Diel movement patterns of Pacific sugar limpet, *Patelloida saccharina* (Gastropoda: Patellogastropoda: Lottiidae) in response to semi-diurnal tides of Samal Island, Philippines

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Abstract. Limpets pursue adaptive responses to persist in harsh conditions of tropical intertidal areas. This study investigated the diel movement patterns of a homing limpet species, *Patelloida saccharina*, subjected to semi-diurnal tides at Catagman, Samal Island, Philippines. Field observations from 27 March 2017 to 19 April 2017 showed that during spring tides, activity commenced when limpets were submerged by the flooding tide at night. All limpets returned to their respective home scars just before sunrise and no further activity or movement was observed even during flood tide in the day. No activity was observed during night-time low tide periods of neap tides. Activity commenced at a later time when the limpets were submerged by the incoming tide and ceased prior to exposure from the outgoing of the tide. Results of Chi-square tests suggest that *P. saccharina* movement patterns were associated with day-night cycles ($x^2 = 19.158$) and tide type ($x^2 = 17.658$). However, movement was not directed ($x^2 = 0.79718$; d.f. = 2; p > 0.05), which may relate to random search for food. Further, Mann-Whitney U tests indicated significant differences in the distance travelled and duration of excursion of limpets between the spring and neap tides. Limpets moved farther and spent a longer time foraging during spring tides than neap tides, although a higher percentage of actively moving limpets was observed during the neap tide. The current study suggests that periods of darkness and submersion are prerequisites to initiate movement of *P. saccharina* limpets. The substantial literature on limpet behaviour considers that variations in activity pattern are adaptive strategies linked to desiccation. Overall understanding of *P. saccharina* movement pattern supports this premise that homing mechanism and movement restricted to nocturnal high tides are possible adaptations for survival on tropical intertidal shores of Samal Island.

Key words. diel movement pattern, Pacific sugar limpet, *Patelloida saccharina*, Samal Island

INTRODUCTION

Herbivorous marine molluscs are commonly found in tropical, rocky, intertidal areas. Their grazing impact allows space for recruitment of other sessile animals (Arrontes et al., 2004; Coleman et al., 2006), contributing to the overall structure and unique assemblage of intertidal environments (Hawkins & Hartnoll, 1983). Intertidal animals have movement patterns characterised by alternating periods of activity and inactivity (Underwood, 1979; Gray & Hodgson, 1999), which relate to day-night and tidal cycles (Naylor, 1988; Little, 1989). In the case of herbivorous limpets, diel cycles (Funke, 1968;

Hirano, 1979b; Branch & Cherry, 1985), tidal regime (Hirano, 1979a; Naylor, 1988; Davies et al., 2006), and zonation (Balaparameswara Rao & Ganapati, 1971; Della Santina et al., 1995) are reported to influence the rhythmicity of their movements.

While movement in limpets is often linked to foraging, different movement patterns were observed in several limpet species (Branch, 1981). For instance, the variable movement patterns observed in *Patella vulgata* (Linnaeus, 1758) were associated with the type of habitat (Little & Stirling, 1985; Williams et al., 1999). These variations allow for optimal use of resources within their periods of activity (Della Santina & Naylor, 1993; Gray & Williams, 2010) and avoidance of predation (Bertness et al., 1981) and heat stress (Williams & Morritt, 1995; Williams et al., 2005).

Branch (1981) summarised limpet activity rhythms as: 1) movement while submerged during day and night; 2) movement while awash during the rising and falling tides, but not while exposed or submerged during day and night; 3) movement at night during low tide; and 4) movement only during submergence at night. However, Little (1989) agreed with Hawkins & Hartnoll (1983) that the criteria may

Table 1. Summary of tide information across all sampling dates of this study based on the Mean Lower Low Water (MLLW), Davao City, Philippines. The minimum and maximum tide heights recorded for Davao are −0.5 m and 2.0 m, respectively (from Tides4Fishing, 2020).

Sampling date	27–28 March 2017 (Spring)		4–5 April 2017 (Neap)		9–10 April 2017 (Spring)		19–20 April 2017 (Neap)	
Tide	Time (hours)	Tide height (m)	Time (hours)	Tide height (m)	Time (hours)	Tide height (m)	Time (hours)	Tide height (m)
First high tide	0521	1.5	1050	1.2	0451	1.4	1001	1.2
First low tide	1123	−0.2	1800	0.3	1054	0.0	0330	0.5
Second high tide	1732	1.7	0026	0.9	1700	1.5	2329	0.8
Second low tide	2345	−0.3	0554	0.5	2310	−0.1	1705	0.3

not be rigid given the behavioural plasticity of animals in the intertidal zone (Branch & Barkai, 1988). Little (1989) then reported the foraging patterns of some grazing molluscs based on tidal periodicity. These were categorised as feeding activity when submerged, emersed, awash, and those with no regular pattern.

