	Pa/Sc/Po/De	96.65/38.0 (11.7–211.0)	47.00 (25.0–118.5)	4.45/65.30 (18.5–129.5)	1.45 (27.2–95.5)
	Siganus javus	18	Pa/Sc/Po/De	0.70/0.50 (30.4–106.4)	0.70 (45.3–77.5)		0.25 (51.5–60.0)
Sphyraenidae	*Sphyraena putnamiae*				0.15 (58.4–60.2)	0/0.15 (64.7–106.5)	
	Sphyraena obtusata			0/0.05 (74.5)			
Paralichthyidae	*Pseudorhombus argus*					0.05/0.20 (59.4–149.1)	
Soleidae	*Pardachirus pavoninus*			0.05/0.30 (53.5–141.6)	0.20 (61.0–130.2)	0/0.05 (39.8)	
Cynoglossidae	*Cynoglossus cynogrossus*						0.05 (110.6)
Triacanthidae	*Triacanthus biaculeatus*					0/0.05 (166.6)	
	Triacanthus sp.					0.05/0.10 (11.9–13.1)	
Monacanthidae	***Monacanthus chinensis***	19	Pa/Sc/De/Mo	4.20/6.05 (10.8–153.3)	2.10 (17.2–165.5)	0.05/2.65 (10.7–150.7)	0.05 (18.3)
	Paramonacanthus choirocephalus				0.05 (73.6)		
Ostraciidae	*Lactoria cornuta*			0.05/0.10 (21.0–188.4)	0.10 (34.7–116.7)	0/0.55 (22.6–123.3)	
Tetraodontidae	*Chelonodon patoca*			0/0.10 (78.3–86.1)	0.70 (59.8–110.5)	0/0.55 (12.2–174.4)	
	Tetraodon nigroviridis					0/0.05 (123.7)	
	Tetraodon fluviatilis					0/0.10 (108.1–123.5)	
	Lagocephalus lunaris			0/0.05 (25.6)		0/0.05 (21.5)	
	Arothron immaculatus				0.05 (66.6)		
Diodontidae	*Diodon liturosus*				0.05 (144.6)		
	Total species number			36/37	41	35/55	21
	Species number per 100 m^2			9.35/10.1	8.25	6.45/11.2	3.1
	Total individual numbers per 100 m^2			157.05/75	66.35	15.45/99.4	6.25

Note: Code = assigned for key species which used in Figure 8; TC = trophic category of the key species; Pa = Planktonic animal feeders; Sc = Small benthic/epiphytic crustacean feeder; Lc = Large benthic/epiphytic crustacean feeder; Pol = Polychaete feeders; De = detritus feeder; Fi = fish feeders; Mo = Molluscs feeder

Table 4. Univariate and multivariate PERMANOVAs analysis results for the total number of fish species, the total number of fish individuals and fish assemblage in studied intertidal or subtidal seagrass beds and open sand/mud flats, Trang Province, Thailand.

		Total no. of fish species			**Total no. of fish individuals**			**Fish assemblage**		
Source	**Df**	**MS**	**Pseudo-F**	**p**	**MS**	**Pseudo-F**	**p**	**MS**	**Pseudo-F**	**p**
Habitat	3	1.0705	41.234	0.001	10.585	30.355	0.001	27,380	15.592	0.001
Season	3	0.055483	2.1372	0.108	1.8953	5.4354	0.004	6,702.9	3.8171	0.001
Habitat×Season	9	0.01579	0.60823	0.799	0.7996	2.2931	0.028	4,331.7	2.4668	0.001
Residual	103	0.025961			0.34869			1,756		

