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Citation	Fisheries science, 83(4), 523-535 https://doi.org/10.1007/s12562-017-1082-4
Issue Date	2017-07
Doc URL	http://hdl.handle.net/2115/71161
Rights	The final publication is available at www.springerlink.com via http://dx.doi.org/10.1007/s12562-017-1082-4
Type	article (author version)
File Information	Fisheries science_83(4)_523-535.pdf

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Importance of outer reef slopes for commercially important fishes: implications for designing a marine protected area in the Philippines

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Abstract A passive acoustic telemetry survey was conducted to determine occurrence patterns of commercially important fishes on a steep reef slope along a marine protected area (MPA) in the southern Philippines, where the outer reef edge is often set as an offshore MPA boundary. Based on 4–61 days of tracking data from 21 detected individuals from five species (*Lutjanus argentimaculatus*, *Lutjanus monostigma*, *Lethrinus atkinsoni*, *Lethrinus obsoletus*, and *Siganus guttatus*; 20.7–69.2 cm fork length) caught near the reef slope of the MPA, *S. guttatus* occurred most frequently on the reef flat of the MPA, whereas all individuals of the four lutjanid and lethrinid species were primarily (99.4–100%) detected near the reef slope, and nine individuals (56.3% of the four species) belonging to three species (other than *L. obsoletus*) most likely used the shallow (≤10 m) and deep (≥20 m) layers and thus, those middle layer of the slope. These findings indicate that commercially important lutjanid and lethrinid species predominantly and vertically used the areas near the reef slope, suggesting the importance of fully including reef slopes in MPAs to enhance their effectiveness by conserving such fishes.

Keywords Acoustic telemetry, Commercially important fish, Coral reef, Depth use, Marine protected area, Reef slope,

Introduction

A fringing coral reef is generally composed of an inner reef flat and an outer reef edge and slope. Offshore boundaries of marine protected areas (MPAs) established on fringing reefs are often set along outer reef edges (e.g., [1–3]) without exception in the Philippines (Philippine MPA Database: www.mpa.msi.upd.edu.ph, Accessed January 2016). Thus, deeper areas of the reef slope are not included in such MPAs and have been used by fishermen as fishing grounds (e.g., [4–6]). The boundary is set along the outer reef edge because the edges are easily recognized navigational landmarks used by fishermen [7] and because conservation benefits to mobile species are expected to be enhanced by limiting "spillover" [8, 9] into unprotected areas if the habitat is restricted by a natural MPA boundary such as a reef edge [10–12].

However, the negative effect of intensive fishing along the MPA boundary known as "fishing the line" is a concern on conservation of fisheries resources [13–16]. In the Philippines, deeper areas of reef slope just outside the MPA boundary are often used by fishermen as fishing grounds and such fishing the line is suggested to decrease MPA effectiveness [17]. Therefore, if many commercially important fishes frequently move between inner shallow reefs (inside MPAs) and outer deep reef slopes (outside MPAs) or if such fishes only use the slopes as their main habitat, fully including slopes inside the MPAs would help conservation efforts. However, little is known about the occurrence patterns of fishes along reef slopes (but see [18–20]).

In this study, we targeted five commercially important and mobile reef-associated fishes (members of the families Lutjanidae, Lethrinidae, and Siganidae) captured near the reef edge of a no-take MPA in the southern Philippines, where the edge contains a steep reef slope and is set as an offshore MPA boundary. We assessed their occurrence patterns near the slope using passive acoustic telemetry, particularly focusing on their vertical depth use.

3

Materials and methods

Study site and acoustic receiver array

The field survey was conducted from August 2012 to October 2013 on a fringing reef with the reef flat zone facing

the open sea off Laguindingan, northern Mindanao Island, the Philippines (Fig. 1). Here, a no-take MPA with a

total area of 0.31 km^2 (length from shore side to offshore side: ca. 760 m, width: 360–450 m) has been allocated

since 2002. The seascape composition of the MPA included near-shore mangroves, a seagrass bed, and an offshore

coral reef. The coral reef was composed of hermatypic corals, such as tabular and branching *Acropora* (living

coral coverage >80%). The seagrass bed and mangroves at the site have been described in Honda et al. [21]. The

offshore boundary of the MPA is set along the reef edge consisting of a steep reef slope, with bottom depth along

the slope of 20–30 m. The horizontal distance between the shallowest and deepest parts along the slope was

generally <5 m. This MPA has been strictly regulated since its establishment in 2002 through an installation of a

watchtower. Fishing the line by hook-and-line is operated legally and regularly along the reef edge of this MPA

(authors' pers. comm., 2011; Fig. 1b).

Twelve acoustic receivers (VR2W; Vemco, Shad Bay, NS, Canada) were deployed at 12 stations located

on the coral reef (on a reef flat and the top and bottom of a reef slope) inside or outside the MPA, as shown in Fig.

1. The stations where receivers were deployed on the reef flat are described from west to east as flat1–flat4,

whereas stations at the top and bottom along the reef slope are described as shallow1–shallow4 and deep1–deep4,

respectively. Flat2, flat3, shallow2, and shallow3 were located inside the MPA, whereas the remaining stations

were located outside the MPA (Fig. 1). Bottom depths at the "flat" stations were 1.0–1.5 m at low tide and 2.0–

4

2.5 m at high tide. When deployed, those at the "shallow" stations (shallow1–shallow4) were 6, 9, 5, and 10 m whereas those at the "deep" stations (deep1–deep4) were 23, 26, 29, and 29 m. However, depth fluctuated depending on the tide. Receivers were deployed in small sandy patches at the flat stations using a concrete anchor, rope, and a buoy. The bottom of each receiver was placed 0.5 m away from the anchor, and the buoy was placed 1 m away from the tip of the receiver. Receivers at the shallow and deep stations were deployed using aluminum cable and two buoys. The cable was locked to coral or rocks at the shallow stations or to a concrete anchor at the deep stations. The bottom of each receiver was placed 1.5 m away from the locked point (shallow stations) or the anchor (deep stations), and the buoys were placed at least 2 m away from the tip of the receiver. All receivers were deployed from 25 August to 26 November 2012 and from 22 May to 10 October 2013.

The detection ranges of the receivers fluctuated depending on bottom topography and sea conditions, such as depth, tide, wave action, and wind speed (e.g., [22–24]). Based on the results of Honda et al. [25], who studied the same site using passive acoustic telemetry and real-time detection, the detection ranges of the receivers were in a radius of 40–120 m at the flat stations, 50–150 m at the shallow stations, and 60–180 m at the deep stations.

Fish capture and tagging

All fish were caught inside or along the offshore boundary (reef slope) of the MPA. The target species were *Lutjanus argentimaculatus*, *Lutjanus monostigma* (Lutjanidae), *Lethrinus atkinsoni*, *Lethrinus obsoletus* (Lethrinidae), and *Siganus guttatus* (Siganidae). These species are listed as "commercial fish" on FishBase (www.fishbase.org, Accessed January 2016) and are regarded as common commercial targets at our study site (authors' pers. comm., 2011).

5

We used hook-and-line and box-shaped fish traps, locally called *bubo*. Five *S. guttatus* [20.7–27.9 cm fork length (FL)] were caught by the former method on reef flats and shallow reef slope inside the MPA, whereas the remaining four species were caught in traps [two *Lutjanus argentimaculatus* (34.2 and 69.2 cm FL), 15 *L. monostigma* (24.5–41.4 cm FL), five *Lethrinus atkinsoni* (21.6–24.8 cm FL), and one *L. obsoletus* (27.9 cm FL); Table 1]. All traps were located on the sandy bottom next to the reef slope of the MPA, at depths of 25–30 m, and were retrieved after 7–14 days of deployment. Traps that contained fish were not recovered immediately but were transferred to shallower depths for 2–3 days to allow the fish to decompress. The captured fish were placed immediately in an aerated tub on the boat before being carried to a fish cage (ca. 1.5 m long × 1.5 m wide × 1.5 m high) installed near the watchtower (Fig. 1a). To allow the fish to recover from the stress of being caught, the fish-tagging operation started 1 h after the fish were caged. Fish were transferred to a tank before tagging and treated with an anesthetic mixture of 0.012‰ eugenol and seawater. After immobilization, a latex-covered coded acoustic transmitter (V8-4L, V9-2H, V9P-6L, or V13-1L; Vemco) was implanted surgically into the abdominal cavity of each fish (Table 1). The V8, V9, V9P, and V13 transmitters were 8, 9, 9, and 13 mm in diameter and 20.5, 29.0, 39.0, and 36.0 mm in length and weighed 2.0, 4.7, 4.6, and 11.0 g, respectively. The expected battery lives were 47, 53, 48, and 339 days and their power outputs were 146 (for the V8) and 147 dB (for others) re 1μPa at 1 m. Fish with a lower power transmitter might have potentially been less detected than fish with higher power tags. The frequency for all transmitter types was 69 kHz, and they randomly transmitted a set of six coded pulses once every 20–40 s. Only the V9P transmitter had a pressure (depth) sensor and transmitted depth data as well. Of all 28 tagged individuals, 25 fish were equipped with a transmitter without a depth sensor, while the remaining three were equipped with the V9P transmitter. After the transmitter was implanted, the fish were sutured with biodegradable silk, and an antibiotic ointment was applied to the incision. The size of each fish was measured before being placed back in the cage. The proportion of transmitter weight to fish body weight was 0.10–1.96%

6

(Table 1). After all fish recovered from the tagging operation for ca. 30 min, they were released near the watchtower at depths of 1–2 m (Fig. 1).

Individual fish were given identifiers based on their abbreviated species name and replicate fish number continued from Honda et al. [25] (see Table 1). Moreover, two *L. monostigma* [Lu-mo5 and Lu-mo7 (37.3 and 41.4 cm FL, respectively when tagged on 10 and 19 May 2012)] tracked in Honda et al. [25] were included because the batteries in their attached transmitters remained active.