The Pacific sugar limpet, *Patelloida saccharina* (Linnaeus, 1758), is a homing limpet species found ubiquitously on Philippine rocky shores. It is widely distributed from the Indian Ocean to the West Pacific and reaches a maximum size of 50 mm (Poutiers, 1998). Based on a summary of limpet activity rhythms, Branch (1981) reported that *P. saccharina* are active while awash during day and night, following the work of Ohgushi (1954). However, it should be noted that Ohgushi (1954) studied the activity of its subspecies, *P. saccharina lanx* (Reeve, 1855) and *Siphonaria japonica* (Donovan, 1824), in relation to tides in Japan. He reported active movement of both species before and after low tide (Ohgushi, 1954).

Studies focusing on tropical limpets or the intertidal zone in general remain scarce and underrepresented in Philippine research (Villarta et al., 2019). The accessibility of the intertidal zone and the abundance of *P. saccharina* on Samal Island, Philippines, provided an opportunity to investigate their diel movement patterns. Their periods of activity and inactivity in relation to day-night cycles and corresponding tidal rhythms over one lunar cycle were documented. Although Ohgushi (1954) had reported the movement patterns for a *P. saccharina* subspecies, this study was nonetheless fundamental for understanding of whether tropical *P. saccharina* populations would conform or deviate from this pattern. Furthermore, the study demonstrates the importance of behavioural ecology as an approach to enhance our understanding of the dynamics of tropical intertidal communities.

MATERIAL AND METHODS

Study site. Field work was conducted in Barangay Catagman, Island Garden City of Samal, Davao del Norte, Philippines (7°3′47.47″N, 125°40′49.14″E; Fig. 1) from 27 March 2017
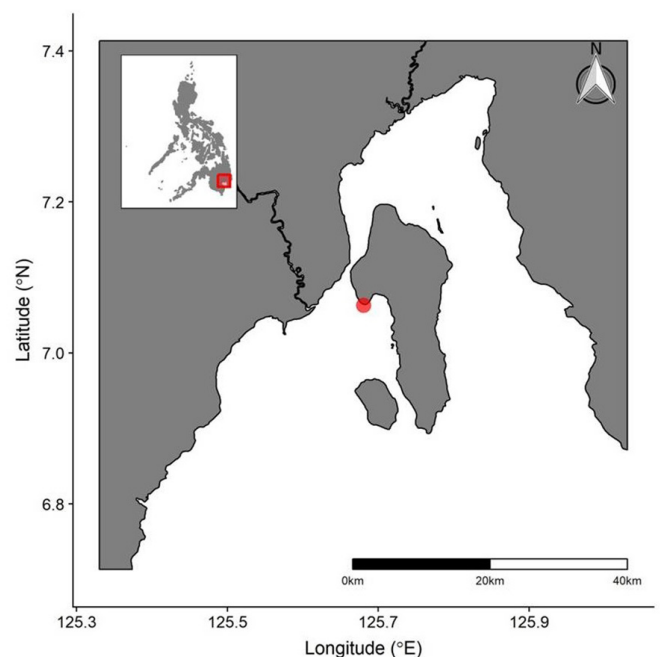

Fig. 1. Map showing the location of the study area in Samal Island, Davao del Norte, Philippines.

to 19 April 2017. The island belongs to Type IV weather classification, characterised by a uniform amount of rainfall throughout the year (Moron et al., 2009). It experiences a semi-diurnal tide, having two low tide and high tide peaks over 24 hours, with the two low or high tides separated by 12-hour intervals. The annual tidal range in Davao is −0.5–2.0 m (Tides4Fishing, 2020). A summary of tide information across all sampling dates is provided in Table 1. The average sea surface temperatures recorded in situ for March and April 2017 were 28.2°C and 28.8°C, respectively. Field observations were done during the new moon, first quarter, full moon, and last quarter to examine the influence of tidal changes on the rhythmicity of limpet movement.