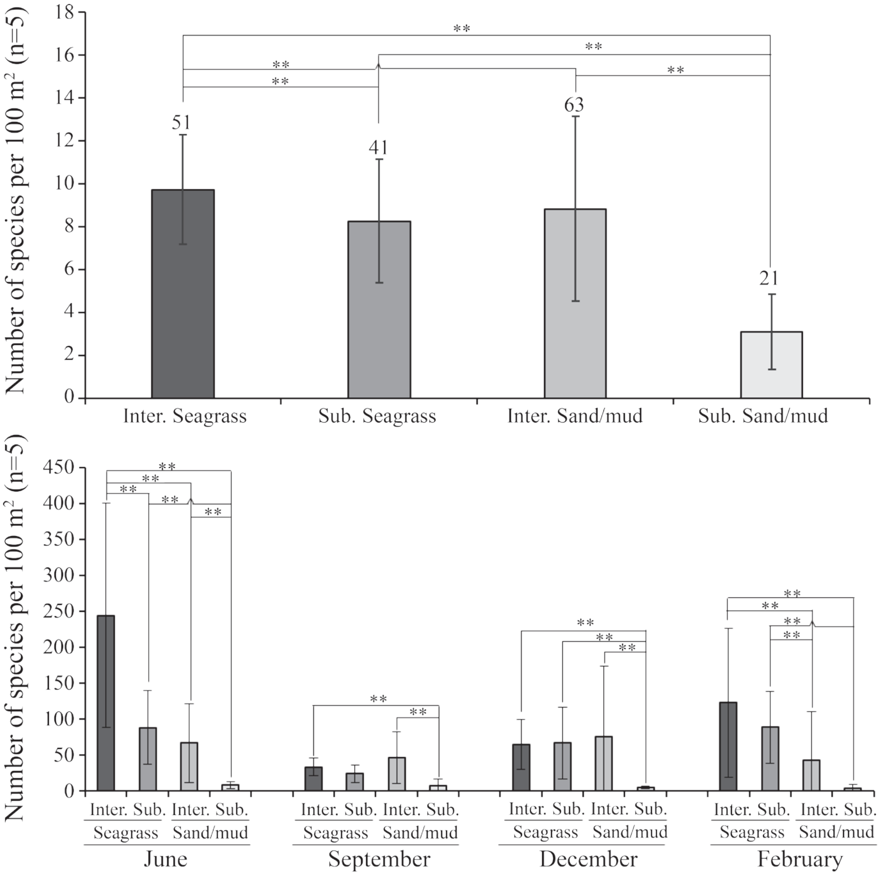

Figure 7. Mean total fish species number (top) in each habitat and mean total density (bottom) recorded in the *Enhalus acoroides* seagrass beds and open sand/mud areas (Intertidal and Subtidal sites were abbreviated as “Inter.” and “Sub.”, respectively) from June 2017 through February 2018. The number on each bar indicates the total species number. Error bars indicate standard deviations. ** = highly significant difference (p<0.01) based on pair-wise comparison in PERMANOVA analysis.

Table 5. Species contributing to the similarity within each habitat group identified by Percentage similarity (SIMPER) analysis, the top 3 species % of contribution are given.

Season	Group	Group Av. Sim.	Species	Contrib.%
June 17	Intertidal seagrass	70.55	*Siganus canaliculatus*	31.35
			Lethrinus lentjan	12.15
			Pelates quadrilineatus	11.81
	Subtidal seagrass	60.52	*Siganus canaliculatus*	40.07
			Monacanthus chinensis	16.06
			Nuchequula gerreoides	12.4
	Intertidal sand/mud	34.56	*Siganus canaliculatus*	37.00
			Gerres macracanthus	11.57
			Lethrinus lentjan	7.21
	Subtidal sand/mud	42.32	*Acanthosphex leurynnis*	51.59
			Sillago sihama	43.76
			Siganus canaliculatus	4.65
Sep 17	Intertidal seagrass	54.81	*Siganus canaliculatus*	45.74
			Monacanthus chinensis	24.02
			Lethrinus lentjan	9.72
	Subtidal seagrass	44.98	*Siganus canaliculatus*	51.49
			Monacanthus chinensis	21.11
			Siganus javus	10.67
	Intertidal sand/mud	38.71	*Siganus canaliculatus*	55.61
			Acanthosphex leurynnis	19.91
			Halichoeres bicolor	5.03
	Subtidal sand/mud	20.00	*Acanthosphex leurynnis*	58.46
			Equulites stercorarius	30.02
			Siganus canaliculatus	5.86
Dec 17	Intertidal seagrass	61.31	*Siganus canaliculatus*	25.37
			Petroscirtes variabilis	22.99
			Monacanthus chinensis	15.57
	Subtidal seagrass	62.17	*Siganus canaliculatus*	51.72
			Petroscirtes variabilis	18.77
			Monacanthus chinensis	11.86
	Intertidal sand/mud	39.73	*Siganus canaliculatus*	32.84
			Upeneus sundaicus	14.84
			Halichoeres bicolor	13.84
	Subtidal sand/mud	20.27	*Siganus canaliculatus*	42.14
			Inegocia japonica	33.2
			Repomucenus schaapii	24.66
Feb 18	Intertidal seagrass	51.05	*Siganus canaliculatus*	24.09
			Halichoeres bicolor	17.09
			Monacanthus chinensis	14.95
	Subtidal seagrass	57.69	*Siganus canaliculatus*	50.49
			Petroscirtes variabilis	26.4
			Syngnathoides biaculeatus	16.08
	Intertidal sand/mud	23.36	*Acentrogobius nebulosus*	20.65
			Halichoeres bicolor	15.58
			Upeneus tragula	13.09
	Subtidal sand/mud	15.15	*Siganus canaliculatus*	52.31
			Stolephurus indicus	23.64
			Halichoeres bicolor	12.03