Data analyses

In this study, considering the negative effect of tagging stress, detection data obtained within 24 h after release were excluded from analyses. Simultaneous detections by multiple receivers (e.g., flat1 and flat2, shallow3 and deep3) were counted as one detection. The individual residence index [26], defined as the quotient between the number of days detected and the period between 1 day after release and the last detection date (tracking period), was calculated to determine how frequently each tracked fish was certainly present in the fixed array [27].

The detections were grouped into five categories based on locational characteristics: 1. reef flat inside the MPA (flatIN: detections by flat2 or flat3 and simultaneous detections between these two stations and between flat2 or flat3 and shallow2 or shallow3); 2. reef slope near the MPA (slopeIN: detections by shallow2, shallow3, deep2, or deep3 and simultaneous detections among these four stations); 3. reef flat outside the MPA (flatOUT: detections by flat1 or flat4 and simultaneous detections between flat1 and shallow1 and between flat4 and shallow4); 4. reef slope outside the MPA (slopeOUT: detections by shallow1, deep1, shallow4, or deep4 and simultaneous detections between the former two stations and between the latter two stations); and 5. others [simultaneous detections between stations inside and outside the MPA (e.g., shallow1 and deep2)]. This

7

categorization was adopted because accurate fish home ranges could not be estimated using our study design (i.e., fish full home ranges were not encompassed by the receivers' array), and thus we aimed to grasp their approximate horizontal occurrence pattern by calculating individual detection frequencies of these five categories.

Depths ≤10 m were defined as the shallow layer because the depth of the reef edge was 5–10 m; thus, fish at these depths were assumed to occur near or on the edge. Depths ≥20 m were defined as the deep layer because the bottom depth along the reef slope was 20–30 m; thus, fish at depths ≥20 m were assumed to occur along the reef slope or on the bottom off the slope. If a tagged fish was detected at flatIN and/or flatOUT two or more times (considering the false detections [28]), such a fish was defined to be using shallow layer.

For the three fish equipped with a V9P transmitter (henceforth, fish with a depth sensor), time-series detected depths dividing them into slopeIN and other four categories were shown. Individual vertical kernel utilization distributions (vKUDs) were estimated in each time period (day, twilight, and night) using *ks* package [29] in R version 3.3.1. Here, twilight duration was regarded as 4 h (2 h each around sunrise and sunset), and day and night comprised the remainder of the day. Sunrise and sunset were determined from Sunrise, sunset, moonrise and moonset times (www.sunrisesunsetmap.com, Accessed September 2015). The vKUDs were illustrated in a linear two-dimensional space to determine the vertical use along the reef slope using average positions [30]. The average positions were calculated every 10 min interval for vertical space use following Currey et al. [18]. In this analysis, we only used detections obtained at shallow and deep stations. The number of movements between the shallow and deep layers (N of shallow-deep movement) were counted individually, and the daily mean values were calculated. Here, shallow-deep movement was defined as ascending or descending between the last detected station in the deep (shallow) layer and the first detected next station in the shallow (deep) layer within 24 h, and the time of the shallow-deep movement was defined as the intermediate value of the movement. The daily mean N of shallow-deep movement was defined as the quotient between total N of shallow-deep movements and the

8

number of days detected. Time-length frequency of ascents and descents and their hourly frequencies using only <1 h time-length data were calculated to examine diel vertical-movement patterns. Difference in detectability in receivers at different times of the day (see [31]) might have affected on the N of shallow-deep movements.

Use of shallow and/or deep depth layers by the 25 fish without a depth sensor was estimated in the following manner. First, the 10-m interval detection frequencies of each receiver at each pair of shallow and deep stations (e.g., shallow1 and deep1) and those of their simultaneous detections (by the same fish) were calculated using the detection data of three fish with a depth sensor. Here, because only one fish with a depth sensor was detected once at >60 m depth according to the results, we defined 60 m as the maximum detectable practical depth in this analysis. Second, if there was a trend that fish at shallower depths were detected more frequently by a shallow receiver and vice versa for fish at deeper depths, detection probabilities at three depth layers (0–10 m, 10–20 m, and 20–60 m) at each shallow and deep station and by their simultaneous detections by each pair of stations were calculated based on the detection frequencies. Third, if the detection probability by shallow or deep receivers at shallow (0–10 m) or deep (20–60 m) depth layers was high (>80%), respectively, fish in the corresponding depth layer were considered to be detected with high likelihood at the station. We counted the total number of detections by each individual only at such stations. Finally, if the summed numbers of detections by a fish at the shallow or deep stations exceeded 50 (liberal estimate), such a fish was considered to have occurred one or more times at the shallow or deep depth layer. All of our target species were visually observed at <10 m depth on the coral reef inside the MPA [21, 25, Honda, personal observation].

Results

A total of 160,371 detections originating from 21 of the 28 tagged fish were recorded during the study (Table 1). Although the tracking periods of six fish (Lu-mo5, Lu-mo11, Le-at8, Si-gu9, Si-gu10, and Si-gu11) lasted 10 or less days, 11 fish from four lutjanid and lethrinid species were tracked for 30 or more days (Table 1). The mean residence index (± standard deviation) of all tracked fish was 0.75 ± 0.29, and the indices of 13 (61.9% of all tracked fish) individuals were 0.75–1.00 (Table 1).

Although Lu-ar6, Lu-mo19, and Le-ob3 were observed at very low detection rates [0.04% (n = 15), 0.02% (n = 1), and 0.61% (n = 63) of all detections, respectively] at flat stations, no other individuals, except *Siganus guttatus*, was detected at those stations. In contrast, although Si-gu10 was detected at deep stations [1.92% (n = 7)], no other *S. guttatus* individuals were detected at those stations. The detection frequencies of all tracked lutjanid and lethrinid individuals mostly (98.5–100%) consisted of slopeIN and slopeOUT (Fig. 2). The mean (± standard deviation) frequency at the former was 69.5 ± 35.4%, and the frequency for 10 fish (62.5%) exceeded 80%. Whereas those of *S. guttatus* were mostly (99.8–100%) consisting of flatIN and slopeIN, and its frequency at the former for three fish (Sigu7, Si-gu8, and Si-gu11) were high (97.9%, 92.5%, and 93.5%, respectively; Fig. 2).

Depth-use patterns by fish with a depth sensor

Each fish showed distinct and wide-ranging depth-use patterns (Fig. 3). Lu-ar6 gradually shifted to deeper layers between 10 and 30 m as the 14 days (26 May–8 June 2013) elapsed soon after tracking started (Fig. 3, upper). Then, the fish stayed mainly at ≤10 m depth and occasionally descended to 30–50 m. The shallowest and deepest depths recorded by Lu-ar6 were 0.0 and 48.4 m, respectively. For this fish, the vertical core area (50% vKUD) and its extent (95% vKUD) ranged mainly 0–10 m and 0–25 m depths, respectively, regardless of time periods

(Fig. 4, upper). The 50% vKUD only ranged near the reef slope along the MPA during the day and twilight, whereas during the night that also ranged outside the MPA. The total N of shallow-deep movements by Lu-ar6 was 120, and its mean daily N was 2.55. Time-length frequencies of both ascents and descents were the highest in 0–5 min, and those within 1 h occupied 84.2% and 77.1%, respectively (Fig. 5a, upper). Hourly movement frequencies became higher during 3:00–5:00 and 12:00–13:00 regardless of ascent or descent and any other remarkable trends were not observed during other time periods (Fig. 5b, upper).

Lu-mo19 exhibited wide-ranging vertical movements between the surface and ca. 60 m depth over 6 days (9–14 June 2013) soon after tracking started (Fig. 3, lower-left). Then, the fish was detected continuously only in the shallow layer for 11 days (15–25 June), followed by depth-use patterns similar to those observed during the first 6 days. The shallowest and deepest depths recorded were 0.6 and 58.2 m, respectively. This fish exhibited similar vertical space use patterns during the day and twilight as those by Lu-ar6 although the 50% vKUD was relatively wider and deeper (Fig. 4, middle). However, both the 50% and 95% vKUDs during the night showed distinct patterns that the former was separated into two areas either one above 30 m depth and the other at 40–50 m and that the latter ranged widely from surface to 60 m. Nonetheless, the 50% vKUDs were mostly distributed near the slope along the MPA in any of time periods. Total and daily mean N values of shallow-deep movements by Lu-mo19 were 148 and 3.08, respectively. Similar to Lu-ar6, high frequencies of ascents (88.9%) and descents (76.7%) were recorded within 1 h (Fig. 5a, middle). The peak of descents was observed during 18:00–21:00 and was five hours earlier than that of ascents (i.e., 23:00–2:00; Fig. 5b, middle). Both ascents and descents were less observed during daytime; in particular, no movement was recorded from 13:00 to 18:00.

Lu-mo20 did not occur near the surface (0–5 m depth) at all and mainly occurred at 10–30 m (Fig. 3, right). The fish descended to deeper layers (>40 m) several times, and the shallowest and deepest depths recorded were 8.5 and 61.3 m, respectively. Unlike Lu-ar6 or Lu-mo19, vertical space use by Lu-mo20 was almost limited

11

to near deep1 (Fig. 4, lower) although the 95% vKUD tended to become larger as it became darker. Total N of

shallow-deep movements by Lu-mo20 was 14, which was much lower than that of Lu-ar6 or Lu-mo19, although

the number of days detected did not differ among the three fish (47, 48, and 50 days for Lu-ar6, Lu-mo19, and

Lu-mo20, respectively). The daily mean N of shallow-deep movements was 0.28, and most of them were recorded

during daytime (Fig. 5b, lower).

Estimate of depth use by fish without a depth sensor

The 10-m detection frequency of each receiver at each pair of stations near the slope and that of simultaneous

detections by each pair of receivers obtained by the three fish with a depth sensor is shown on Fig. 6a. Fish that

occurred in the 0–10 m depth layer were detected with high frequency by shallow1 and shallow2, and fish at 20–

60 m depth layer were mainly detected by deep1 and deep2. This trend was also true for each individual to a

greater or lesser extent (Online Resource 1). In contrast, shallow3 and shallow4 detected fish with high frequency

not only at 0–10 m depth layer but also at 30–60 m (Fig. 6a). The probabilities that shallow1 and shallow2 detected

fish at 0–10 m depth layer were 93.7% and 82.7%, respectively (Fig. 6b), whereas deep1 and deep2 detected fish

at 20–60 m with 83.1% and 80.7% probabilities, respectively.