The study site is characterised by vertical boulders on the high intertidal zone that abruptly descend to an extensive rocky reef platform with shallow tide pools and crevices carved by *Echinometra mathaei* (Blainville, 1825). The lottiid limpet *Patelloida saccharina* is usually found on the reef flat just below the vertical boulders at the high and
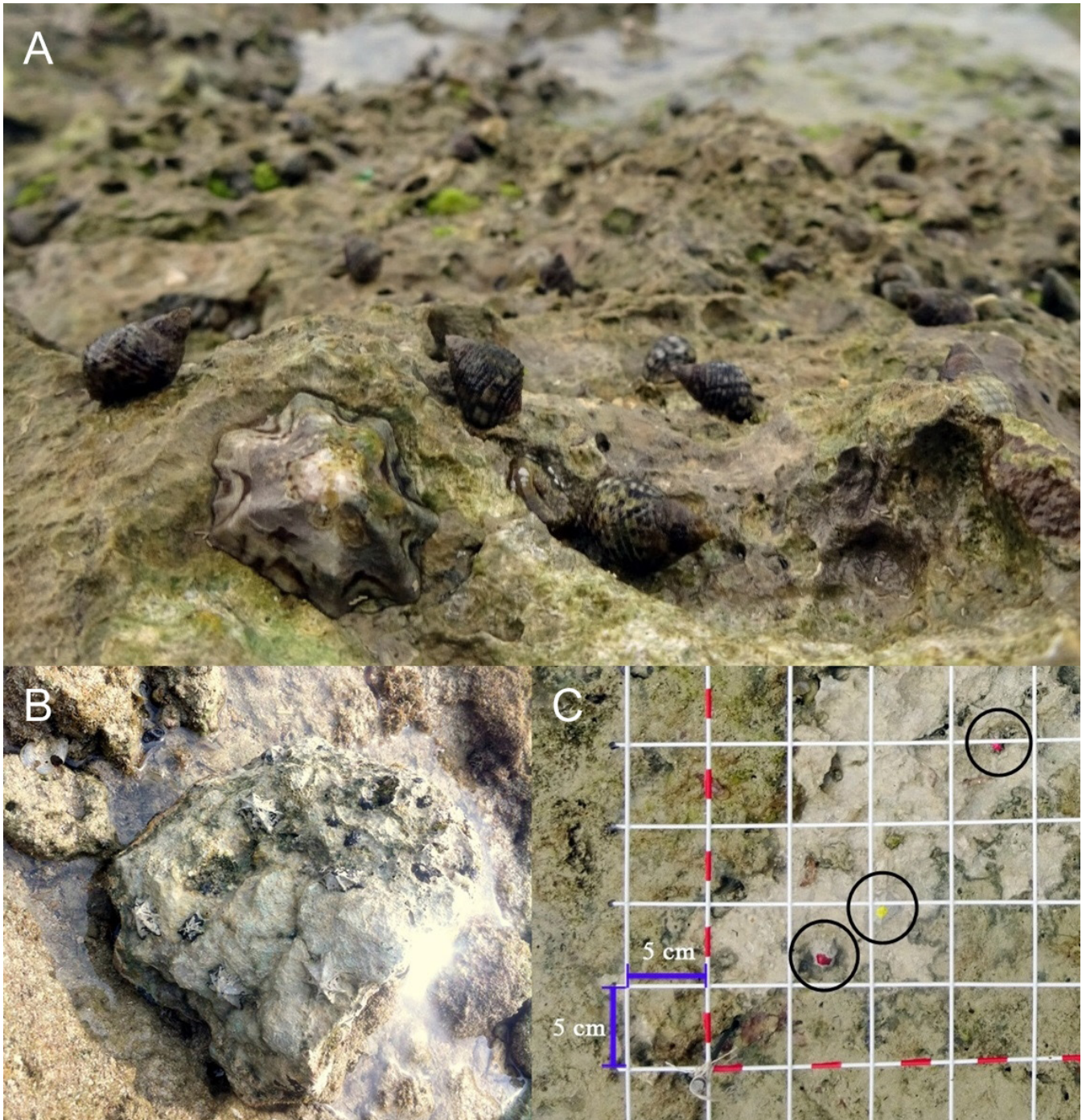
Fig. 2. *Patelloida saccharina* clamped on: A, bare rock face; B, rock covered with sand and turf algae. C, portion of the 5 × 5 cm grid quadrat laid on a reef patch with three *P. saccharina* individuals. Apices of limpet shells were painted with nail polish. Photographs by EY Zapanta and MA Fortaleza.

mid-intertidal zones, with smaller individuals (less than 1.5 mm) often found at the low intertidal zone. Along the high intertidal zone (0.9–2.2 m above chart datum), they are typically clamped on bare rocky substrate or on rocks with sand, turf algae, and patches of *Padina* spp. (Adanson, 1763; Fig. 2A, B). An average of 16 (± 3.01 s.d.; n = 260 quadrats) individuals per 0.25 m² may be observed on reef patches at the high intertidal zone (Pilay, 2019). This area is totally exposed during low tide periods.