Monacanthus chinensis were normally found as key species of the intertidal and subtidal seagrass beds. However, these species were occasionally found as the major proportion in the intertidal and subtidal sand/mud habitats during some sampling months. Fish species such as *Pelates quadrilineatus, Lethrinus lentjan, Nuchequula gerreoides, Siganus javus, Halichoeres bicolor* and *Syngnathoides biaculeatus* were unique species found in both intertidal and subtidal habitats. The species that most contributed to the differences between these habitats were identified (Table 6). The degree of fish assemblage dissimilarity increased from the seagrass to sand/mud habitats. The fish species such as *Siganus canaliculatus, Siganus javus, Petroscirtes variabilis, Pelates quadrilineatus, Nuchequula gerreoides, Lethrinus lentjan, Monacanthus chinensis, Hippichthys cyanospilus, Halichoeres bicolor, Equulites stercorarius* and *Acanthosphex leurynnis* discriminated the intertidal seagrass from other habitats with variation in the sampling season. These species such as *Petroscirtes variabilis, Pelates quadrilineatus, Monacanthus chinensis, Hippichthys cyanospilus, Halichoeres bicolor* and *Equulites stercorarius* were found at higher densities in the intertidal seagrass bed. In comparison with the intertidal seagrass, *Nuchequula gerreoides* and *Siganus javus* were found at higher densities in the subtidal seagrass, whereas, species such as *Siganus canaliculatus* and *Lethrinus lentjan* were occasionally found in higher numbers in the intertidal seagrass habitat. The *Acanthosphex leurynnis* was collected in greater numbers in the intertidal sand/mud area.

The Canonical Analysis of Principal Coordinates (CAP) results of each sampling month showed a correlation between the density of available prey and key fish species among habitats (Figure 8). In June, there was a significant ($p = 0.001$) correlation between the prey abundance data cloud and habitats. The first two canonical correlations were both greater than 0.75 ($\delta_1 = 0.93$, $\delta_2 = 0.79$). The fish assemblage in the intertidal seagrass bed showed a strongly association with available prey variables of benthic fauna, such as small crustaceans and molluscs (Figure 8, see samples of the intertidal seagrass bed). The key fish species in the intertidal seagrass assemblage such as *Lethrinus lentjan* and *Pelates quadrilineatus* were associated with these prey types. Conversely, the fish assemblage gradient in the subtidal seagrass beds correlated with the availability of planktonic shrimp and epiphytic large crustaceans. Species such as *Nuchequula gerreoides* were associated with planktonic shrimp and epiphytic large crustaceans (Figure 8).

In September, there was a significant correlation between prey abundance and key species among habitats (Figure 8, $p = 0.001$). The first two canonical correlations are both greater than 0.80 ($\delta_1 = 0.92$, $\delta_2 = 0.82$). Planktonic copepods and epiphytic small crustaceans had a strong association with the intertidal seagrass beds (Figure 8). The key fish species associated with these habitats was *Monacanthus chinensis* (Figure 8).

In December, prey abundance and key fish species among habitats showed a significant correlation (Figure 8, $p = 0.001$). The first two canonical correlations are both greater than 0.75 ($\delta_1 = 0.93$, $\delta_2 = 0.80$). The epiphytic small crustacean was strongly associated with the gradient of key fish species in the intertidal seagrass beds (Figure 8). The key fish species of the habitat, associated with this prey, were *Monacanthus chinensis* and *Petroscirtes variabilis* (Figure 8).