Lu-ar6, Le-ob3, and all *S. guttatus* were detected two or more times at flatIN and/or flatOUT (Table 2).

Except for fish with a depth sensor, six fish (Lu-mo3, Lu-mo9, Lu-mo11, Lu-mo16, Lu-mo18, and Le-at10) were

detected more than 50 times at shallow1 and/or shallow2 and deep1 and/or deep2. Thus, nine individuals (56.3%

of four lutjanid and lethrinid species), including three fish with a depth sensor belonging to two lutjanid and one

lethrinid species, were likely to use both the shallow and deep layers (Table 2). *S. guttatus* used only the shallow

layer (Table 2).

Discussion

According to the residence indices of tracked individuals, 61.9% of them occurred in the study area during >75% of their tracking periods, indicating that they used the area frequently. We also found that all individuals of the four lutjanid and lethrinid species were most often (99.4–100%) detected near the reef slope and more than half of the individuals of the four species and one or more individuals of the three species (other than *Lethrinus obsoletus*) were likely to use the shallow and deep layers along the steep reef slope of the MPA. Moreover, although all lutjanid and lethrinid fishes were captured by fish traps located on the bottom next to the reef slope, considering that we did not bait any of the traps, it was unlikely that the trap itself triggered movement of fish toward a deep layer. Thus, Le-ob3, which was detected at flatIN but not at deep1 or deep2, may also have used both depth layers. Further, two of the three fish with a depth sensor exhibited frequent shallow-deep movements near the slope. These findings suggest that not a few individuals of the four species used the slope vertically. *Siganus guttatus* caught from the MPA were assumed to occur mostly inside the MPA, as suggested by Honda et al. [25]. However, the detection ranges of the receivers in the MPA did not cover the entire MPA.

In this study, the shallow3 and shallow4 stations tended to detect fish in the 30–60 m depth layer with higher frequency than shallow1 and shallow2. However, the trend in the detection frequency at the 0–30 m depth layer did not differ much among the four receivers (Fig. 6a). Because depth >30 m indicates a sandy bottom area off the reef slope, it was possible that shallow3 and shallow4 were located under a specific topographic condition that made it easy to detect fish at such place (e.g., fewer coral barriers between the receiver and fish at >30 m depth).

13

The three fish with a depth sensor showed distinct vertical space use patterns among individuals, indicating that these patterns differed among individuals and between species. In particular, Lu-mo19 (37.8 cm FL) and Lu-mo20 (32.8 cm FL) showed completely different patterns within the same species, although they were of similar sizes. These vertical space use variations among individuals have been reported in some reef fishes (e.g., [19, 20, 32]). For example, Currey et al. [33] acoustically tracked 26 *Lethrinus miniatus* (37.2–48.6 cm FL) implanted with a depth sensor in the southern Great Barrier Reef and reported that their depth use varied highly among individuals regardless of differences in size. Thus, considering our small sample size, we cannot conclude that the trends we observed represented all individuals of the two species. Moreover, it should be noted that vertical space use outside the detection range of our receivers' array was not estimated.

Nevertheless, Lu-ar6 mainly occurred at the shallow layer regardless of time period. Lu-mo19 utilized the area along the reef slope (0–20 m depth) in any of time period and also used at 40–50 m as a core area during the night. Because some reef fishes move toward sandy areas far from reefs during the night to feed [34], detecting Lu-mo19 and two other fish (Lu-ar6 and Lu-mo20) at >30 m may have been due to their movement toward offshore sandy areas or coral bommies to forage. The daily mean N of shallow-deep movements by Lu-mo6 and Lu-mo19 exceeded 2.5, indicating that those fish practiced ca. one shuttle shallow-deep movement per day. Although Lutjanidae species are generally known to be nocturnal [35], only Lu-mo19 showed a nocturnal movement pattern. The peak of hourly frequency of descents for Lu-mo19 was ca. five hours earlier than that of ascents during the night, indicating that the fish stayed in deep during the periods of the time gap. Meanwhile, most shallow-deep movements were observed during daytime by Lu-mo20 although the total number of movements was small. These suggest that large variabilities in diel activity as well as the depth-use patterns may have occurred among individuals and species. On the other hand, most shallow-deep movements were completed

14

within 1 h and those modes for Lu-ar6 and Lu-mo19 ranged within 10 min (Fig. 5a), suggesting such movements were triggered by some purpose, such as feeding or resting.

The triggers for the irregular depth-use patterns by Lu-ar6 during the 2 weeks after tracking started and the finding that we only detected Lu-mo19 in the shallow layer during the 11 days are unclear, although these behaviors may have been related to capturing or tagging stressors (e.g., [36]). Currey et al. [37] reported that the abovementioned 26 acoustically tracked *Lethrinus miniatus* tended to occur more often on the southern Great Barrier Reef slope when water temperature was cooler. Further study is needed to reveal their depth-use patterns in more detail by increasing the number of tracked fish and by specifying the purpose for visiting deeper (>30 m) areas.

This study demonstrated that the four lutjanid and lethrinid species mainly used the area near the steep reef slope of the MPA, and that three of the four species most likely used the slope vertically. Therefore, conservation benefits may only be minimal unless fishing the line along the reef edge is restricted (Fig. 1b). In fact, the core ranges of two fish with a depth sensor used in this study were mostly distributed along the slope of the MPA. We propose that MPA boundaries in this country should be moved to >50 m on the offshore side to cover the entire outer reef slope. Otherwise, we propose no or restricted fishing activities along offshore MPA boundaries consisting of the reef edges.

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Table 1 Fish IDs, measurements, tagging and basic detection information for tagged fish captured beside the steep reef slope or on the reef flat of the marine protected area off Laguindingan. Residence index was defined as the quotient between number of days detected and tracking period

Species	Fish ID	Tag type	Fork length (cm)	Body weight (kg)	Tag /body weight (%)	Capture method	Tagged and released date	Total number of detections	Tracking period (d)	No. of days detected (d)	Residence index
Lutjanus argentimaculatus	Lu-ar5	V9	34.2	0.58	0.81	Fish trap	29 Aug 2012	46	17	10	0.59
	Lu-ar6	V9P	69.2	4.66	0.10	Fish trap	25 May 2013	35,996	50	47	0.94
Lutjanus monostigma	Lu-mo3	V13	41.4	1.18	0.93	Fish trap	10 May 2012	34,430	61	61	1.00
	Lu-mo5	V13	37.3	0.68	1.62	Fish trap	19 May 2012	731	9	9	1.00
	Lu-mo8	V9	26.4	0.29	1.62	Fish trap	29 Aug 2012	0	-	-	-
	Lu-mo9	V9	26.6	0.35	1.34	Fish trap	29 Aug 2012	1,668	30	29	0.97
	Lu-mo10	V9	26.0	0.28	1.68	Fish trap	29 Aug 2012	0	-	-	-
	Lu-mo11	V9	27.1	0.38	1.24	Fish trap	29 Aug 2012	424	10	4	0.40
	Lu-mo12	V9	24.5	0.29	1.62	Fish trap	29 Aug 2012	2,216	36	9	0.25
	Lu-mo13	V9	28.0	0.37	1.27	Fish trap	19 Sep 2012	0	-	-	-
	Lu-mo14	V9	27.8	0.36	1.31	Fish trap	19 Sep 2012	0	-	-	-
	Lu-mo15	V9	26.3	0.32	1.47	Fish trap	19 Sep 2012	0	-	-	-
	Lu-mo16	V9	26.4	0.31	1.52	Fish trap	19 Sep 2012	1,852	59	43	0.73
	Lu-mo17	V13	34.5	0.61	1.80	Fish trap	19 Sep 2012	0	-	-	-
	Lu-mo18	V9	29.7	0.43	1.09	Fish trap	19 Sep 2012	374	58	16	0.28
	Lu-mo19	V9P	37.8	0.97	0.47	Fish trap	8 Jun 2013	5,120	50	49	0.98
	Lu-mo20	V9P	32.8	0.52	0.88	Fish trap	12 Jul 2013	44,600	50	50	1.00
Lethrinus atkinsoni	Le-at6	V9	23.2	0.24	1.96	Fish trap	19 Sep 2012	13,230	57	52	0.91
	Le-at7	V8	21.6	0.22	0.91	Fish trap	8 Jun 2013	0	-	-	-
	Le-at8	V8	24.8	0.29	0.69	Fish trap	12 Jul 2013	41	4	3	0.75
	Le-at9	V8	22.8	0.24	0.83	Fish trap	22 Jul 2013	17	36	4	0.11
	Le-at10	V8	22.1	0.23	0.87	Fish trap	22 Jul 2013	5,614	23	11	0.48
Lethrinus obsoletus	Le-ob3	V9	27.9	0.42	1.12	Fish trap	19 Sep 2012	10,204	58	56	0.97
Siganus guttatus	Si-gu7	V8	21.6	0.23	0.87	Hook and line	25 May 2013	286	29	20	0.69
	Si-gu8	V8	26.3	0.43	0.47	Hook and line	25 May 2013	1,484	22	22	1.00
	Si-gu9	V8	20.7	0.19	1.05	Hook and line	25 May 2013	13	4	3	0.75
	Si-gu10	V8	27.3	0.48	0.42	Hook and line	25 May 2013	260	10	9	0.90
	Si-gu11	V8	22.1	0.28	0.71	Hook and line	25 May 2013	1,765	10	10	1.00

Lu-mo3 and Lu-mo5 were used also in Honda et al. [25]

Table 2 Total number of detections at flatIN, flatOUT, shallow1, shallow2, deep1, and deep2 by each tracked individual