Sampling methodology. At the high intertidal zone, reef patches with at least two or more *P. saccharina* individuals were identified and selected. The apices of limpet shells were painted with nail polish for identification and their shell sizes were measured to the nearest 0.1 mm using a Vernier caliper. Ten to twelve 0.5 × 0.5 m grid quadrats were placed on reef patches where limpets were observed. The grid quadrats were anchored to the reef substrate by hammering concrete nails in every corner of the quadrat and securing it with cable tie. The grid quadrats were elevated such that they would not hamper limpet movement along the rocky substrate. A floater was attached on one side of each grid quadrat to locate them easily during the rising tide. After fixing the grid quadrats, each setup was photographed to

record the reference points or the limpets' homing positions to the nearest 5 × 5 cm grid (Little et al., 1988; Fig. 2C).

Field observations commenced at 1700 hours, in anticipation of limpet activity towards sunset, and concluded after 12 hours. The measurement of tidal height in situ and documentation of movement were conducted at 30-minute intervals to allow movement of observers from one grid quadrat to another. This tidal height refers to the water level above the reef substrate where *P. saccharina* limpets were located. During each time of observation, three tidal height measurements were recorded using a wooden metre rule. The tide heights recorded in situ were then converted to tide heights in metres above chart datum (C.D.) as predicted for Davao City (Table 2). During the rising tide, improvised glass-bottom buckets were used to observe limpet activity until the water level became suitable for snorkelling. Underwater flashlights were used to aid night-time observations. In movement documentation, "no movement" was indicated when limpets were observed to be tightly clamped to their homes, as described by Little & Stirling (1985). Movement was noted when the resident limpets left their respective home scars (Little et al., 1988) and their new positions were recorded. A coordinate system was used to track their movement, with changes in limpet position with respect to the x- and y-axes recorded (see Hirano, 1979b). Additionally, the direction of their movements, described as landward, seaward, or lateral, was noted.

Data analysis. To compute the percentage of active limpets in every lunar phase, the total number of limpets that moved was divided by the total number of limpets observed. The percentages were represented in vertical bars and plotted against the average values of tidal heights recorded per grid quadrat in situ. The mean difference between the Mean Lower Low Water (MLLW) and Mean Higher High Water (MHHW) recorded for Samal Island for each sampling date was used to obtain the tidal range where the *P. saccharina* limpets were usually found.

Movement was measured using several metrics: 1) binary movement scores; 2) distance travelled (d; mm); 3) duration of excursion (τ; min); and 4) average speed (s; mm min^{-1}). First, limpet movement was assigned binary scores (0 = no movement, 1 = with movement). Afterwards, a computer software, ImageJ (Schneider et al., 2012), was used to analyse the photographs and estimate d of individual limpets, assuming that they moved along a straight line (Little et al., 1988). τ was recorded as the duration from when the limpet left until it returned and turned to fit in its home scar. Lastly, s was calculated using the formula, $s = d/\tau$.

All statistical analyses were executed in Paleontological Statistics (PAST) version 4.03 software (Hammer et al., 2001). Chi-square Test of Independence was used to determine associations of movement with day-night cycle and tide type. Similar tests were conducted to assess the relationship between direction of limpet movement and tide type. Lastly, the Mann-Whitney U Test was used to determine whether d and τ varied between spring and neap tides.

RESULTS

An average of 40 (± 3.4 s.d., n = 161) *P. saccharina* individuals was observed every lunar phase, with limpet shell size ranging from 10 to 30 mm. This accounted for 83 individuals observed during the new moon and full moon, and 78 individuals during the first quarter and last quarter (Table 3). It should be noted that some limpets first observed during the earlier lunar phase were also included in observations during the later lunar phases and that the low-density records can be explained by their patchy distribution in the high intertidal zone. Other grazers observed sharing the same area with *P. saccharina* limpets were the fringed false limpet, *Siphonaria laciniosa* (Linnaeus, 1758) and the spiny chiton, *Acanthopleura spinosa* (Bruguière, 1792).

Movement in relation to day-night cycles. The diel and 12-hour observations conducted across four lunar phases showed that *P. saccharina* activity was restricted to periods of darkness, beginning at sunset and lasting until dawn. The limpets observed in all grid quadrats remained stationary during daylight hours (0600–1630 hours; Fig. 3). During the new moon, limpet movement commenced at 1700 hours, when sunset became night-time (Fig. 3A). The percentage of moving limpets increased gradually until the activity peaked at 49% at 1830 hours (Fig. 3A; Table 2). The actively moving limpets started homing between 2030 and 2100 hours, a brief period before the outgoing tide left the high intertidal zone dry. All limpets that moved had returned to their respective home sites at 2130 hours. On the following day, limpets began their second outward journey at 0400 hours when it was still dark, and 49% of the population was actively moving at 0500 hours. No movement was recorded beyond 0530 hours, which corresponded to the time when daylight broke.