In February, prey abundance and key fish species among habitats showed a significant correlation (Figure 8, $p = 0.001$). The first two canonical correlations are both greater than 0.85 ($\delta_1 = 0.94$, $\delta_2 = 0.86$). The epiphytic small crustacean remained strongly associated with the gradient of key fish species in the intertidal seagrass beds (Figure 8). The key fish species associated with this prey are *Monacanthus chinensis* and *Petroscirtes variabilis* (Figure 8). Additionally, the availability of benthic polychaetes was associated with the gradient of key fish species in the subtidal seagrass beds, with *Siganus canaliculatus* being the fish species associated with this prey (Figure 8).

Table 6. Fish species contributing to the dissimilarity between habitat pairs identified by SIMPER analysis, the top 3 species % of contribution are given.

Season	Group	Group Av. Diss.	Species	Contrib.%
June 17	Intertidal seagrass & Subtidal seagrass	50.86	*Pelates quadrilineatus*	11.9
			Lethrinus lentjan	11.65
			Nuchequula gerreoides	11.56
	Intertidal seagrass & Intertidal sand/mud	68.45	*Siganus canaliculatus*	10.81
			Pelates quadrilineatus	8.36
			Halichoeres bicolor	6.76
	Intertidal seagrass & Subtidal sand/mud	97.60	*Siganus canaliculatus*	20.77
			Lethrinus lentjan	9.85
			Pelates quadrilineatus	9.39
	Subtidal seagrass & Intertidal sand/mud	70.77	*Nuchequula gerreoides*	8.78
			Siganus canaliculatus	8.29
			Monacanthus chinensis	6.11
	Subtidal seagrass & Subtidal sand/mud	95.57	*Siganus canaliculatus*	21.08
			Nuchequula gerreoides	11.16
			Monacanthus chinensis	9.1
	Intertidal sand/mud & Subtidal sand/mud	87.63	*Siganus canaliculatus*	15.14
			Sillago sihama	8.35
			Gerres macracanthus	7.05
Sep 17	Intertidal seagrass & Subtidal seagrass	56.84	*Siganus javus*	8.97
			Siganus canaliculatus	8.38
			Lethrinus lentjan	7.54
	Intertidal seagrass & Intertidal sand/mud	67.62	*Acanthosphex leurynnis*	11.73
			Monacanthus chinensis	10.32
			Siganus canaliculatus	7.58
	Intertidal seagrass & Subtidal sand/mud	85.99	*Siganus canaliculatus*	21.5
			Monacanthus chinensis	13.23
			Equulites stercorarius	7.75
	Subtidal seagrass & Intertidal sand/mud	71.92	*Acanthosphex leurynnis*	12.53
			Siganus canaliculatus	9.41
			Siganus javus	7.42
	Subtidal seagrass & Subtidal sand/mud	89.47	*Siganus canaliculatus*	20.69
			Siganus javus	9.1
			Monacanthus chinensis	9.08
	Intertidal sand/mud & Subtidal sand/mud	80.72	*Siganus canaliculatus*	22.94
			Acanthosphex leurynnis	12.53
			Nuchequula gerreoides	6.76

Table 6. Continued.