Fish ID	Total number of detections					
	flatIN	flatOUT	shallow1	shallow2	deep1	deep2
Lutjanus argentimaculatus						
Lu-ar5	0	0	0	1	0	23
Lu-ar6*	1	14	59	8724	86	5023
Lutjanus monostigma						
Lu-mo3*	0	0	1	66	41	2590
Lu-mo5	0	0	0	0	0	0
Lu-mo9*	0	0	1	1462	90	69
Lu-mo11*	0	0	2	201	35	115
Lu-mo12	0	0	6	33	1791	108
Lu-mo16*	0	0	0	449	44	239
Lu-mo18*	0	0	5	75	193	79
Lu-mo19*	1	0	436	73	39	99
Lu-mo20*	0	0	2029	15	35733	268
Lethrinus atkinsoni						
Le-at6	0	0	0	0	0	0
Le-at8	0	0	13	0	0	0
Le-at9	0	0	0	1	0	13
Le-at10*	0	0	31	4597	4	912
Lethrinus obsoletus						
Le-ob3	63	0	0	144	0	0
Siganus guttatus						
Si-gu7	279	0	0	0	0	0
Si-gu8	1373	0	3	106	0	0
Si-gu9	4	0	0	9	0	0
Si-gu10	36	0	0	210	0	7
Si-gu11	1651	2	0	112	0	0

FlatIN and flatOUT indicate reef flat inside and outside the MPA, respectively. Details are described in the manuscript. Shallow1, shallow2, deep1, and deep2 indicate stations (see Fig. 1). These four stations were selected because shallow1 and shallow2 (deep1 and deep2) tended to detect fish at shallower (deeper) depths (see Fig. 6). Refer to Table 1 for fish ID abbreviations. Asterisks indicate fish likely used both shallow ($\leq$10 m) and deep ($\geq$20 m) layers

Figure Captions

Fig. 1 (a) Geographic location of the study site, Laguindingan, northern Mindanao Island, the Philippines. Stars and a solid triangle indicate the receivers' deployment stations and the watchtower, respectively. F1–F4 (1.0–2.5 m bottom depth), S1–S4 (5–10 m), and D1–D4 (23–29 m) indicate each station. Capital letters "F", "S", and "D" indicate reef Flat, Shallow, and Deep, respectively. Depth contour was made using bathymetry data (LPC. Bernardo, Tokyo Institute of Technology; unpubl. data). (b) Vertical schematic view of the study site. Intensive fishing operations along the boundary of the marine protected area known as "fishing the line" operate legally and regularly

Fig. 2 Detection frequency in each location type used by the tracked fish during the study period. FlatIN, slopeIN, flatOUT, slopeOUT, and others indicate reef flat inside the marine protected area (MPA), reef slope near the MPA, reef flat outside the MPA, reef slope outside the MPA, and remaining detections, respectively. Details are described in the manuscript. Refer to Table 1 for fish ID abbreviations

Fig. 3 Time series of the depths detected for the three fish equipped with a depth sensor (fish ID: Lu-ar6, Lu-mo19, and Lu-mo20) by all 12 acoustic receivers during the study period. Grey dotted lines indicate 10 and 20 m depths. SlopeIN and other categories indicate reef slope near the MPA and remaining detections, respectively. Details are described in the manuscript

Fig. 4 Vertical space use (kernel utilization distributions, KUDs) along the reef slope in each time period by the three fish equipped with a depth sensor (fish ID: Lu-ar6, Lu-mo19, and Lu-mo20), represented as mean depth by mean reef distance (setting shallow1&deep1 as 0 m). Solid and grey colors indicate 50% and 95% KUDs, respectively, Receiver positions are shown by triangles (shallow1&deep1–shallow4&deep4 locates form left to right). Two dotted lines indicate western (left) and eastern (right) borders of the marine protected area
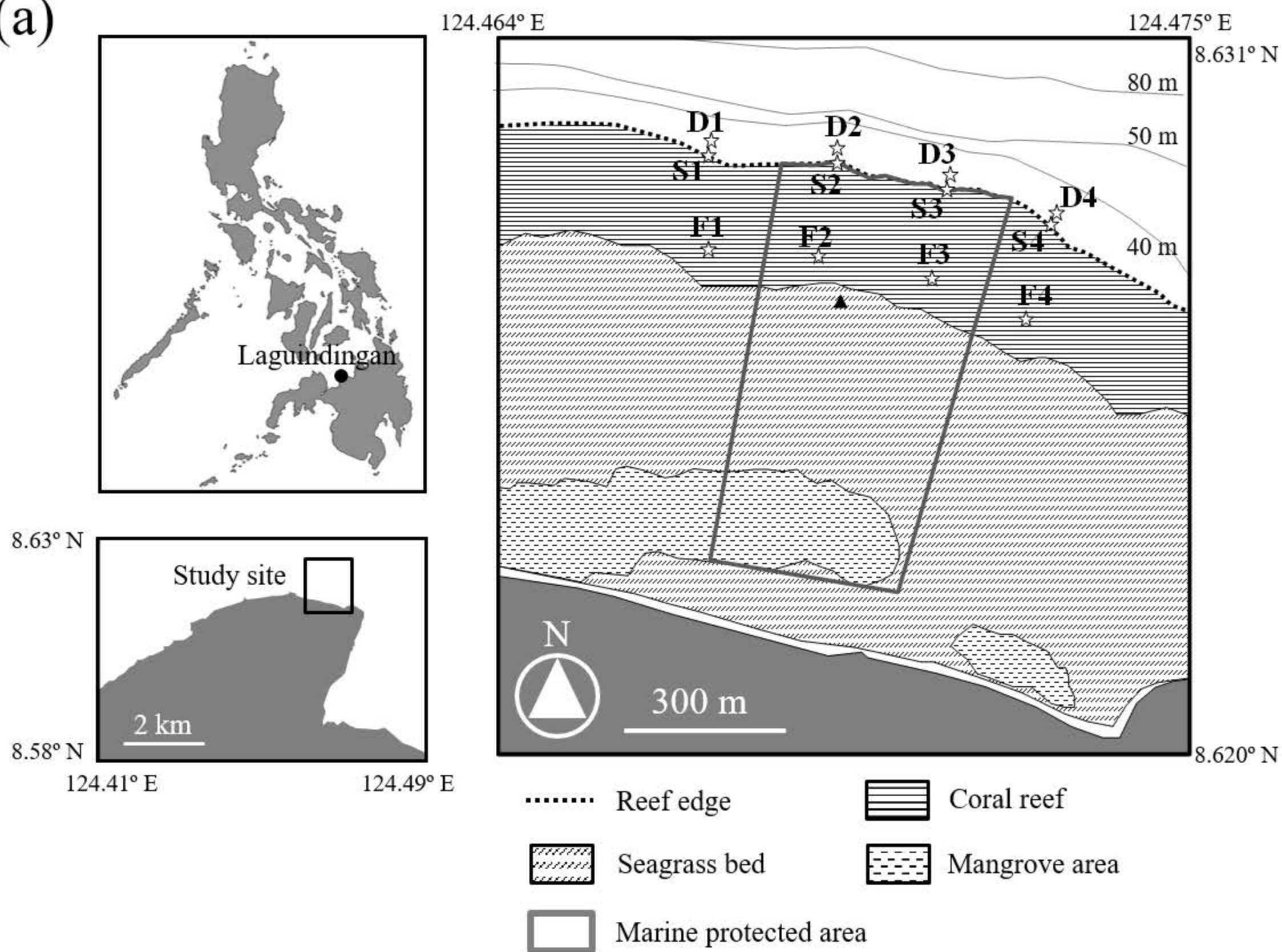
Fig. 5 Time-length frequencies of ascents and descents between shallow (≤10 m) and deep (≥20 m) layers for the three fish equipped with a depth sensor (fish ID: Lu-ar6, Lu-mo19, and Lu-mo20) (a) and their hourly
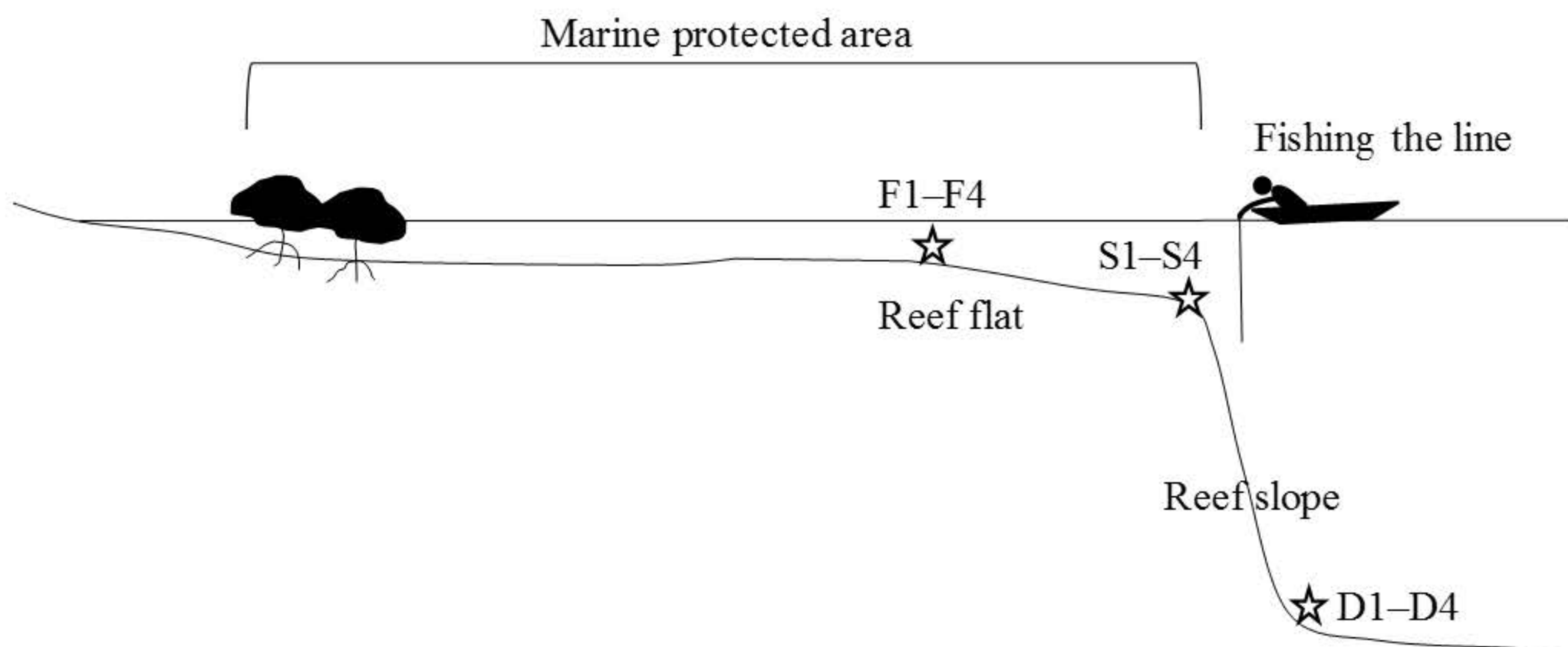
23