Similarly, no *P. saccharina* limpets moved during daylight hours in the first quarter. Limpet activity was first recorded at 2200 hours and it took about two and half hours for 79% of limpets to be actively moving (Table 2). A decrease in activity began at 0130 hours and all limpets started their homeward journey at 0230 hours (Fig. 3B). Only one outward journey was observed during the first quarter.

The movement patterns observed during the new moon and first quarter were comparable to those observed during the full moon and last quarter, respectively. During the full moon, movement commenced when it was dark at 1800 hours. 59% of the population was actively moving at 1900 hours (Fig. 3C; Table 2). Movement started to decrease at 1930 hours until no movement was recorded at 2000 hours. The second outward journey of the limpets commenced at 0400 hours, but this was halted abruptly when dawn transitioned to sunrise after 0430 hours (Fig. 3C). This prompted the limpets to return to their home scars before daylight.

Observations during the last quarter were limited to hourly intervals because of the difficulties experienced by the observers during a tropical storm. This also explains the limited data collected during this moon phase. Limpets were

Table 2. Overview of *Patelloida saccharina* activity in relation to tide heights converted into metres above chart datum (C.D., Davao City). The *P. saccharina* limpets are typically found between 0.9 and 2.2 m above C.D.

Sampling date	Number of limpets observed	Time and tide height when limpets were first active			Time and tide height when limpets were most active			Time and tide height when limpets last moved		
		(hours)	(m)	(%)	(hours)	(m)	(%)	(hours)	(m)	(%)
27 March 2017 PM	37	1700	1.56	35	1830	1.51	49	2100	0.96	11
28 March 2017 AM	37	0400	1.53	46	0500	1.82	49	0530	1.89	46
4 April 2017 AM	39	2200	1.07	3	0030	1.22	79	0230	1.07	36
9 April 2017 PM	46	1800	1.25	20	1900	1.49	59	1930	1.29	57
10 April 2017 AM	46	0400	1.78	28	0400	1.78	28	0430	1.85	9
19 April 2017 PM	39	2300	1.15	20	0000	1.12	33	0100	1.06	18

Table 3. Total number of *Patelloida saccharina* limpets observed, percentage of active limpets, and movement parameters between spring and neap tides at Samal Island, Philippines. The movement parameters indicate the median and range of distance travelled (*d*), duration of excursion (τ), and calculated speed (*s*) of *P. saccharina* limpets.

Observations and movement parameters	Spring tide	Neap tide
Number of limpets observed	83	78
Percentage of active limpets	48–59%	33–79%
Distance travelled (*d*; mm)	104.06 (26.55–405.31)	15.70 (0-210)
Duration of excursion (τ; min)	60.00 (30–240)	15.00 (0–210)
Speed (*s*; mm min^{-1})	1.26 (0.89–1.69)	0.22 (0.00–2.02)

first observed moving at 2300 hours; 33% of the population had moved at 0000 hours (Fig. 3D; Table 2). No more movement was recorded beyond 0100 hours (Fig. 3D). Limpet movement during the last quarter was also limited to one excursion, which was similar to what was observed during the first quarter.

Movement in relation to tides. As observed during the daylight hours (0600–1630 hours), no movement was recorded for *P. saccharina* limpets across all lunar phases regardless of the flooding and ebbing of tides (Fig. 3). During the new moon, *P. saccharina* movement commenced at 1700 hours, corresponding to 35% of activity when the falling tide was at 1.56 m above C.D. (Fig. 3A; Table 2). The limpets began their homeward journey while still submerged from 2030 to 2100 hours when the tidal height fell further to 0.96 m above C.D. No movement was recorded during the entire low tide period from 2130 to 0330 hours when the limpets were exposed to air. When the tide turned, 46% of limpets moved from 0400 to 0430 hours when the rising tide was between 1.53 and 1.71 m above C.D. At 0530 hours, although the tidal height was still increasing, all limpets had returned to their home sites. During the full moon, the first activity was observed at 1800 hours when the rising tide was 1.25 m above C.D. (Fig. 3C; Table 2). This reached 59% activity at 1830 hours when the tidal height further increased to 1.69 m above C.D. Activity started to decline at 1930 hours

when the tidal height decreased to 1.29 m above C.D. No movement was recorded at 2000 hours when the tide fell to 1.08 m above C.D. After the tide turned, and although the tidal height increased from 1.78 to 1.85 m above C.D. from 0400 to 0430 hours, only 28% of the limpets moved during the second excursion (Fig. 3C; Table 2). The limpets returned quickly to their home scars while still submerged in the rising tide just before sunrise.