Season	Group	Group Av. Diss.	Species	Contrib.%
Dec 17	Intertidal seagrass & Subtidal seagrass	48.32	*Lethrinus lentjan*	13.44
			Siganus canaliculatus	9.41
			Monacanthus chinensis	7.61
	Intertidal seagrass & Intertidal sand/mud	63.15	*Petroscirtes variabilis*	11.66
			Siganus canaliculatus	9.63
			Lethrinus lentjan	8.79
	Intertidal seagrass & Subtidal sand/mud	91.56	*Petroscirtes variabilis*	15.2
			Siganus canaliculatus	13.67
			Monacanthus chinensis	11.67
	Subtidal seagrass & Intertidal sand/mud	61.06	*Siganus canaliculatus*	14.75
			Petroscirtes variabilis	10.04
			Hippichthys cyanospilus	6.88
	Subtidal seagrass & Subtidal sand/mud	87.77	*Siganus canaliculatus*	27.63
			Petroscirtes variabilis	13.4
			Monacanthus chinensis	9.47
	Intertidal sand/mud & Subtidal sand/mud	83.83	*Siganus canaliculatus*	18.39
			Upeneus tragula	9.05
			Halichoeres bicolor	7.99
Feb 18	Intertidal seagrass & Subtidal seagrass	55.29	*Halichoeres bicolor*	12.5
			Siganus canaliculatus	10.75
			Pelates quadrilineatus	9.82
	Intertidal seagrass & Intertidal sand/mud	83.1	*Siganus canaliculatus*	11.87
			Petroscirtes variabilis	9.35
			Halichoeres bicolor	8.23
	Intertidal seagrass & Subtidal sand/mud	87.90	*Siganus canaliculatus*	12.09
			Petroscirtes variabilis	11.62
			Halichoeres bicolor	11.09
	Subtidal seagrass & Intertidal sand/mud	82.87	*Siganus canaliculatus*	22.26
			Petroscirtes variabilis	12.41
			Syngnathoides biaculeatus	9.44
	Subtidal seagrass & Subtidal sand/mud	84.92	*Siganus canaliculatus*	27.77
			Petroscirtes variabilis	16.76
			Syngnathoides biaculeatus	12.08
	Intertidal sand/mud & Subtidal sand/mud	89.11	*Siganus canaliculatus*	12.60
			Acentrogobius nebulosus	8.09
			Halichoeres bicolor	7.20