frequencies only using <1 h time-length movements (b). Grey shaded areas indicate average periods from sunset to sunrise of days recorded movements
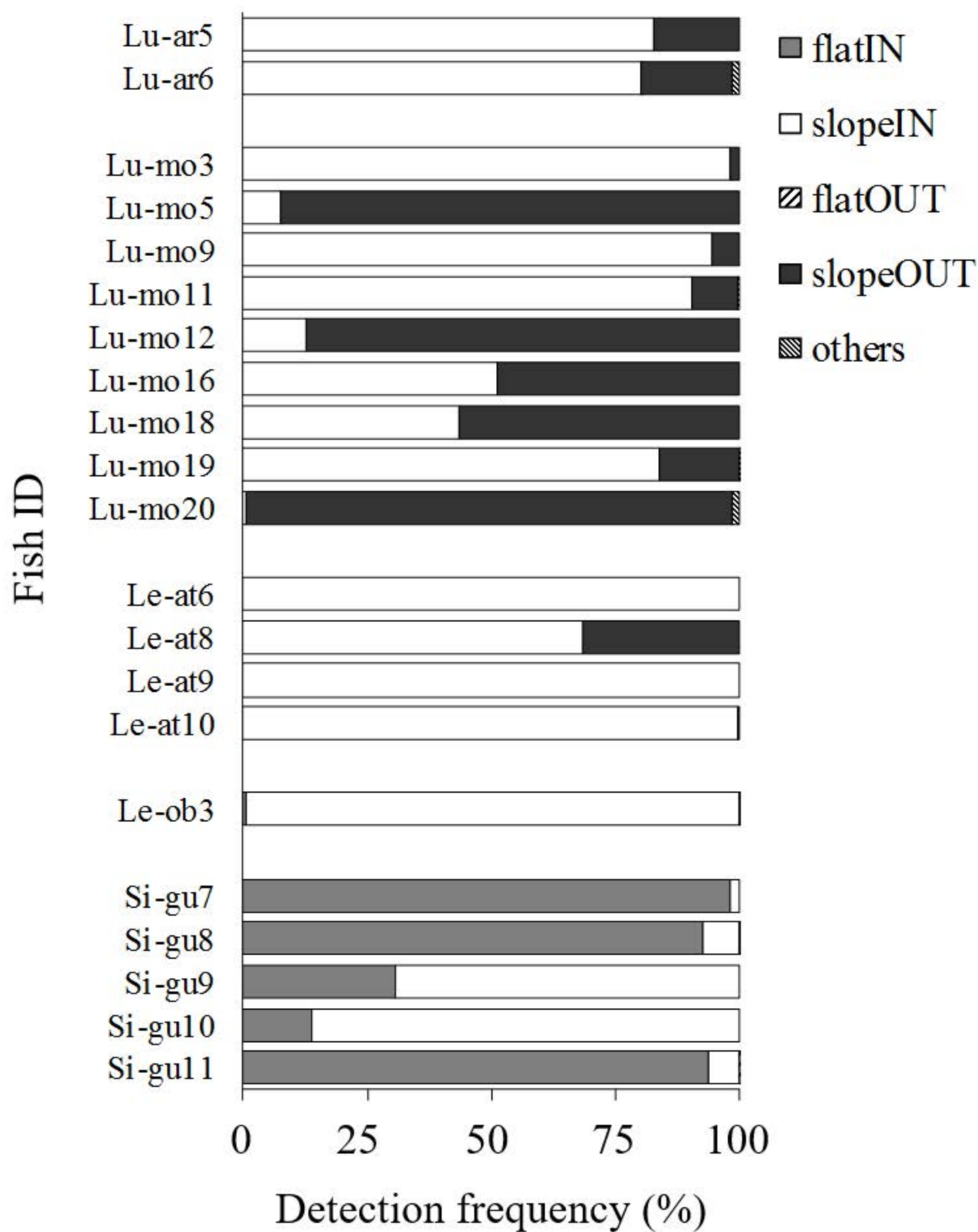
Fig. 6 Detection frequencies in each 10-m depth range (0–60 m) at each pair of shallow and deep stations (e.g., S1 and D1) by three tagged fish equipped with a depth sensor (a), and detection probabilities in the 0–10, 10–20, and 20–60 m depth ranges at each pair of stations based on detection frequency (b). The probabilities at the stations were calculated only when there was a tendency that fish in a shallow (deep) area were detected more frequently at a shallow (deep) station. S&D in the figures indicates simultaneous detections by S and D receivers. S1–S4 and D1–D4 indicate station locations (see Fig. 1)
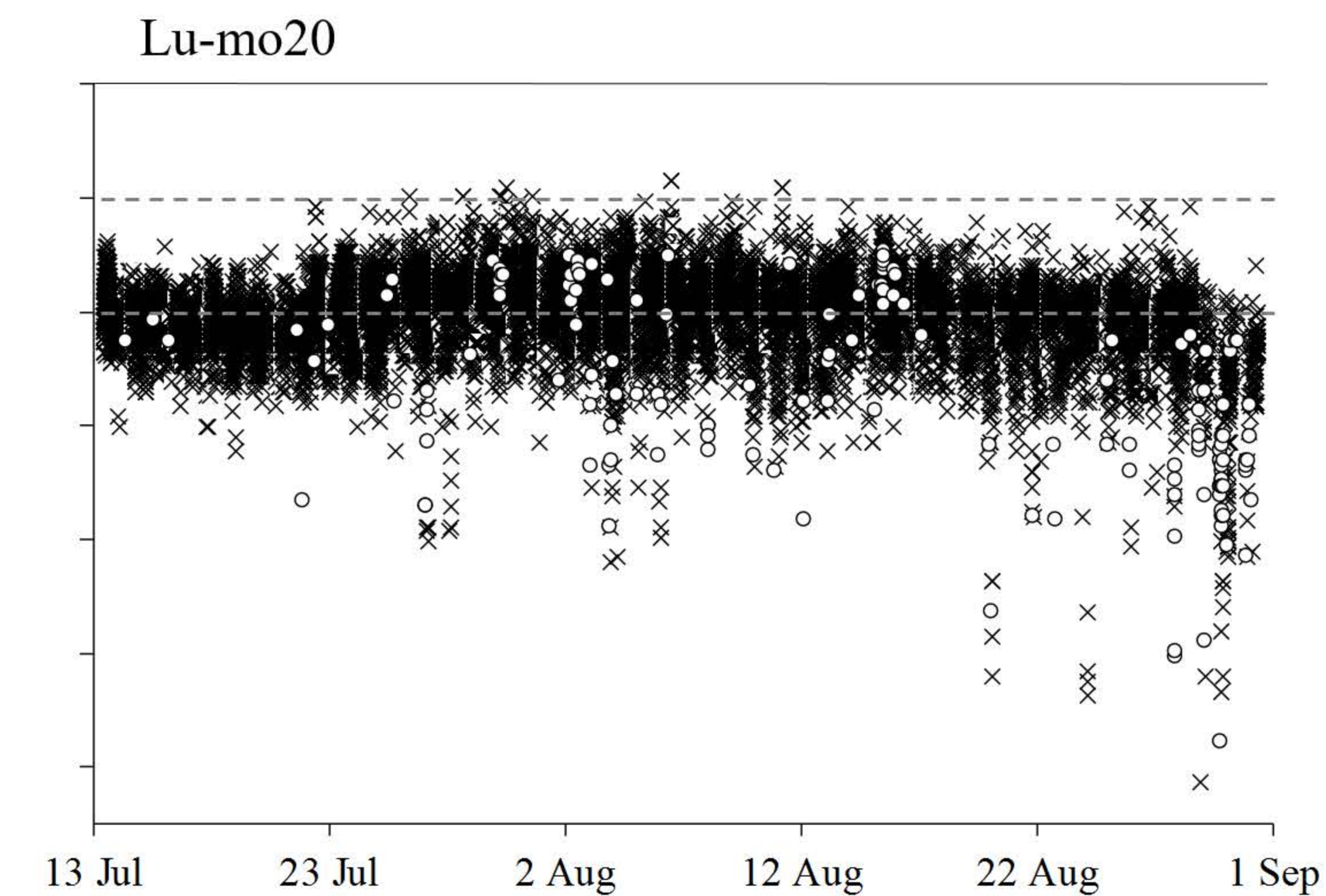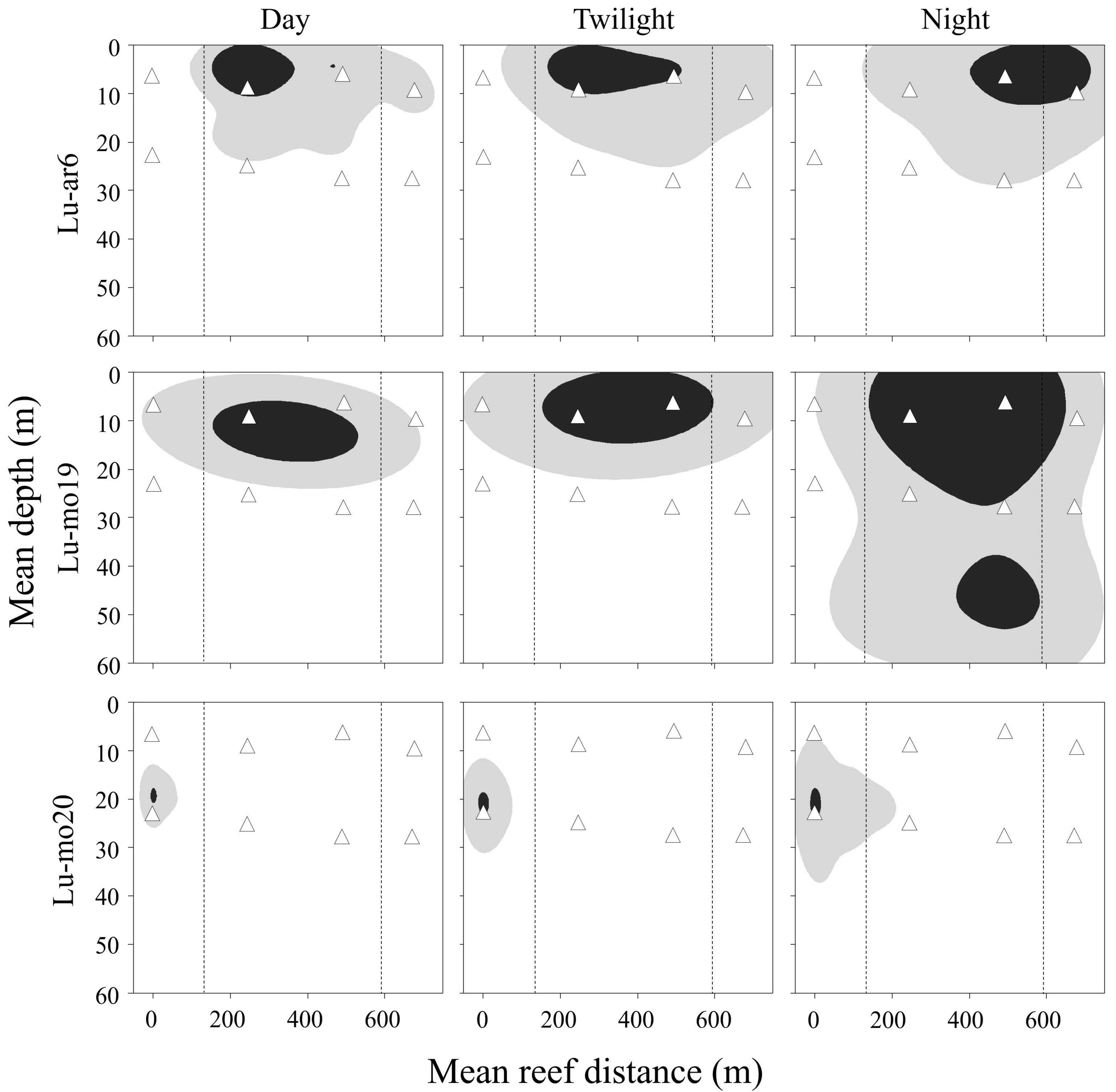
(a)