During the first quarter, no activity was observed during the entire low tide period from 1800 to 2130 hours (Fig. 3B). Activity commenced at 2200 hours when 3% of limpets moved underwater, at 1.07 m above C.D (Table 2). The activity increased to 79% at 0030 hours, when the limpets were submerged at 1.22 m above C.D., and this lasted until 0230 hours, when limpets were submerged at 1.07 m above C.D. Similarly, no movement was observed during the night-time low tide period of the last quarter, when limpets were totally exposed from 1730 to 2000 hours and awash from 2030 to 2100 hours (Fig. 3D). Most limpets moved at 2300 hours when they were submerged at a tidal height of 1.15 m above C.D. (Table 2). All limpets started their homeward journey at 0100 hours while still underwater at 1.06 m above C.D. No further movement was recorded when the tidal height eventually decreased to 0.95 m above C.D. at 0200 hours.
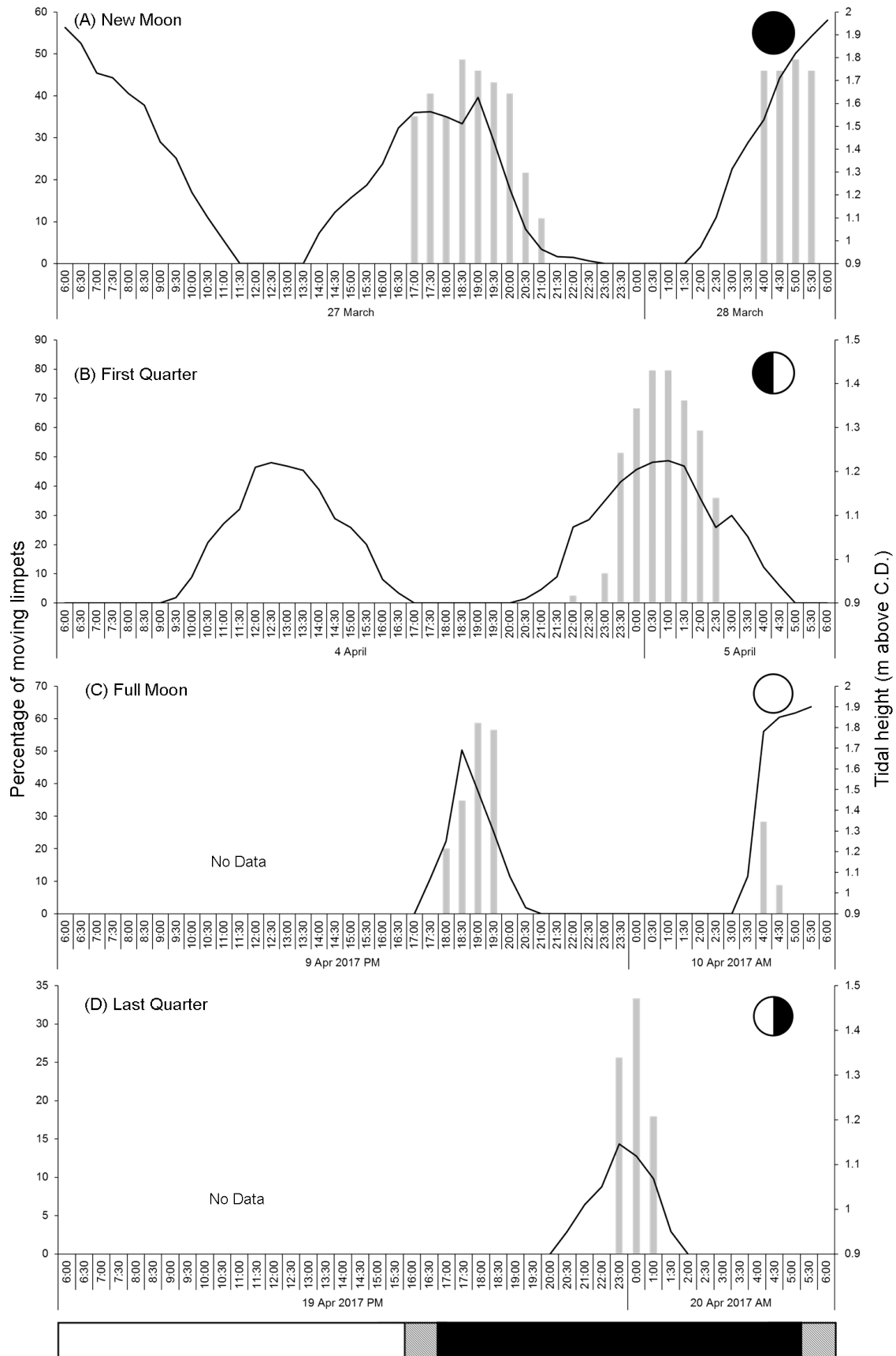
Fig. 3. Movement patterns of *Patelloida saccharina* limpets in Catagman, Samal Island, during various lunar phases. A, New Moon, 27–28 March 2017; B, First Quarter, 4–5 April 2017; C, Full Moon, 9–10 April 2017; D, Last Quarter, 19–20 April 2017. The left and right y-axes correspond to the percentage of moving limpets and tidal height measurements in metres above chart datum (C.D.), respectively. Grey vertical bars represent the percentage of actively moving limpets during each lunar phase. The bar at the bottom corresponds to the day-night cycle: (from left to right) white = daytime, grey = transitioning to sunset, black = night-time, grey = sunrise. Note that the activity of *P. saccharina* limpets was observed during dark periods only, from sunset to night-time until before sunrise, as long as they were covered by the tide.

