



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

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ABSTRACT

Intertidal seagrass beds occur throughout the tropical Indo-Pacific region and several studies have shown that small fishes inhabit them when inundated during the tidal regime. However, there is a lack of evidence regarding the trophic importance of these habitats to different fish populations at such times. In this study, we examined the feeding behavior of the juvenile fish communities during an incoming tide at two intertidal seagrass bed sites in northern Mindanao, Philippines, during both wet and dry seasons, by deploying remote underwater video cameras. The video footages (3 h) revealed that nearly half of all fish species arrived within 30 min from the start of recording (ca. 30–40 cm water depth, 10–20 cm above the seagrass canopy), and that species richness gradually increased with rising tide, reaching 80% of recorded species within 120 min at both sites in both seasons. Small juvenile (< 10 cm total length) 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. The fishery target families Labridae, Lethrinidae, Siganidae, and Lutjanidae foraged during the rising tide, pointing to the importance of intertidal seagrass beds as a foraging habitat for at least 17 species. Because these habitats are disappearing due to expanding coastal developments for human use, the results highlight the ecological importance as a foraging area for multiple fish species to which it may help support developing conservation and management policies in coastal zones.

1. Introduction

Seagrass beds are globally the most widespread shallow marine habitat (Green and Short, 2003). In tropical regions, they serve as important nursery and foraging grounds for a diverse array of marine organisms, including commercially important species (Krumme, 2009; Nagelkerken, 2009). For example, juvenile reef fishes (Lethrinidae, Lutjanidae and Scaridae) utilize seagrass beds as nursery areas, where survival rates and prey densities are high, before moving to nearby coral reefs where they remain as adults (Berkström et al., 2013; Grol et al., 2011; Nakamura et al., 2012). In the Caribbean Sea, Haemulidae and Lutjanidae migrate (during day and night) to seagrass beds from adjacent coral reefs or mangroves due to the greater availability of prey, such as small crustaceans, in the former (Nagelkerken et al., 2000;

Ogden and Ehrlich, 1977; Verweij et al., 2006). Because seagrass habitats are vital for many economically important fish species, they provide critical ecosystem services to tropical coastal economies (Nordlund et al., 2017; Orth et al., 2006).

Most studies highlighting the importance of tropical seagrass beds as nursery and foraging grounds have been conducted on subtidal beds in the Caribbean (Grol et al., 2011; 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), where many intertidal beds get exposed for several hours during low tide (Unsworth et al., 2007). However, few studies have focused on the habitat use of fishes in intertidal seagrass beds (Davis et al., 2017; Unsworth et al., 2007).

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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. Intertidal salt marsh and mangrove creek habitats are frequented by small fishes during an early incoming tidal phase, with larger fishes (including piscivorous species) arriving later (Bretsch and Allen, 2006; Ellis and Bell, 2008). Accordingly, it might be reasonably expected that small fishes and their piscivorous predators move onto intertidal seagrass beds for foraging when the latter are inundated. However, direct qualitative and quantitative evidence showing fishes engaged in foraging activities in intertidal seagrass is lacking. Therefore, it is unclear how fishes utilize intertidal seagrass beds, despite the importance of such information to fully understand the ecological roles of seagrass habitats in tropical regions.

Recently, loss of seagrass habitat has been occurring on a variety of spatial scales, ranging from square meters to square kilometers (Orth et al., 2006). Because seagrass beds exist at the land-sea interface, they are subject to damage by many human-related activities, including agricultural runoff, coastal development, dredging and vessel grounding (Orth et al., 2006; Waycott et al., 2009). Waycott et al. (2009) reported that a rapid decline of seagrass habitats has occurred worldwide, with a loss rate (detected by inter-decadal analysis) estimated at 7% per year since the 1900s. The Philippine archipelago has been identified as an epicenter of nearshore marine fish biodiversity, the island chain supporting more species than any other tropical country in the Indo-Pacific region (Carpenter and Springer, 2005). However, subtidal and especially inter-tidal seagrass beds in the Philippines are severely threatened by expanding coastal development (Fortes, 2013), risking to destroy important fish habitats. In light of this, the present study aimed to assess the trophic interactions of the fish communities inhabiting intertidal seagrass beds using an in situ video recording method (Becker et al., 2012; Ellis and Bell, 2008). Specifically, we describe the temporal changes in (1) fish composition, (2) species diversity, (3) abundance, and (4) fish behavior (swimming and feeding), on incoming tides.

2. Methods

2.1. Study sites

This study was conducted at Plaridel (8° 25' N, 123° 45' E) and Laguindingan (8° 37' N, 124° 27' E), located 79 km apart on northern Mindanao Island, Philippines (Fig. 1). Both study areas included fringing reefs with extensive seagrass beds and adjacent mangrove swamps, the tidal regime for both sites being predominantly mixed semidiurnal. At Plaridel, several subtidal seagrass beds were intermingled within intertidal seagrass bed areas. The former occurred approximately 50–600 m offshore, the distance from the shoreline to the reef edge ranging from 500 to 1700 m. At the Laguindingan study site, a clear transition existed between the intertidal and subtidal seagrass beds, the latter being separated by ca. 200 m from the back edge of the coral reef (ca. 800 m from shoreline to reef edge).

The rainy season (wet season) in the study areas extends from November to February, the warmest months (dry season) typically extending from March to August. Sea surface temperature (28–30 °C) and salinity (34–36) were similar between the two sites and between the two sampling seasons during the study period. Both seagrass areas were

dominated by *Thalassia hemprichii* (Pacific turtlegrass), which coexisted with other seagrass species, such as *Enhalus acoroides*, *Cymodocea rotundata* and *Halodule uninervis*. Mean shoot density (\pm standard deviation) of *T. hemprichii* was 255.2 ± 62.8 per m² at Plaridel and 438.4 ± 66.5 per m² at Laguindingan during the wet season, and 172.0 ± 51.2 per m² at Plaridel and 398.4 ± 124.5 per m² at Laguindingan during the dry season (0.5 m \times 0.5 m quadrat, $n = 5$). The mean canopy height of *T. hemprichii* was 19.5 ± 2.8 cm at Plaridel and 19.3 ± 2.4 cm at Laguindingan during the wet season, and 20.7 ± 2.4 cm at Plaridel and 19.7 ± 1.5 cm at Laguindingan during the dry season ($n = 15$). Little or no fishing activity being observed over the seagrass beds during the study period, the potential effects of such activities on fish behavior was negligible.

2.2. Underwater video assessment

The underwater video cameras were deployed during incoming tides between December 2017 and January 2018 (wet season), and between April and May 2018 (dry season). Three or four video deployments were conducted simultaneously in the intertidal seagrass beds over two consecutive census days at each site. The cameras were deployed randomly in different areas each day, being positioned at least 50 m apart (Lefcheck et al., 2019; Unsworth et al., 2014). Independency of each video was also checked by confirming that each replicate video footage showed different fish sizes and species occurrence in each time segment (30 mins). Seven replicate deployments were made in the wet season (three cameras deployed on the first day, four cameras on the second) and six in the dry season (three cameras deployed on both days) at each site, a total of 26 deployments for both sites.