124.464° E
124.475° E
8.631° N
80 m
50 m

D1
D2
D3
S1
S2
D4
S3
F1
F2
S4
F3
40 m
F4

Laguindingan

8.63° N
Study site
8.58° N
124.41° E
124.49° E

2 km

N
300 m
8.620° N

.... Reef edge   ▭ (horizontal lines) Coral reef

▨ Seagrass bed   ▨ Mangrove area

▭ Marine protected area

(b)

Marine protected area

Fishing the line

F1–F4
☆
S1–S4
☆
Reef flat

Reef slope

☆ D1–D4

Lu-ar6
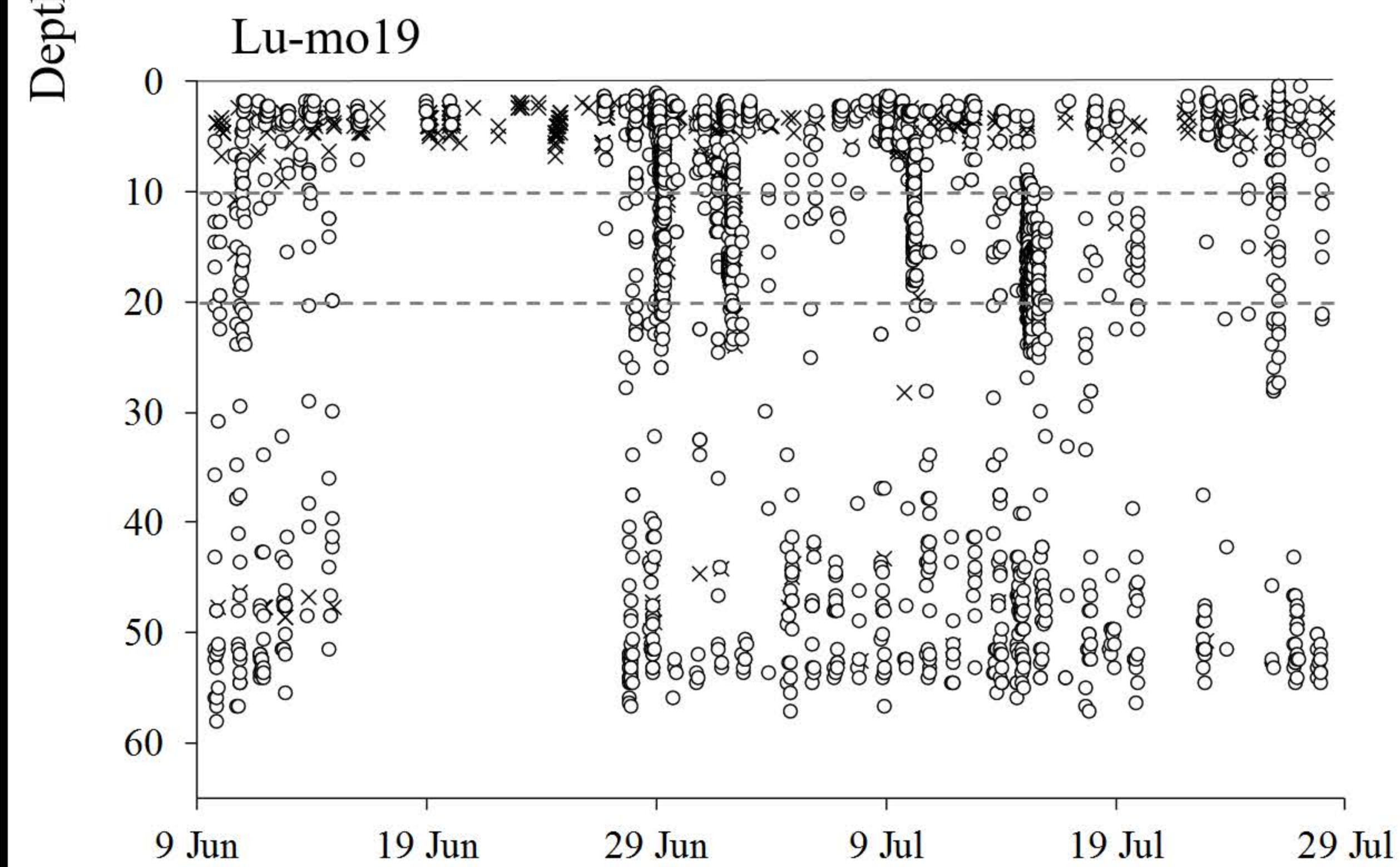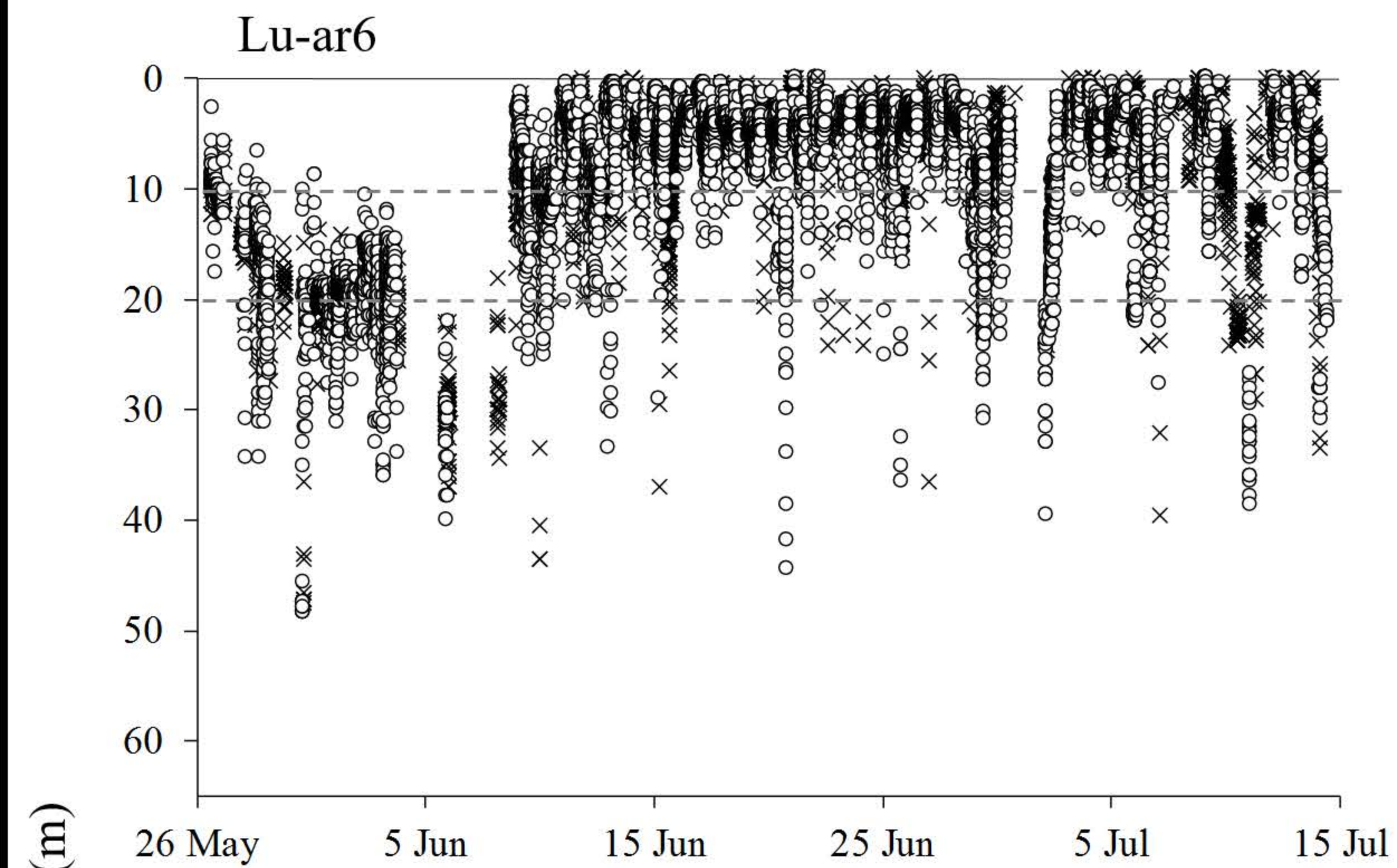
○ slopeIN