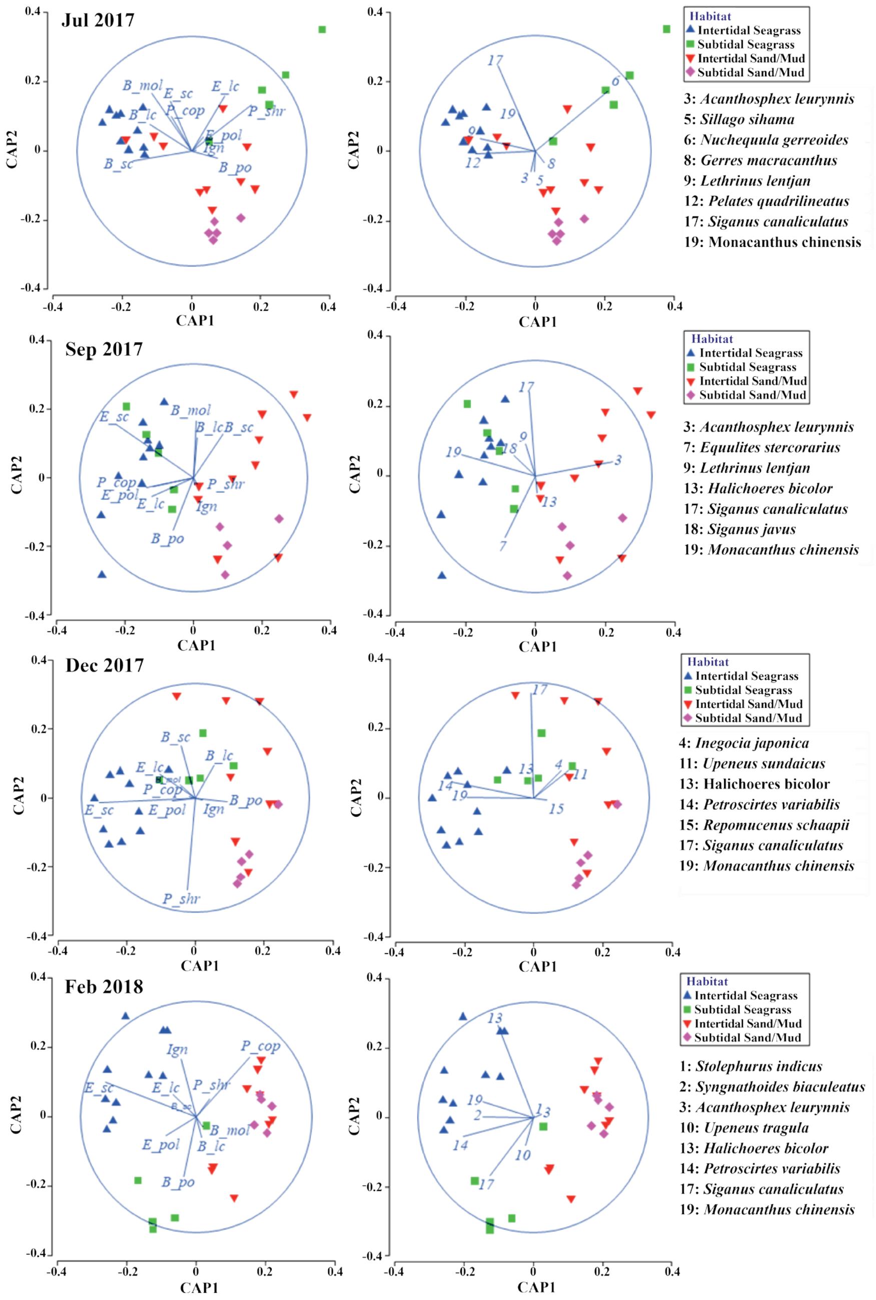

Figure 8. Canonical Analysis of Principal Coordinates (CAP) plot of correlation of key fish species and their prey collected in the intertidal or subtidal seagrass habitats, sampling season between June 2017 and Dec 2018. Data were log(x+1) transformed and similarities were based on a Euclidean distance matrix. Vectors overlaid on CAP plots indicate the direction of Pearson correlations between individual prey and CAP axes (left plots) and the direction of Multiple correlations between individual key fish species and CAP axes (right plots).

Note: Benthic animals: B_SC = Small crustaceans, B_pol = Polychaetes, B_LC = Large crustaceans, B_mol = Molluscs; Planktonic animals: P_cop = Planktonic copepods, P_shr = Planktonic shrimps; Epiphytic prey animals: E_SC = Small crustaceans, E_pol = Polychaetes, E_SC = Small crustaceans, E_LC = Large crustaceans; In = Ignition loss.

DISCUSSION

Our study discovered that the fish diversity, total fish density and density patterns of each fish species differ between the intertidal and subtidal seagrass beds. These differences are occasionally found when compared with the intertidal sand/mud but not with the subtidal sand/mud. The distinct fish assemblages between the intertidal and subtidal seagrass beds may be related to the availability of food resources. The intertidal seagrass may provide sufficient food for the dietary needs of fish. Then, factors such as their prey items are considered important aspects. We found that the prey available in these habitats showed a substitutive pattern with slight seasonal variations. In some seasons, the epiphytic animals associated with seagrass canopies, such as small and large crustaceans in the intertidal seagrass bed, demonstrated greater abundance. The availability of other food resources, such as detritus, small benthic crustaceans, molluscs, and planktonic copepods and shrimps, also reflected a substitutive pattern between the intertidal and subtidal seagrass beds. Benthic animals, such as small crustacean and molluscs, were found in higher densities in the intertidal seagrass bed. The variability and replacement of macrofauna species associated with a seascape have been recognized (Magni *et al*., 2006; Rodil *et al*., 2021). Then, the discrimination based on the assemblage of key fish species may be inconsistent following the temporal change of prey items in each habitat. The multivariate discriminant plot and the variation plot between the two seagrass habitats were notable. It may be common to summarize that it is difficult to clarify associations of fish distribution with specific habitat characteristics because small fish exhibit temporal and ontogenetic diet preferences that vary on a small spatial scale (Livingston, 1982; Shimizu *et al*., 2022). Shimizu *et al*. (2022) concluded that dietary flexibility might increase the adaptability of fish to seagrass beds characterized by significant variations in available food resources. However, multivariate analyses between the density of prey items and key fish species can be found in specific habitats due to the prey preference of each fish species, based on their prey abundance in each habitat. In cases where the same species inhabits both habitats, our study found that some fish species show an association with either subtidal seagrass or intertidal seagrass based on food availability. The key fish species associated with intertidal seagrass beds show similarities with those found in subtidal seagrass beds. For example, *Monacanthus chinensis* was identified as a key species in both subtidal and intertidal seagrass habitats, with samples collected within a similar body size range. This fish species feeds on detritus, planktonic, epiphytic, and benthic animals, including crustaceans and molluscs. There was a strong correlation between this species and epiphytic small crustaceans in the intertidal seagrass bed, particularly from September to December, even though these prey items are also found in the subtidal seagrass habitat. This suggests that the availability of prey can attract fish abundance in both habitats, albeit occasionally. Additionally, the availability of food resources in the intertidal seagrass habitat may have a significant correlation with fish abundance. Key species such as *Lethrinus lentjan* and *Pelates quadrilineatus* showed a high correlation with their prey items (benthic crustaceans) that were abundant in the intertidal seagrass bed, especially in June. *Petroscirtes variabilis*, another key species, primarily feeds on detritus and small crustaceans, and its abundance correlates with the abundance of its prey, epiphytic small crustaceans. This species showed high density in the intertidal seagrass habitat, especially in December and February. However, these correlations have only discovered benthic or epiphytic prey, which were not found in correlation with the planktonic prey in the intertidal seagrass habitat. The correlation between the fish and the planktonic prey was found only in the case of *Nuchequula gerreoides* in the subtidal seagrass habitat. Therefore, the similar occurrence of the key fish species between the intertidal and subtidal seagrass habitats was displayed because the intertidal seagrass has sufficient food resources to maintain a substitutional manner with the subtidal seagrass habitat. Then, fish that live in the intertidal seagrass habitat are alternatively buffeted, which is associated with seagrass as the available in the subtidal seagrass habitat.