Results of the Chi-square test supported the associations between limpet movement and day-night cycle (i.e., limpet movement was observed only during the night; $x^2 = 19.158$; d.f. = 2; p < 0.05), and limpet movement and tide type (i.e., more limpets moved during spring tide ($x^2 = 17.658$; d.f. = 2; p < 0.05). Although movement was associated with the tides, the direction of movement appeared to be random ($x^2 = 0.79718$; d.f. = 2; p > 0.05). Furthermore, *P. saccharina* travelled longer distances and undertook longer excursion periods during spring tides ($d_{median} = 104.06$ mm; $\tau_{median} = 60$ min) compared to during neap tides ($d_{median} = 15.70$ mm; $\tau_{median} = 15$ min) (Mann-Whitney U test; d: U = 2348, d.f. = 1, p < 0.05; τ: U = 1965.5, d.f. = 1, p < 0.05). Lastly, travel speed was greater during the spring tides ($s_{median} = 1.26$ mm min^{-1}) compared to during neap tides ($s_{median} = 0.22$ mm min^{-1}) (Table 3).

DISCUSSION

Nocturnal habit of *Patelloida saccharina*. Diel observations over one lunar cycle allowed documentation of *Patelloida saccharina* movement patterns in Catagman, Samal Island. Results showed that throughout the daylight hours in both spring and neap tides, limpets did not move away from their home site. During the spring tides, limpets returned to their home sites before daylight, and seemed to seize the opportunity to forage during the rising tide, despite the short period of darkness before daylight. Daylight or illumination appeared to be a contributing factor to the cessation of *P. saccharina* movement. Although the level of illumination that may facilitate limpet movement was not measured, the initial observation presents an opportunity to investigate this aspect, as demonstrated by the works of Rogers (1968) and Ross (1968) on acmaeid limpets. Acmaeid limpets possess eyespots that act as photoreceptors (Rogers, 1968), and, interestingly, light reception through the shell in *Notoacmaea persona* (Rathke, 1833) facilitates its phototactic response (Lindberg et al., 1974). Limpet species are generally perceived as nocturnal animals (Lord, 2008). The diel observations confirmed the nocturnal habit of *P. saccharina* limpets; they are only active during the night because illumination during the day would cause cessation of movement (i.e., negative phototaxis). Negative phototaxis is an equally important factor in limpet behaviour (Lindberg et al., 1974) and investigating the light responses in limpets would demand similar field and laboratory experiments.

Tidal rhythmicity of limpet movement. In addition to movement during periods of darkness, results indicated that tidal rhythms also influence *P. saccharina* movement. During spring tides, movement commenced when *P. saccharina* were submerged by the flooding tide at dusk, and ceased just before the ebbing tide left the high intertidal zone dry (Fig. 3; Table 2). This was also the lowest recorded tidal height that influenced cessation of limpet movement. Despite the increasing tidal height during their second activity in spring tides, limpet movement stopped just before sunrise.

During neap tides, no movement was observed in the night-time low tide period when limpets were emersed. Movement only commenced later when *P. saccharina* were submerged by the flooding tide. These observations support our hypothesis that limpet movement occurred only during nocturnal high tides.

Factors that dictate the movement and homing patterns of limpets cannot be isolated given that the intertidal zone faces environmental gradients that occur in day and night cycles and changing tidal regimes (Underwood, 1979; Branch & Cherry, 1985). While Ohgushi (1954) reported that the subspecies of *P. saccharina* in Japan moved day and night while awash (Branch, 1981), our results suggest that *P. saccharina* in Samal Island, Philippines, moved when submerged and only at night. Little (1989) mentioned similar patterns in the chiton *Chiton pelliserpentis* (Quoy & Gaimard, 1835) (see Horn, 1986) and the pulmonate limpet, *Siphonaria laciniosa* (Linnaeus, 1758) (see Hulings, 1985), which also moved on rocky habitats when submerged at night.