× other categories
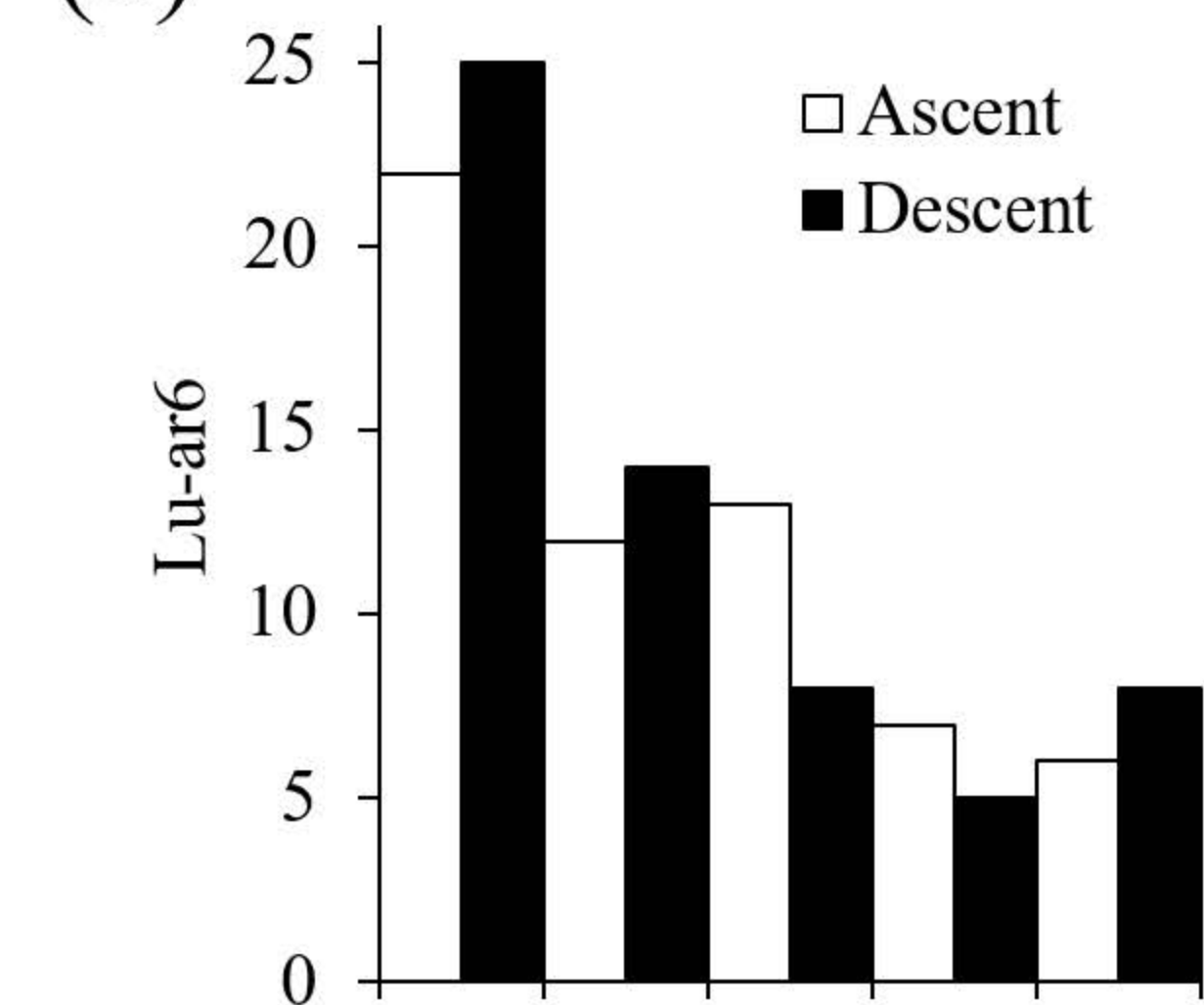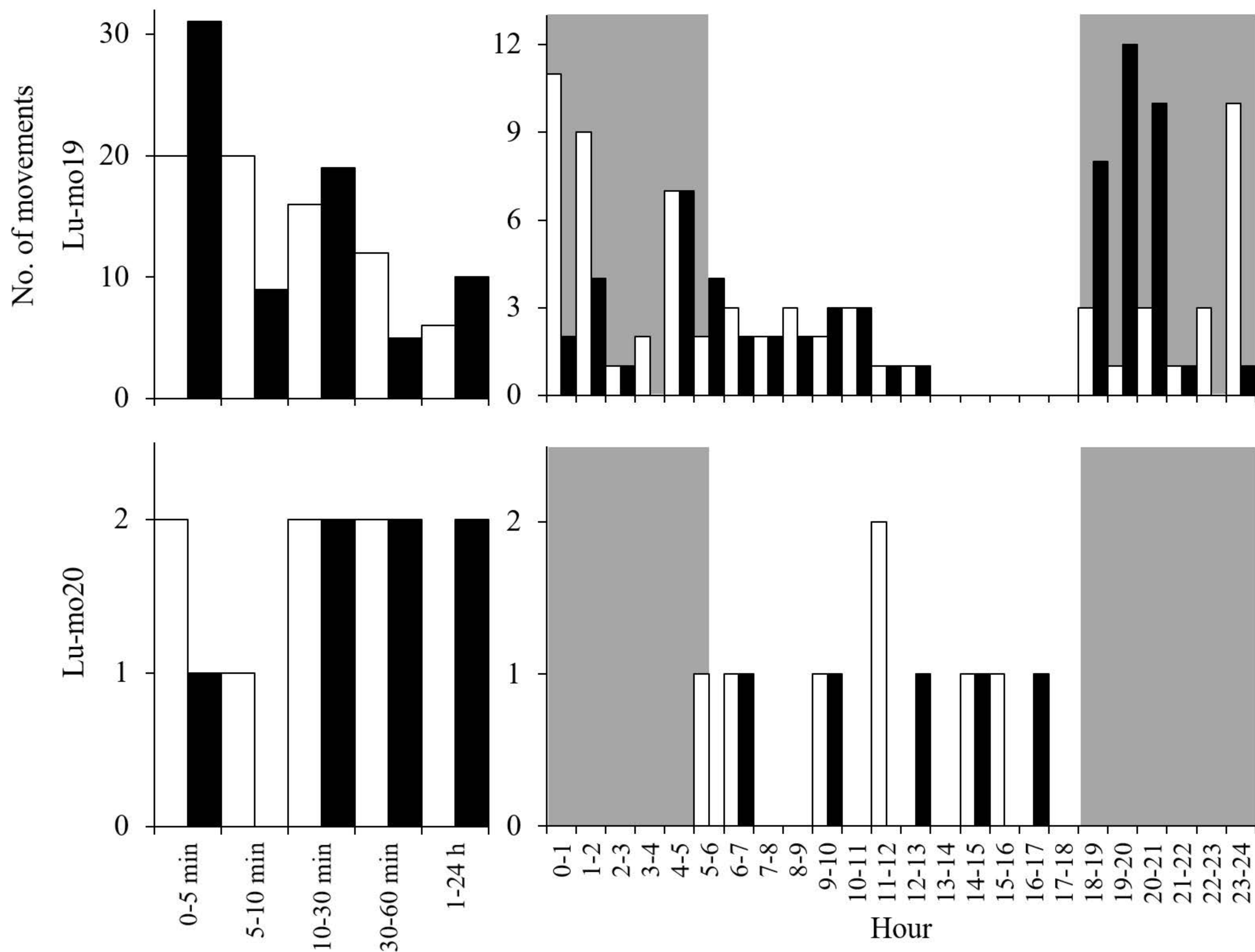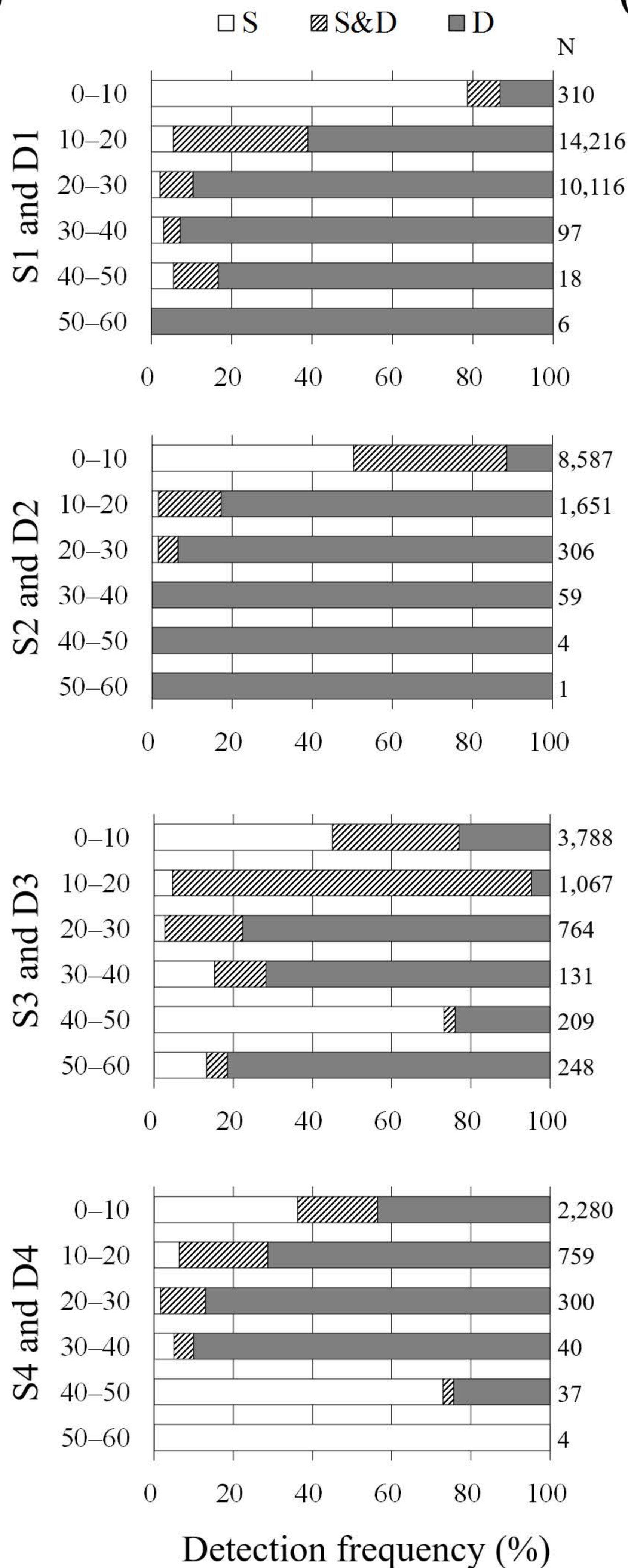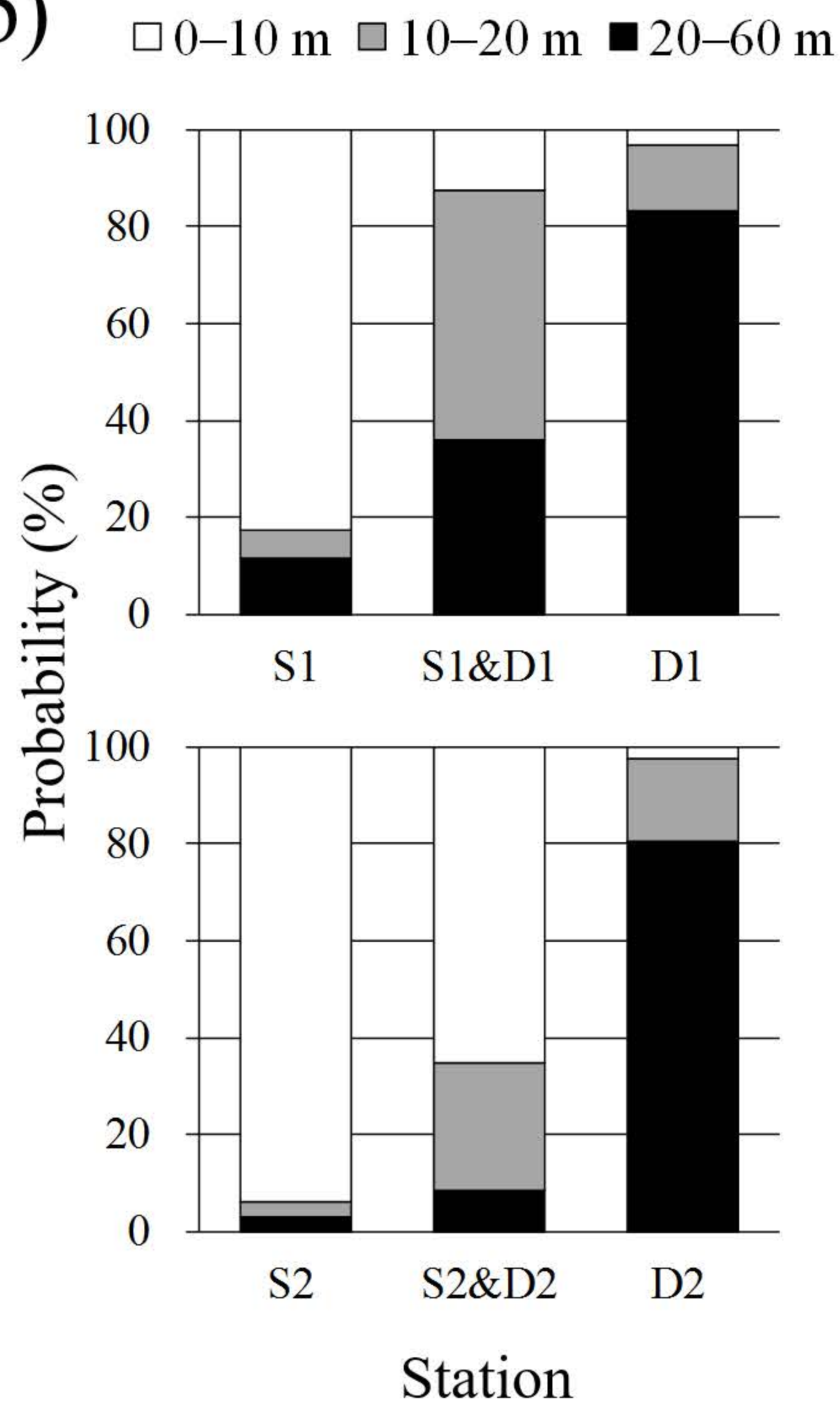
Lu-mo19