The complexity of the seagrass bed is generally considered the major factor responsible for the faunal richness of seagrass habitats because this complexity provides a variety of food resources (Saenger *et al*., 2013; Hayes *et al*., 2020). Our case may be further described because the complexity of the seagrass, in terms of leaf height and the number of shoots of *E. acoroides*, was a differentiating factor between the two habitats (the intertidal and subtidal seagrass beds). Consequently, the substitution in fish diversity and density between comparable dried-up and wet seagrass areas, such as subtidal and intertidal seagrass habitats, may reflect the equivalence in seagrass complexity. However, fish assemblage characteristics, typified among habitats, were found with a gradient of the presence or absence of seagrass. The composition of fish species was distinct across habitat gradients. Therefore, the structural complexity of the habitat and the food resources provided may not suffice to explain our findings.

Other potential factors not identified in this study may also be relevant. These substitution patterns suggest that several fishes may utilize the intertidal area not only for the benefits of seagrass complexity as food resources but also to exploit other habitat characteristics for their daily activities. The abundance of fish in the intertidal area also attracts shallow-water predators when the water depth increases (Staveley *et al*., 2017). To reduce predator pressure, small fishes in the intertidal area engage in micro-scale movements to shallower waters when the incoming tide rises and inundates those areas, then move back to the adjacent areas during low tide (Mclvor and Odum, 1988). Fish assemblages, especially small and juvenile fishes, select shallow depositional habitats where prey availability is greatest and a predator presence is minimal. Thus, the advantage of intertidal and subtidal areas may be to provide a refuge for schools of small and juvenile fishes seeking shelter from predators and accessing their associated food resources (Jenkins *et al*., 1997; Verdiell-Cubedo *et al*., 2007).

In comparison with seagrass habitats, the fish diversity in the intertidal sand/mud area is relatively high but low density in some seasons. The fish assemblage in the intertidal sand/mud also showed a similar structure to seagrass habitats, but differed from the subtidal sand/mud habitat. The multivariate community structure of the intertidal sand/mud responded to mixing between associated seagrass or associated sand/mud fishes, which varied depending on the sampling season. Small and juvenile fishes may prefer shallow intertidal habitats where prey is available and predators are less abundant. However, our study did not find a correlation between fish species and prey available in this habitat.