The underwater video cameras (GoPro Hero3 with BacPac batteries) were attached with cable ties to iron stakes driven into the substrate, at a fixed position 10 cm above the seagrass canopy, at each census location (Fig. S1). The video cameras were positioned to point horizontally facing the incoming tide to record fish movement into the seagrass bed and subsequent behavior. The intertidal seagrass beds under video surveillance were located about 100–200 m and 100 m, respectively, from the subtidal beds at Plaridel and Laguindingan. All video deployments were done during daylight hours, between 0600 h and 1500 h. 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) (Becker et al., 2012). Video cameras were deployed during spring tides (maximum tide height, 1.3–1.5 m) at Plaridel and during neap tides (maximum tide height, 0.8–0.9 m) at Laguindingan. Although neap and spring tide classifications differed between the two study sites, the substrate was exposed in the intertidal zones of both at low tide.

2.3. Video analysis

The video footage resolution was 1280×960 pixels per frame at 30 frames per second, with a minimum recording capacity of 3 h. The recorded footage was edited with GoPro video editing software (Quik v2.6.2).

Only fishes that swam within a 1.2 m wide frame of view and 2.0 m distance in front of the camera were subjected to the analyses, since most recorded images of fishes outside that area were unclear. Each fish was identified to the lowest possible taxonomic level, following Allen et al. (2003) and Nakabo (2002), and the arrival time and total length (TL) noted. TL was estimated by comparison with nearby *Thalassia hemprichii* leaves (width ca. 1.0 cm). Some individuals could be identified to genus only (i.e., *Acanthurus* sp., *Pteragogus* sp., *Lethrinus* spp., *Lutjanus* spp., *Pomacentrus* spp., *Pentapodus* sp., *Scarus* spp., *Siganus* spp., and *Arothron* spp.), each genus being considered as a separate taxon in later analyses.

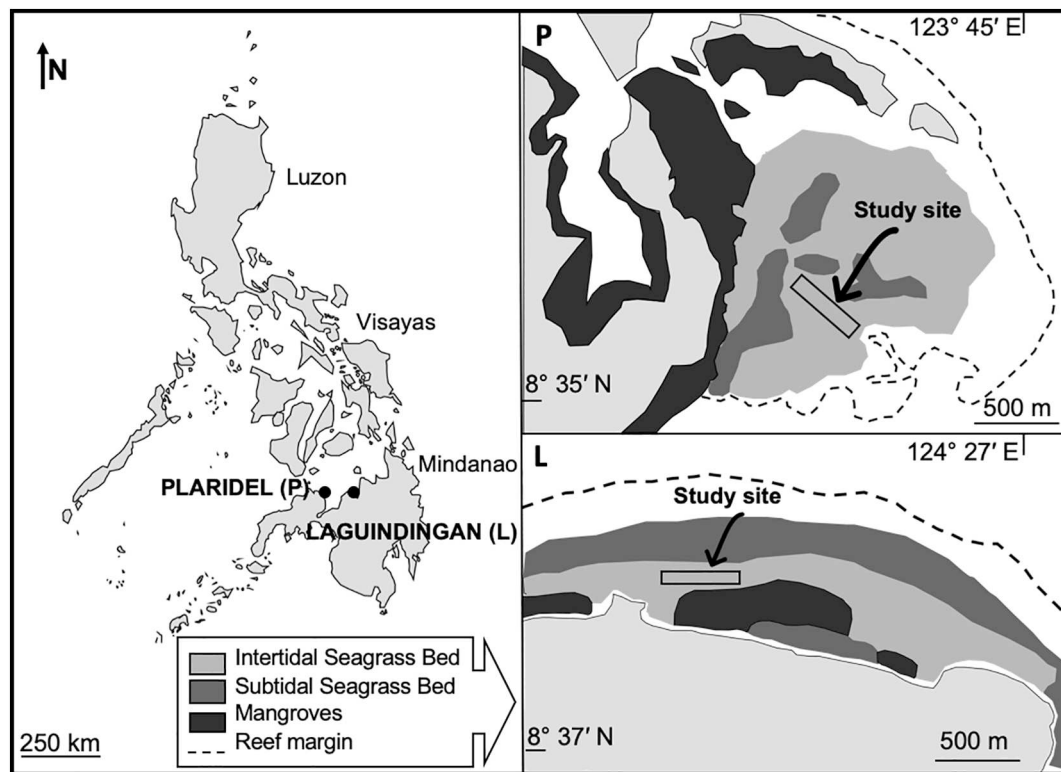


Fig. 1. Location of the seagrass bed sites at Plaridel (P) and Laguindingan (L), northern Mindanao, Philippines.

Compiled data were also used to calculate fish abundance based on the MaxN method (Becker et al., 2012; Cappo et al., 2007), where MaxN is defined as the maximum number of individuals of each taxon present in a single frame within a given period (this study, every 30 min), being a conservative estimate of relative abundance which avoided double counting. Individuals (representing a single taxon) from more than one frame were summed up if they clearly differed in body-size within each period (Zarco-Perello and Enríquez, 2019). Fish size data was collated based on the MaxN calculated abundance. Species richness was determined from the total number of taxa present within each period.

Three behavioral types for tallied fishes were identified, based on dominant movements: (1) feeding behavior - fishes observed feeding directly on seagrass leaves and seagrass-associated epiphytes, (2) swimming behavior (rapid swimming and/or meandering through seagrass leaves without stopping); and (3) unidentified behavior, a behavior of unidentified function - motionless or very slowly swimming but not seen in the act of capturing prey and picking behavior [fishes freely darting in and out of seagrass blades]. If more than one behavioral category was observed for any given fish, only one category was noted, based on the following ranking order: (1) feeding, (2) swimming, and (3) unidentified. This ranking was used to focus the analyses on behavior associated with feeding.

2.4. Data analysis

The duration of video deployments varied due to variations in camera battery life ($3:27 \text{ h} \pm 0:14 \text{ h}$, range from 3:06 h to 3:55 h). Accordingly, only imagery data collected during the first 3 h of each census was used. To obtain a clear and simple portrayal of temporal fluctuations in fish occurrence on incoming tides, each 3 h time span was divided into six 30 min periods (i.e., 0–30 min, 30–60 min,

60–90 min, 90–120 min, 120–150 min, and 150–180 min, hereafter referred as 30 min, 60 min, 90 min, 120 min, 150 min, and 180 min time periods, respectively). Fish MaxN was averaged across replicates for each site and season, and expressed as mean abundance per 30 min period.

Among the top eight dominant fish families based on MaxN abundance data and of the most abundant species in the seagrass beds (Table 1), four families (Labridae, Lethrinidae, Lutjanidae, and Siganidae) and eight species (*Siganus fuscescens*, *S. guttatus*, *Halichoeres argus*, *Lethrinus harak*, *Choerodon anchorago*, *Cheilodactylus inermis*, *Lutjanus fulviflamma*, and *Sphyrna barracuda*) were selected for analyses, since they were common at both sites in both seasons. Furthermore, to determine the migration patterns of different fish sizes, two body-length classes (<10 cm and >10 cm TL) were utilized.