Lu-mo20

Depth (m)

Date (in 2013)

Day   Twilight   Night

Title: Importance of outer reef slopes for commercially important fishes: implications for designing a marine protected area in the Philippines

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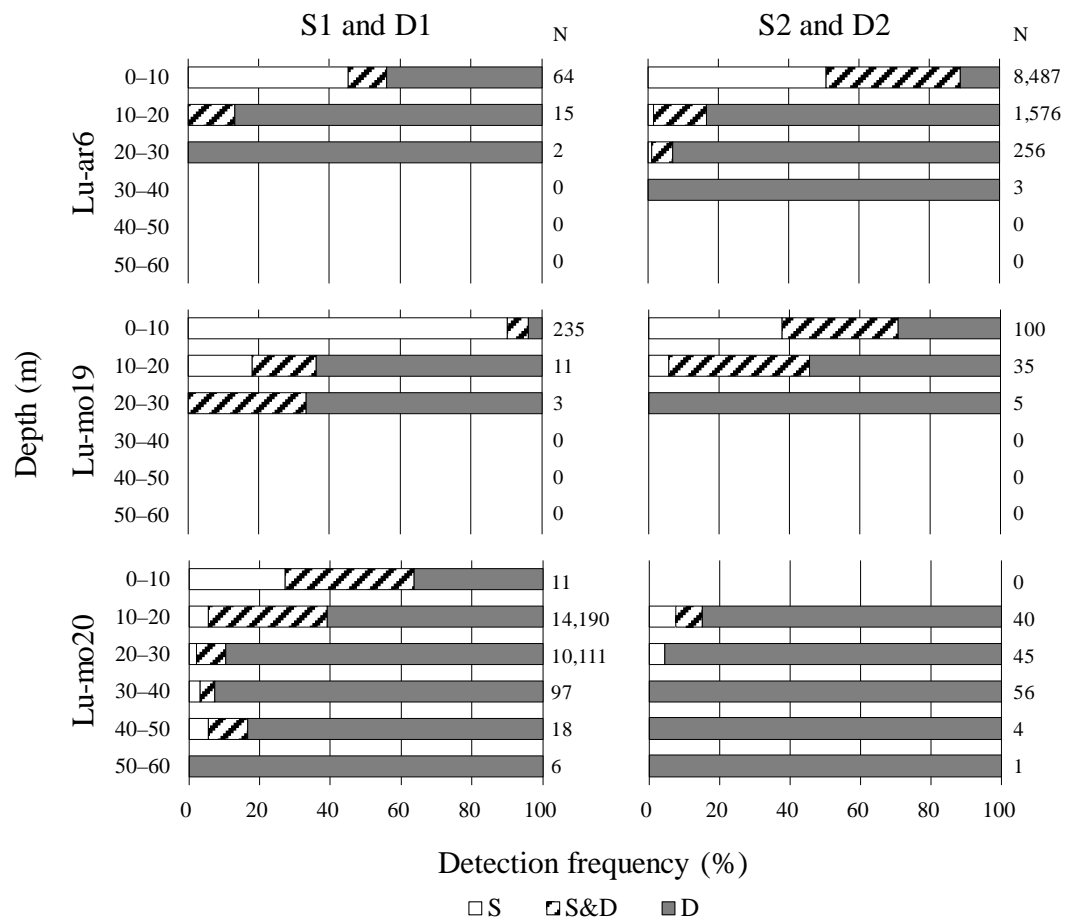
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Online Resource 1. Detection frequencies in each 10-m depth range (0–60 m) at two pairs of shallow and deep stations (i.e., S1 and D1, or S2 and D2) by each of three tagged fish equipped with a depth sensor (fish ID: Lu-ar6, Lu-mo19, and Lu-mo20). S&D in the figures indicates simultaneous detections by S and D receivers. S1, D1, S2, and D2 indicate station locations (see Fig. 1)