Franco *et al*. (2006) identified the sand/mud area around the seagrass as a transition habitat with highly variable fish assemblages, influenced by adjacent habitats and serving as buffer zones and migration routes for many fish species. The study also described how fish assemblages may have a similar structure among these habitats due to tidal variation, especially for small and juvenile fishes in tidal shallow waters. Species diversity and density were observed to be low in the intertidal substrate during low tide but increased during high tide (Lee *et al*., 2014). On the other hand, the subtidal sand/mud area had more uniform assemblages due to the sandy beach environment. Fish species like *Acanthosphex leurynnis, Sillago sihama, Stolephurus indicus, Inegocia japonica, Repomucenus schaapii, Equulites* stercorarius, *Upeneus sundaicus* and *U. tragula* made significant contributions to the intertidal sand/mud habitat. These species are also found in sandy beach habitats (Ikejima *et al*., 2003; Srichum *et al*., 2013) and their prey items consist of both planktonic and benthic animals. Even though these food resources were high-density, peaking in some seasons compared to seagrass habitats, no evidence detects the correlation between these fish and their prey items in our study. In addition, most of these fishes were almost juveniles. The short-distance moving or temporary settling in the intertidal tide pool may be one of the life strategies of the associated intertidal fishes, especially in the juvenile stage. Unsurprisingly the intertidal sand/mud supports diverse fish for their transition both from seagrass and other habitats compared to the subtidal sand/mud area.

The present study concludes that the intertidal seagrass bed serves as an important habitat substitute for the subtidal seagrass bed. The diversity and density of fish and fish assemblage characteristics are similar between the intertidal and subtidal seagrass beds. However, fish diversity and density in the intertidal sand/mud area are occasionally equal to those of the two seagrass beds, while the subtidal sand/mud area has the lowest diversity and density, making it uncomparable to the seagrass beds. The substitution in fish assemblages between the intertidal seagrass and subtidal seagrass beds is reflected by the similarity of fish prey resources. Prey available in the intertidal seagrass bed is enough to sustain fish, suggesting that the intertidal habitat may serve as an alternative for subtidal dependent fishes. Key species of the seagrass habitats may also be found in nearby intertidal sand/mud areas, but they rarely venture into more distinct habitats such as intertidal mangroves, sandy beaches and river estuary systems (Ikejima *et al*., 2003; Jutagate *et al*., 2009; Saheem *et al*., 2015). Most of the fishes observed in this study were juveniles, indicating that short-distance moving or temporary settling in the intertidal tide pool may be a common life strategy for associated intertidal fishes, especially during the juvenile stage. These fish species are important for local fisheries, despite their relatively small sizes. The intertidal seagrass bed provides food for fish assemblages and limited fish predators for small fishes, highlighting the importance of establishing and applying intertidal fishing management based on this information.

CONCLUSIONS

In summary, the present study was conducted to sample fish with differences in both the physical and biological characteristics of their habitats. Seagrass habitats, including both subtidal and intertidal areas, exhibit truly different complexities compared to sand/mud area. However, fish diversity and density are not always different between seagrass and nearby sand/mud habitats, as equal fish diversity was found between intertidal seagrass and intertidal sand/mud habitats. Fish assemblages indicated that key species found in subtidal seagrass are similar to those in intertidal seagrass and occasionally similar to those in intertidal sand/mud areas. The transition between subtidal and intertidal seagrass may provide sufficient living requisites for fish, as prey items such as epiphytic fauna appear to be abundant in both habitats. The similarity of intertidal sand/mud with seagrass fish assemblages occurs when associated seagrass fishes have a high density in the sand/mud area. However, these similarities do not seem to be influenced by the abundance of prey items, as these prey items appear to be related to seagrass habitats in both subtidal and intertidal areas. The intertidal sand/mud may act as a transitional habitat for fish from nearby seagrass habitats, while the fish assemblage of subtidal sand/mud is distinguished by fish taxa found in the sandy beach assemblages. A new finding of our study is that intertidal seagrass plays a substitutive role in terms of fish assemblages, as both habitats have compensatory food resources. Our findings indicate that intertidal seagrass is equally important as subtidal seagrass. These findings suggest that intertidal areas support a greater number of fish species and individuals compared to subtidal areas, even when they dry up during low tide. The observed correlation between key fish species and their food resources in both intertidal and subtidal seagrass habitats demonstrates that these areas provide essential food resources throughout the fishes' life cycles in the coastal area. Therefore, the scientific understanding of intertidal habitats should be integrated into the design of seagrass bed management programs. Further, management plans for seagrass conservation must include intertidal seagrass within the sanctuary's scope.

ACKNOWLEDGEMENTS

The Nagao Natural Environment Foundation, Japan, financially supported this study. We would like to thank Natthita Rojchanaprasart for supporting data analyses.

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