To identify distinct fish behavioral patterns, the number of observations based on multiple frames of each behavior category (i.e. feeding, swimming and unidentified) of species richness, abundance and of the four dominant fish families among the six 30-minute periods were analyzed. Also, the feeding behavior observations of the two size classes of the four dominant fish families and eight fish species were selected for further analysis.

One-way, repeated-measures ANOVA was used to examine differences in mean species richness and mean abundance among the six 30-minute periods within each site and season, as well as, differences in mean abundance and the number of observations exhibiting each behavioral traits of the four dominant fish families and eight fish species (among time periods of incoming tides). Sphericity was analyzed using Mauchly's test, and the Greenhouse-Geisser test (Becker et al., 2012) when assumptions were violated. When assumption of normality (Shapiro-Wilk) of raw and log transformed data ($\log(x + 0.5)$) failed, a non-parametric Friedman test was performed. All statistical analyses were performed using SPSS software (18.0).

Table 1

Fish abundance per hour (\pm SD) for all species in intertidal seagrass beds recorded with underwater videography at Plaridel and Laguindingan during the wet and dry seasons.

Family	Species	MaxN	Plaridel		Laguindingan		Behavior
			Wet	Dry	Wet	Dry	
Acanthuridae	<i>Acanthurus</i> sp.	1	0.05 \pm 0.13				S
Apogonidae	<i>Cheilodipterus quinquelineatus</i>	6		0.06 \pm 0.14	0.10 \pm 0.25	0.17 \pm 0.28	S
	<i>Fibramia thermalis</i>	76	3.33 \pm 8.82		0.29 \pm 0.76		S
	<i>Ostorhinchus ishigakiensis</i>	45		0.06 \pm 0.14	1.24 \pm 3.313	1.00 \pm 1.37	S
	<i>Sphaeramia orbicularis</i>	84			0.86 \pm 1.70	3.67 \pm 4.50	S, F
	<i>Rhinecanthus verrucosus</i>	5	0.24 \pm 0.63				S
Balistidae	<i>Petroscirtus breviceps</i>	35	0.43 \pm 0.60	0.06 \pm 0.14	1.14 \pm 0.60	0.06 \pm 0.14	S, F
Blenniidae	<i>Petroscirtus variabilis</i>	20	0.29 \pm 0.23	0.33 \pm 0.56	0.14 \pm 0.18	0.28 \pm 0.53	S, F
	<i>Aeoliscus strigatus</i>	22	0.81 \pm 1.41	0.22 \pm 0.34	0.05 \pm 0.13		S, F
Fistulariidae	<i>Fistularia commersonii</i>	4	0.19 \pm 0.38				S, F
Gerreidae	<i>Gerres oyena</i>	14	0.67 \pm 0.43				S, F
Gobiidae	<i>Amblygobius phalaena</i>	5	0.24 \pm 0.42				S
	<i>Exyrias puntang</i>	2	0.10 \pm 0.25				S, F
Labridae	<i>Cheilio inermis</i>	54	0.86 \pm 0.57	0.94 \pm 0.39	0.62 \pm 0.52	0.33 \pm 0.30	S, F
	<i>Choerodon anchorago</i>	62	0.76 \pm 1.10	0.39 \pm 0.68	0.95 \pm 0.52	1.06 \pm 0.44	S, F
	<i>Halichoeres argus</i>	149	2.57 \pm 1.81	2.56 \pm 1.03	0.67 \pm 0.67	1.94 \pm 0.53	S, F
	<i>Halichoeres papilionaceus</i>	95	1.57 \pm 0.63	1.50 \pm 0.78	0.24 \pm 0.32	1.67 \pm 0.60	S, F
	<i>Halichoeres scapularis</i>	26	0.95 \pm 0.83	0.33 \pm 0.67			S
	<i>Oxycheilinus bimaculatus</i>	5	0.19 \pm 0.33			0.06 \pm 0.14	S, F
	<i>Pteragogus</i> sp.	1	0.05 \pm 0.13				F
	<i>Stethojulis strigiventer</i>	15	0.52 \pm 0.72	0.22 \pm 0.54			S, F
	<i>Stethojulis trilineata</i>	3	0.10 \pm 0.16	0.06 \pm 0.14			S
	<i>Lethrinus genivittatus</i>	3	0.14 \pm 0.26				S
	<i>Lethrinus harak</i>	82	0.90 \pm 0.71	0.50 \pm 0.55	0.90 \pm 0.50	1.94 \pm 0.74	S, F
	<i>Lethrinus obsoletus</i>	3	0.05 \pm 0.13		0.10 \pm 0.25		S, F
Lethrinidae	<i>Lethrinus spp.</i>	82	1.95 \pm 1.10	0.33 \pm 0.67	0.62 \pm 0.52	1.22 \pm 0.89	S, F
	<i>Lethrinus variegatus</i>	7	0.33 \pm 0.47				S, F
	<i>Lutjanus decussatus</i>	7	0.19 \pm 0.33		0.05 \pm 0.13	0.11 \pm 0.17	S
	<i>Lutjanus fulviflamma</i>	52	0.43 \pm 0.46	0.06 \pm 0.14	1.61 \pm 1.02	0.72 \pm 0.49	S, F
Lutjanidae	<i>Lutjanus spp.</i>	2	0.05 \pm 0.13			0.06 \pm 0.14	F
	<i>Acreichthys tomentosus</i>	55	1.48 \pm 0.72	1.28 \pm 0.49		0.06 \pm 0.14	S, F
Monacanthidae	<i>Ellochelon vaigiensis</i>	9				0.50 \pm 1.22	S
Mugilidae	<i>Mugil cephalus</i>	39	1.14 \pm 1.10		0.05 \pm 0.13	0.78 \pm 1.60	S, F
	<i>Mulloidichthys flavolineatus</i>	1			0.05 \pm 0.13		F
Mullidae	<i>Parupeneus barberinoides</i>	7	0.24 \pm 0.32	0.11 \pm 0.27			S, F
	<i>Parupeneus barberinus</i>	74	2.76 \pm 2.23	0.89 \pm 0.72			S, F
	<i>Parupeneus heptacanthus</i>	3	0.14 \pm 0.18				S
	<i>Pentapodus bifasciatus</i>	4	0.19 \pm 0.50				S
Nemipteridae	<i>Pentapodus sp.</i>	2	0.10 \pm 0.25				S
	<i>Scolopsis bilineatus</i>	3				0.17 \pm 0.41	S
	<i>Scolopsis ciliatus</i>	8	0.38 \pm 0.87				S, F
	<i>Scolopsis lineatus</i>	5				0.28 \pm 0.44	S
	<i>Parapercis cylindrica</i>	10	0.33 \pm 0.38	0.17 \pm 0.28			S
Pinguipedidae	<i>Pomacentrus</i> spp.	2	0.05 \pm 0.13			0.06 \pm 0.14	S
Pomacentridae	<i>Pomacentrus tripunctatus</i>	26	0.48 \pm 1.26		0.24 \pm 0.32	0.61 \pm 0.71	S
	<i>Leptoscarus vaigiensis</i>	7	0.33 \pm 0.88				S, F
Scaridae	<i>Scarus</i> spp.	108	2.57 \pm 3.45	2.78 \pm 5.86		0.22 \pm 0.17	S, F
Siganidae	<i>Siganus fuscescens</i>	1292	36.33 \pm 8.19	17.17 \pm 8.30	5.52 \pm 2.15	5.78 \pm 1.63	S, F
	<i>Siganus guttatus</i>	110	0.19 \pm 0.50	0.39 \pm 0.65	2.86 \pm 2.92	2.17 \pm 1.13	S, F
	<i>Siganus puellus</i>	1			0.05 \pm 0.13		F
	<i>Siganus</i> spp.	4	0.14 \pm 0.38	0.06 \pm 0.14			S, F
Sphyraenidae	<i>Sphyraena barracuda</i>	24	0.05 \pm 0.13	0.28 \pm 0.68	0.57 \pm 0.50	0.33 \pm 0.21	S
Syngnathidae	<i>Corythoichthys haematopterus</i>	14	0.67 \pm 0.51				F
	<i>Syngnathoides biaculeatus</i>	3	0.05 \pm 0.13	0.06 \pm 0.14	0.05 \pm 0.13		F
Terapontidae	<i>Terapon jarbua</i>	7	0.24 \pm 0.50	0.06 \pm 0.14		0.06 \pm 0.14	S
Tetraodontidae	<i>Arothron hispidus</i>	11	0.14 \pm 0.26	0.06 \pm 0.14	0.14 \pm 0.18	0.22 \pm 0.27	S, F
	<i>Arothron manilensis</i>	2	0.05 \pm 0.13			0.06 \pm 0.14	S, F
	<i>Arothron</i> spp.	4	0.05 \pm 0.13		0.10 \pm 0.25	0.06 \pm 0.14	S
	<i>Canthigaster compressa</i>	16	0.14 \pm 0.18	0.61 \pm 0.88		0.11 \pm 0.27	S, F
Total no. of families	23		23	15	13	14	
Total no. of species	59		51	28	26	31	

Abbreviations indicate fish behavior (S swimming, F feeding). Data expressed as means for all video deployments [wet season ($n = 7$), dry season ($n = 6$)].

3. Results

3.1. Species richness and abundance

Overall, 59 fish species representing 23 families were recorded in the 26 video deployments (53 species in 23 families at Plaridel, 37 species in

17 families at Laguindingan) (Table 1). The number of species continued to increase until the conclusion of recording (Fig. 2). Nearly half of all species recorded occurred within the camera's frame of view within the first 30 min of recording (as tide height increased from ca. 0.3 to 0.4 m, Fig. 2). Furthermore, 80% of all species recorded occurred within the first two hours of each recording for both sites and seasons (Fig. 2).

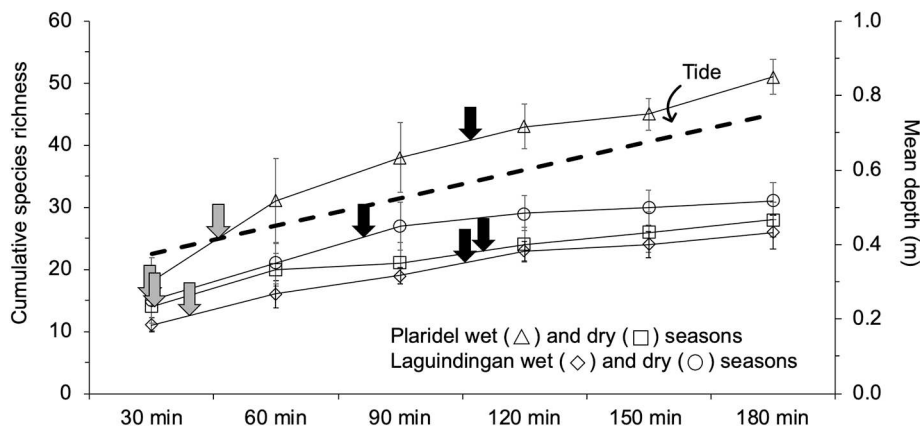


Fig. 2. Cumulative species richness for each study site during flood tides over two seasons. Gray arrows indicate 50% of total species richness recorded for each site and season; black arrows indicate 80% of species richness. Data expressed as mean value for each video deployment [wet season ($n = 7$), dry season ($n = 6$)]. Tidal state expressed as mean depth for both sites and seasons in each time period.

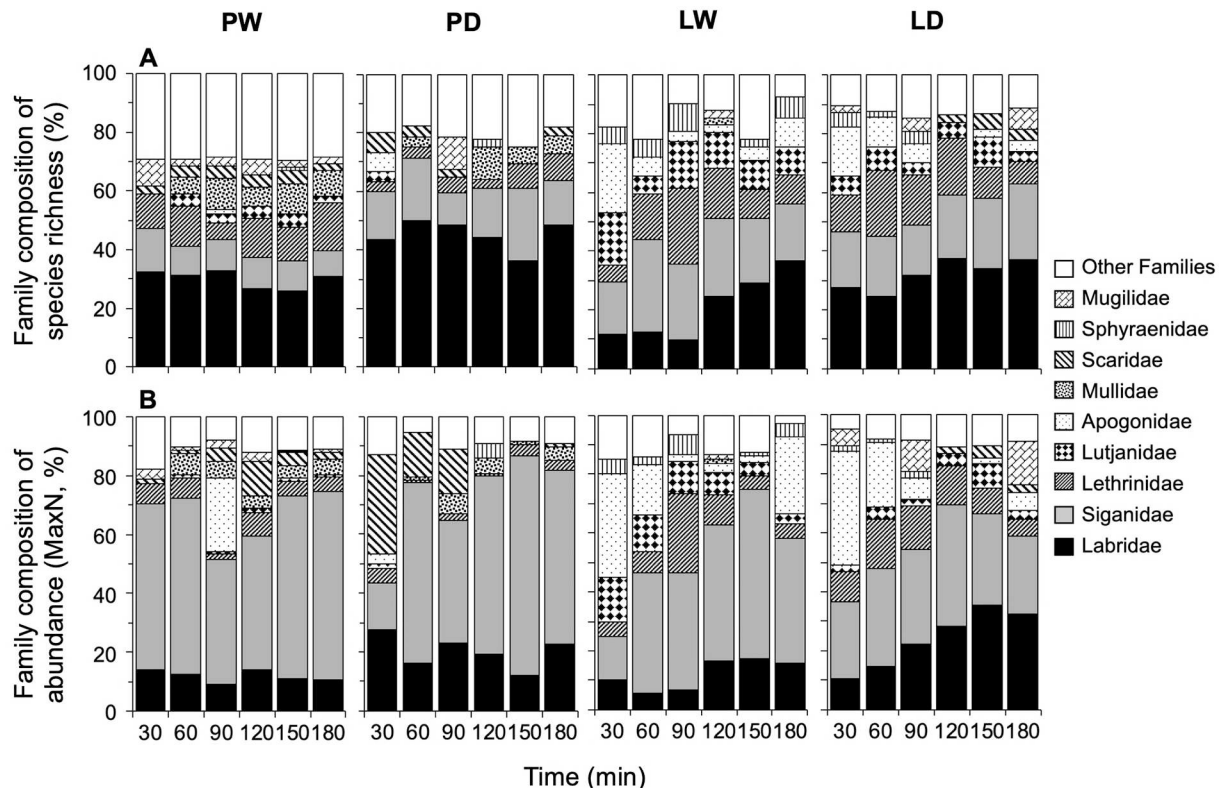


Fig. 3. Relative family composition of fish species richness (A) and abundance (B), by time period at Plaridel (P) and Laguindingan (L) in the wet (W) and dry (D) seasons. Data expressed as means for all video deployments [wet season ($n = 7$), dry season ($n = 6$)].

Relative to both site and season, Labridae was the most speciose family throughout the recorded time periods, followed by Siganidae and Lethrinidae (Fig. 3A), whereas Siganidae was represented by the highest fish abundance throughout the same time periods, followed by Labridae (except for the first two time periods at Laguindingan, during which Apogonidae was the most abundant in both seasons) (Fig. 3B). Nonetheless, each fish family was comprised of a few (one or two) dominant species.

Mean species richness and abundance varied temporally in some cases (Fig. 4); mean species richness and mean abundance showed increasing trend during the wet season at Plaridel (one-way repeated measures ANOVA, both $p < .05$) and at Laguindingan (one-way repeated measures ANOVA, $p < .001$) among time periods.

The four dominant fish families showed nonsignificant difference in fish abundance among time periods in both sites and seasons (one-way repeated measures ANOVA or Friedman test, all $p > .05$, Fig. 5).

However, few exceptions were Labridae and Siganidae showed an increased in abundance among time periods during the wet season at Laguindingan (Friedman test, $p < .01$ for both families) and at Plaridel (Friedman test, $p < .05$ for Labridae), while, Lethrinidae showed decreasing trend during the dry season at Laguindingan (Friedman test, $p < .05$).

3.2. Fish behavioral patterns

Mean species richness and abundance of fishes indicated feeding and unidentified behaviors did not differ significantly among time periods by site or season (one-way repeated measures ANOVA or Friedman test, all $p > .05$, Fig. 4), except in mean abundance exhibited feeding behaviors at Plaridel during the wet season (Friedman test, $p < .05$). However, the observed number of swimming behavior varied temporally in mean species richness at Plaridel during the wet season

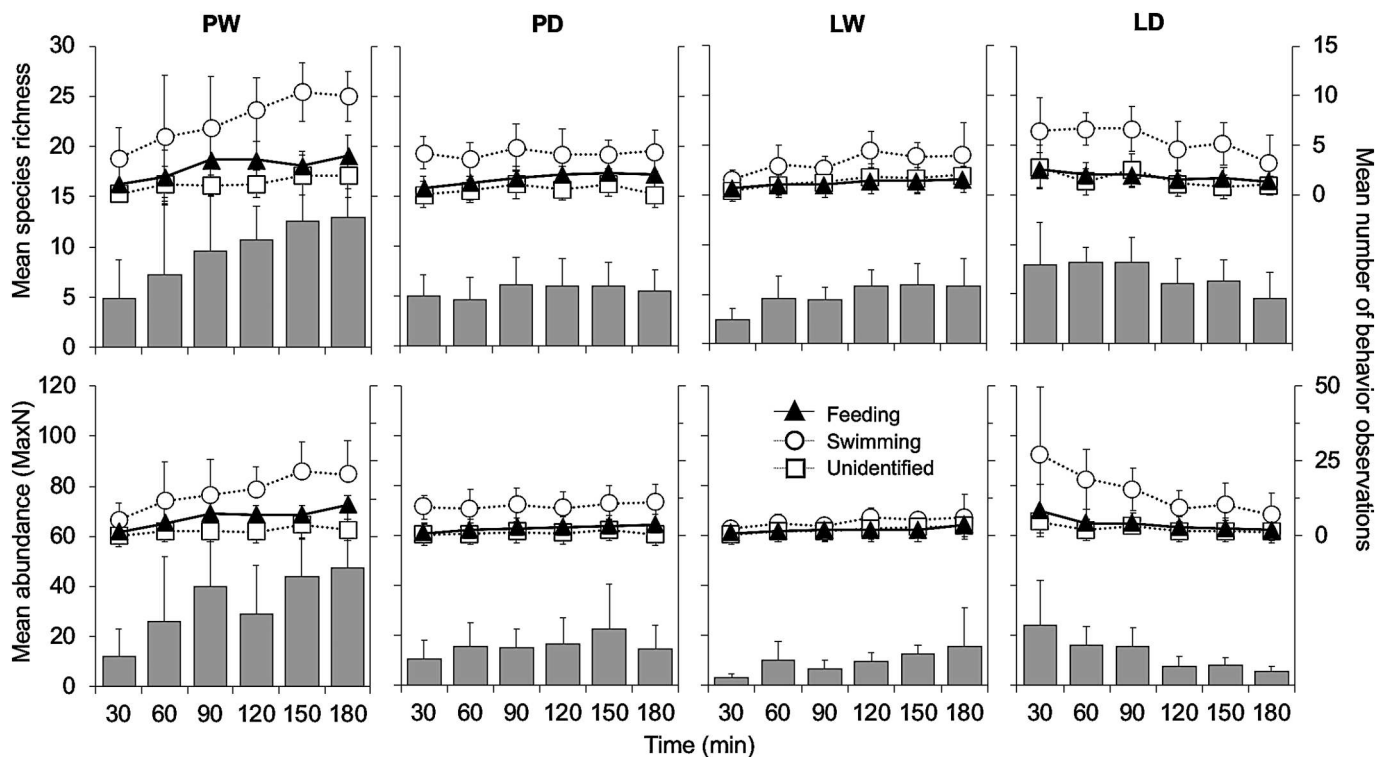


Fig. 4. Mean species richness, abundance and number of behavior observations, by time period at Plaridel (P) and Laguindingan (L) in wet (W) and dry (D) seasons. Data expressed as means for all video deployments [wet season ($n = 7$), dry season ($n = 6$)]; vertical bars depict one standard deviation of mean. Please note differences in y-axis scale between graphs. The primary y-axis was based on a single frame per species within the 30-min period, while the secondary y-axis based on multiple frames.

(one-way repeated measures ANOVA, $p < .01$), and in mean abundance at Plaridel and Laguindingan during the wet season (one-way repeated measures ANOVA, both $p < .05$).

Among the four most abundant (individual numbers) fish families, Labridae, Lethrinidae, and Siganidae began to exhibit feeding behavior just after video recording commenced, whereas Lutjanidae exhibited feeding behavior at different time periods at each site in each season, most notably from 90 min onwards (Fig. 5). The observed number of feeding behavior varied temporally for Siganidae during the wet season at Plaridel (Friedman test, $p < .01$), as did swimming behavior exhibited by Labridae during wet season at both sites (Friedman test, $p < .05$), and by Lethrinidae during the wet season at Plaridel and during the dry season at Laguindingan (Friedman test, $p < .05$, both). On the other hand, lutjanids exhibiting feeding, and swimming behavior did not differ significantly by site or season (Friedman test, all $p > .05$). Swimming was the dominant behavior of Labridae, swimming and unidentified behavior the dominant behavior of Lethrinidae and Lutjanidae, and feeding the dominant behavior of Siganidae, throughout incoming tides (Fig. 5).

3.3. Body-length classes of dominant families

In each family, fishes in the <10 cm body-length (TL) class were most abundant throughout incoming tides (Fig. 6). Fish abundance varied temporally for <10 cm TL Labridae during the wet season at Plaridel and at Laguindingan (one-way repeated measures ANOVA, $p < .05$ and Friedman test, $p < .01$, respectively) and for Lethrinidae and Siganidae during the dry season at Laguindingan (Friedman test, $p < .05$, both families), although fish abundance in the large size class >10 TL cm did not differ by site or season in any of the four most dominant fish families for the six-time periods associated with the first 3 h of incoming tide (Friedman test, all $p > .05$).

The timing of feeding behavior of <10 cm TL size class of Labridae

and Siganidae began within the first two time periods recorded for both sites and seasons. However, the timing of feeding behavior of <10 cm TL Lethrinidae varied at each site in each season. That of Lutjanidae began relatively later, usually from the 90 min period onwards, except at Plaridel during the dry season when no feeding was observed. Large size class (>10 cm TL) labrids, lethrinids and lutjanids appeared relatively late at both sites in both seasons, mostly appearing from 90 min onwards throughout the incoming tide, and few exhibited feeding behaviors. On the other hand, >10 cm TL large siganids appeared in the seagrass beds within the first 30 min period, exhibiting mostly feeding behavior throughout the incoming tide. Small juveniles of <10 cm TL Siganidae exhibiting feeding behavior varied temporally during the wet season at Plaridel (one-way repeated measures ANOVA, $p < .001$). On the other hand, labrids, lethrinids and lutjanids feeding behavior did not differ temporally in both size classes throughout the incoming tide in each site and season (Friedman test, all $p > .05$).

3.4. Body-length classes of dominant species

Among the eight target species, most individual *Sphyrna barracuda* and *Siganus guttatus* belonged to the >10 cm TL class, whereas fishes of the other six species belonged mostly to the <10 cm TL class (all recordings) (Fig. 7). Although most size classes of the eight species showed no significant differences in abundance over a tidal cycle (one-way repeated measures ANOVA or Friedman test, all $p > .05$), exception was found for <10 cm TL *Siganus fuscus* at Laguindingan during both seasons (one-way repeated measures ANOVA and Friedman test, $p < .05$).

The timing of feeding behavior in each species varied between body size classes. For instance, the <10 cm TL classes of *Halichoeres argus*, *Lethrinus harak*, *S. fuscus* and *S. guttatus* started feeding in the 30 min time period. On the other hand, <10 cm TL *Cheilodactylus inermis*, *Lutjanus fulviflamma* and *Choerodon anchorago* exhibited feeding

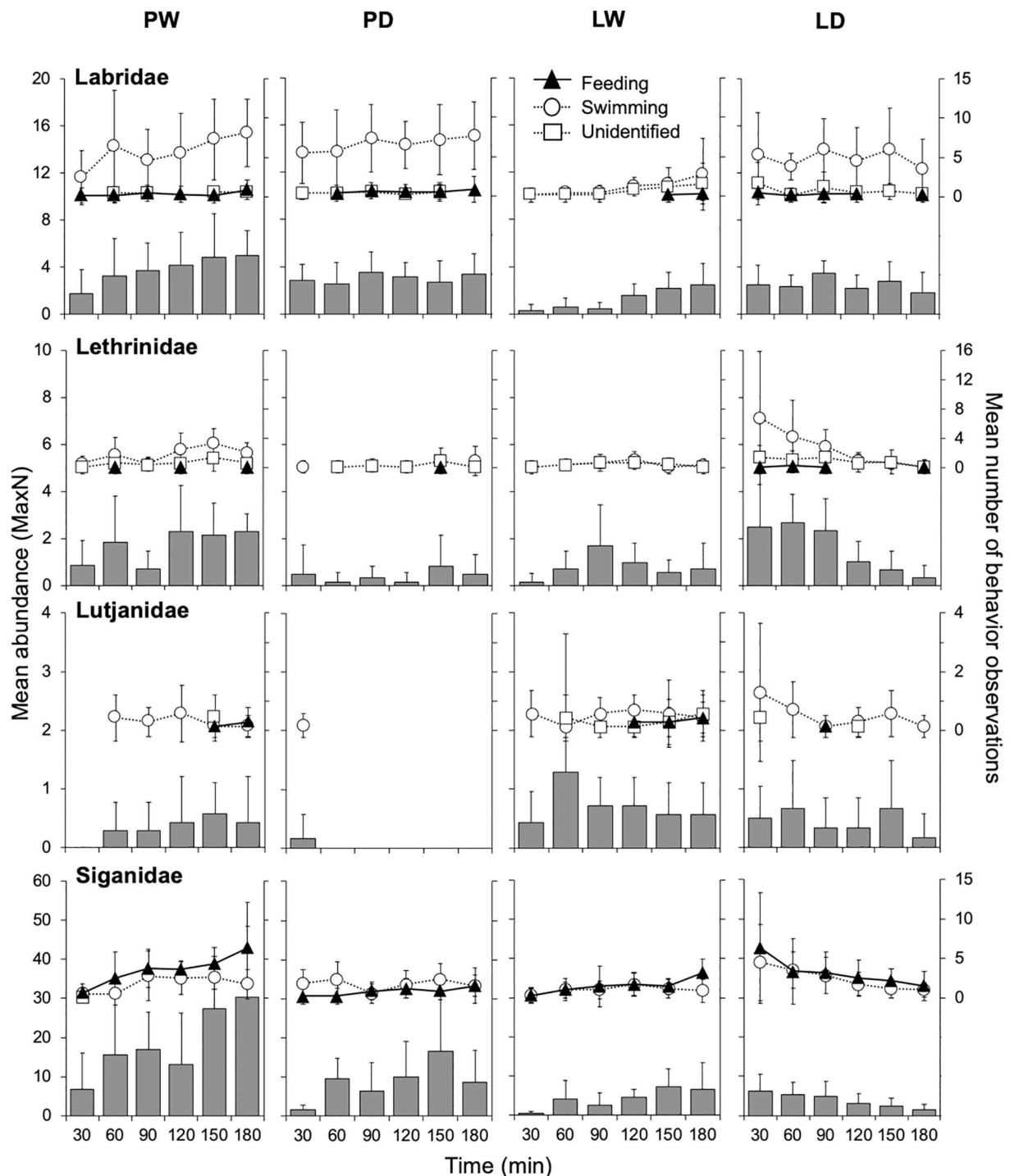


Fig. 5. Mean abundance and number of behavior observations of the four most dominant fish families, by time period at Plaridel (P) and Laguindingan (L) in the wet (W) and dry (D) seasons. Data expressed as means for all video deployments [wet season ($n = 7$), dry season ($n = 6$)]; vertical bars depict one standard deviation of mean. Please note differences in y-axis scale between graphs. The primary y-axis was based on a single frame per species within the 30-min period, while the secondary y-axis based on multiple frames.

behavior during a later time period. The large size class (> 10 cm TL) of *S. fuscescens* and *S. guttatus* started feeding at the onset of recording. While, > 10 cm TL piscivorous species *C. inermis* and *S. barracuda* tended to be more abundant later in the tidal cycle, the former appearing to feed during a later time period (Fig. S1). Small juveniles of < 10 cm TL *Siganus fuscescens* exhibited feeding behaviors varied among time periods during the wet season at Plaridel (one-way repeated measures ANOVA, $p < .001$), while the other seven target species exhibited feeding behavior did not differ significantly among

the time periods in both sites and seasons (Friedman test, all $p > .05$).

4. Discussion

The study revealed that many small fishes, particularly species of Labridae, Siganidae, Lethrinidae and Lutjanidae, migrated to intertidal seagrass habitats immediately after the rising tide had inundated the beds, being contrary to the conventional belief that few fishes utilize seagrass beds in the early (shallow) phase of a rising tide (Unsworth

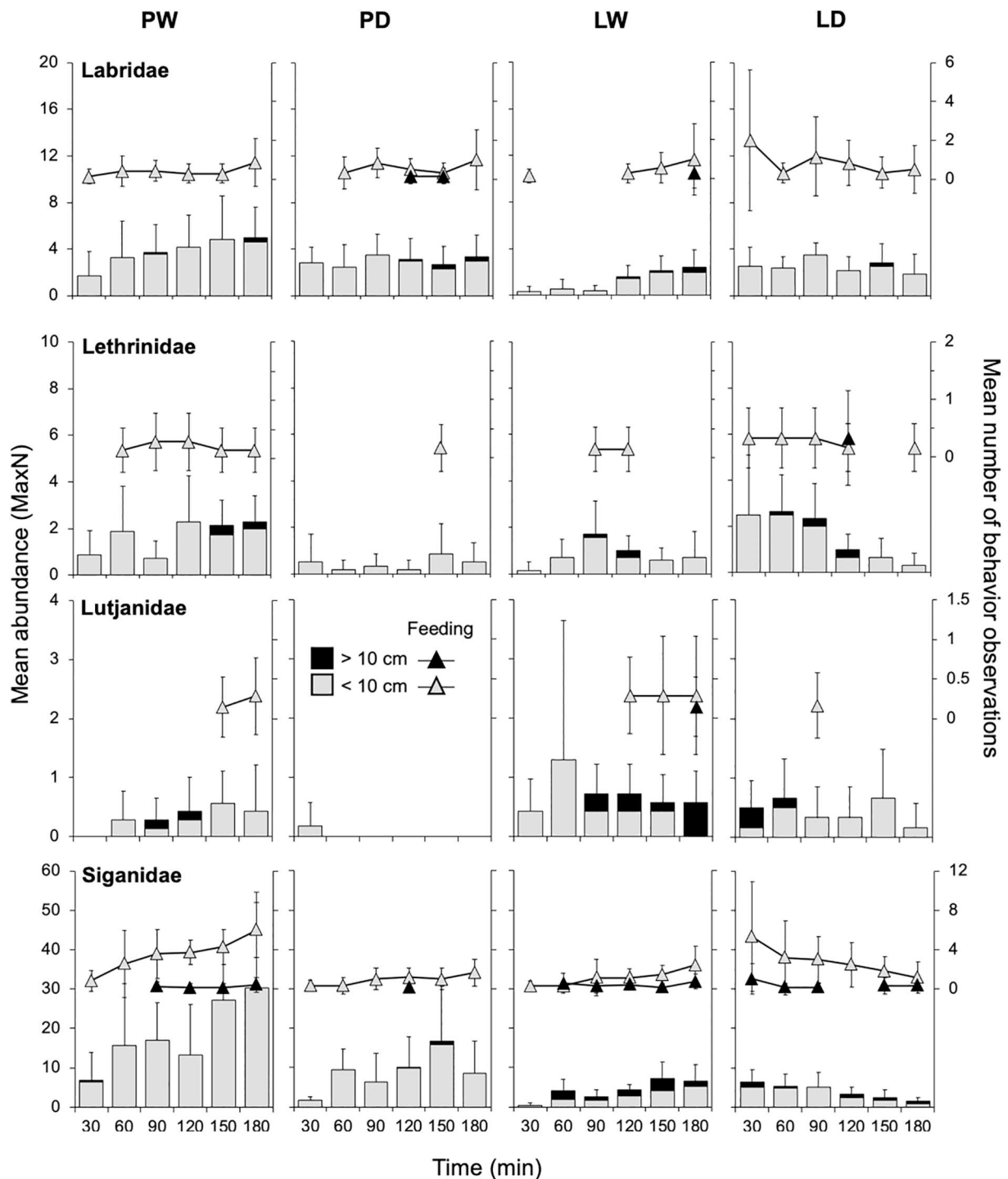


Fig. 6. Mean abundance and number of feeding behavior observation of the four most dominant fish families, by body-length class and time period at Plaridel (P) and Laguindingan (L) in the wet (W) and dry (D) seasons. Data expressed as means for all video deployments [wet season ($n = 7$), dry season ($n = 6$)]; vertical bars depict one standard deviation of mean. Please note differences in y-axis scale between graphs. The primary y-axis was based on a single frame per species within the 30-min period, while the secondary y-axis based on multiple frames.

et al., 2007). Such movement into shallow (intertidal) seagrass beds with incoming tides is probably ubiquitous throughout the Philippine archipelago, because fish family composition found in other seagrass bed sites across the country were similar, dominated particularly by that of Labridae (Ramos et al., 2015) and Siganidae (Salita et al., 2003). Smaller juveniles (<10 cm TL) of a wide variety of species dominated the intertidal seagrass habitats, especially during the incoming tide, supporting Krumme's (2009) speculation that smaller fishes would be more common in shallower water.

In addition, we found that more species continually arrived in intertidal seagrass habitats during rising tide levels. Even juveniles of some species thought to exhibit site fidelity, also exploited shallow seagrass habitat as it became available. For example, although small *Lethrinus harak* (<20 cm TL) exhibit strong site fidelity in subtidal seagrass beds during the day (Nanami and Yamada, 2009), <10 cm TL juveniles were most common in the intertidal seagrass habitats. This phenomenon (i.e., juveniles with high site fidelity accessing intertidal seagrass habitats when possible), in addition to evidence here of new

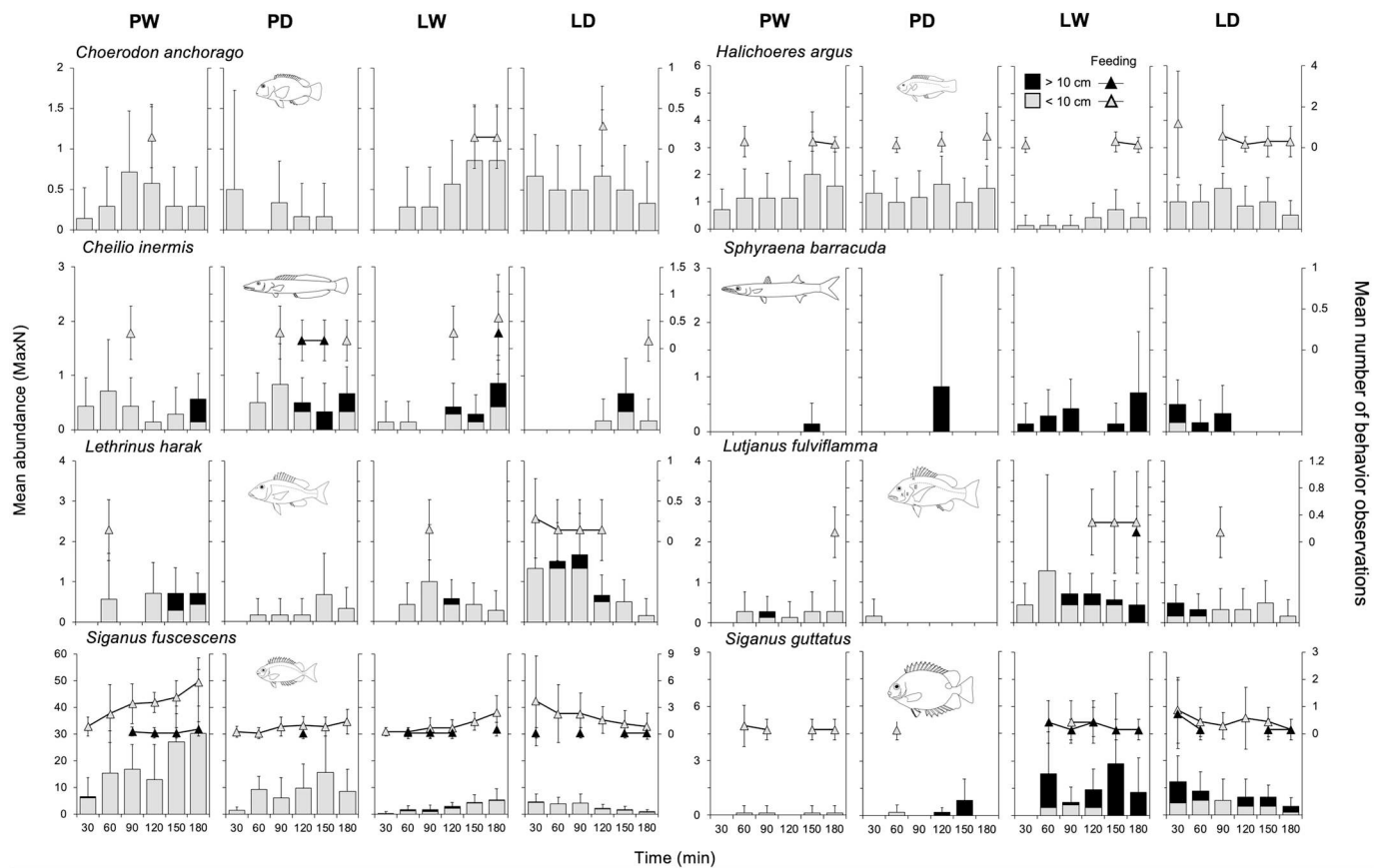


Fig. 7. Mean abundance and number of feeding behavior observation of eight target fish species, by body-length class and time period at Plaridel (P) and Laguindingan (L) in the wet (W) and dry (D) seasons. Data expressed as means for all video deployments [wet season ($n = 7$), dry season ($n = 6$)]; vertical bars depict one standard deviation of mean. Please note differences in y-axis scale between graphs. The primary y-axis was based on a single frame per species within the 30-min period, while the secondary y-axis based on multiple frames.

species continuously arriving as tide levels rose, strongly suggests that small fishes benefit from exploiting intertidal seagrass habitats.

Feeding behavior observed in the dominant fish families and species throughout the incoming tidal regime indicated that they utilized intertidal seagrass beds as a foraging ground. Studies have identified that the food items consumed by most of the target species included small crustaceans i.e. harpacticoid copepods, gammaridean amphipods, tanaids, and shrimps by *Choerodon anchorago*, *L. harak*, *Halichoeres argus* and *Lutjanus fulviflamma*, filamentous algae and seagrasses by *Siganus fuscus* and *S. guttatus* (Nakamura et al., 2003), and fishes by *Cheilio inermis* (Nakamura et al., 2003) and *Sphyræna barracuda* (Lee et al., 2014). Because intertidal seagrass habitats in tropical regions sometimes harbor abundant prey, including small epiphytic animals and microalgae (Nakamura and Sano, 2005), otherwise unavailable food resources become accessible when the beds are inundated by incoming tides, which may motivate fish to migrate to the latter from adjacent subtidal areas. Small individuals of piscivorous *S. barracuda* may also migrate to intertidal seagrass habitats for foraging, often remaining still and quickly attacking passing prey (Grubich et al., 2008; Porter and Motta, 2004). A complex seagrass structure sometimes favors such ambush hunting strategy (Horinouchi et al., 2009), enhanced when the predator merges into the background. Changing body color patterns were recorded in *S. barracuda* whilst remaining motionless close to seagrass leaves, possibly preparing for an ambush attack. Similar hunting behavior has been reported from fish studies on subtidal seagrass beds (Canion and Heck, 2009; Schultz and Kruschel, 2010) and sponge habitats (Scharf et al., 2006). Improved hunting efficiency, in addition to an increasing abundance of small prey fish, may be at least partly responsible for the frequent occurrence of *S. barracuda* in

intertidal seagrass habitats. Nevertheless, to date, supporting data are lacking.

This study revealed that larger fishes seldom entered intertidal seagrass habitats in the early phase of rising tide, instead frequenting them during higher tide levels, probably being constrained by size during lower tide levels. Davis et al. (2017) also reported the arrival times of large fish, such as *Sphyræna obtusata* and *Tylosurus gavioides*, as being mostly during later periods of incoming tides on intertidal seagrass beds. Such phenomena have been reported in other intertidal habitats, Ellis and Bell (2008), for example, finding that large transient fish species such as snapper (*Lutjanus synagris*) and spadefish (*Chaetodipterus faber*) migrated into intertidal mangroves at peak high tide. In addition, Bretsch and Allen (2006) reported that large sized *Leiostomus xanthurus* and *Mugil curema* were more abundant at later tides in intertidal salt marsh creeks. Late arrivals of larger fishes are probably the norm for intertidal habitats.

The study revealed that intertidal seagrass habitats in the southern Philippine archipelago constitute foraging grounds for a diverse array of fish species in juvenile stage, including some fishery target families (Lethrinidae, Lutjanidae and Siganidae). It is likely that intertidal seagrass beds are equally utilized by fishes in other areas of the tropical Indo-Pacific, with fish fauna similar to those at the present study sites (Dorenbosch et al., 2005; Nakamura and Tsuchiya, 2008; Pogoreutz et al., 2012). However, nearshore intertidal seagrass habitats are rapidly disappearing in much of the Indo-Pacific region due to increasingly widespread anthropogenic alterations to nearshore habitats (Kirkman and Kirkman, 2002). As coastal developments expand to support ever larger human populations in coastal zones of tropical Indo-Pacific countries (Mora et al., 2011), further information on the ecological benefits of intertidal seagrass habitats is vital for future

conservation and management of such coastal areas.

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