Distance, duration, and direction of limpet movement. Following the results of the Mann-Whitney U Test, the significant difference in distance travelled and duration of limpet movement between spring and neap tides may relate to the number of excursions each tide type allows. During spring tides, limpets may move in either or both of the night-time and dusk submersions, resulting in greater distances moved and increased time spent foraging than during neap tides. Furthermore, Neumann (1981) emphasised that low water values during neap tides do not provide longer soaking periods for limpets compared to during spring tides (Table 3). Little & Stirling (1985) reported similar observations for the temperate limpet, *Patella vulgata* (Linnaeus, 1758), in semi-diurnal tides of Cork, Ireland, where they moved for 6 hours during the spring tides and only 2.5–3 hours during the neap and declining spring tides. Another study by Little et al. (1988) showed that *P. vulgata* spent longer times away from home during spring tides (137.5 min) than in neap tides (40.8 min).

Although the distance and duration of *P. saccharina* excursions were relatively greater in spring tides than in neap tides, a higher percentage of moving individuals was observed during the neap tides (Table 3). It is probable that the limpets maximise their foraging during the spring tides given that they have two feeding opportunities. Limpets are capable of anticipating their feeding schedules (Little et al., 1988) and feed depending on their needs, as observed in *P. vulgata* (Evans & Williams, 1991). Results indicated that the direction of movement of *P. saccharina* in Catagman, Samal Island, was random, but the limpets still returned to their home scars after every outward journey. Moreover, the duration and direction of outward and homeward trips were not the same. The trails of some *P. saccharina* limpets were observed overlapping with those of their neighbouring conspecifics.

Chelazzi et al. (1988) presented three models of feeding excursions, namely, the ranging pattern, zonal shuttling or tidal migration, and central place foraging. They further proposed that most limpets and chitons fall under central place foraging, characterised by utilisation of natural shelters and site fidelity (Chelazzi et al., 1988). Just like the summarised limpet movement patterns, these models may not accurately represent foraging patterns of intertidal animals; an ethological approach is important to avoid generalisations on homing mechanisms (Hirano, 1979b). From here, the preliminary findings of the study appear to support the central foraging theory, as demonstrated by the homing performance of *P. saccharina* on rocky substrates in Catagman, Samal Island.

Loop excursions were also observed for *Cellana nigrolineata* (Reeve, 1854) in Japan, where the outward and return trips of the limpets were different (Hirano, 1979b). Trail-following in limpets has different underlying mechanisms, including foraging (Branch, 1981; Gray & Hodgson, 1997), communication (Chelazzi et al., 1987), or even mate-searching (Hirano & Inaba, 1980). Although we are unable to determine whether *P. saccharina* movement is associated with any of the abovementioned contexts, homing mechanism is the most important aspect for animals following the central foraging theory (Chelazzi & Vannini, 1988).

Movement of *P. saccharina* in response to disturbance. During field work in the last quarter, a low-pressure area at the eastern side of Mindanao brought heavy rains and strong winds. The strong waves detached some of the grid quadrats and removed the nail polish markings on some limpets, thus restricting the scope of observations. While fixing the detached grid quadrats underwater, it was observed that a large limpet lifted itself and moved away from its home scar to the leeward side of the rock to avoid dislodgement. Similar behaviour was observed in two large *P. saccharina* limpets from other grid quadrats that were reinstated. These limpets remained in their new sheltered locations during the low tide observation. Such movements observed among large *P. saccharina* limpets during heavy rains and strong waves validate the occasional activity pattern that may occur among intertidal animals, as described by Chelazzi et al. (1988).

Activity patterns in gastropods could be occasional, continuous, or rhythmic (Chelazzi et al., 1988). Continuous and rhythmic activities are associated with the processes occurring along the sea-land axis (i.e., diel cycles and tidal fluctuations). Hence, their movements become predictable and recurrent in response to the physical environment (Underwood, 1979; Little et al., 1988; Santini et al., 2011). On the other hand, occasional activity refers to responses elicited during unforeseeable events. Chelazzi et al. (1988) discussed that this may occur in the sudden presence of predators or during unfavourable weather conditions. While periods of darkness and submersion in water are prerequisites to *P. saccharina* movement on the rocky intertidal shores of Samal Island, the strong wave action brought by heavy rains can also induce their movement, even during daytime. Such movement is important to prevent dislodgment by the strong waves (Little, 1989) or avoid osmotic stress brought by rain water dilution (Wolcott, 1973; Branch & Cherry, 1985). These deviations from the usual rhythmic patterns have adaptive value and are necessary for survival (Chelazzi et al., 1988; Naylor, 1988).

Overall, activity patterns are variable in response to competitive interactions (Underwood, 1979, 1984), predation (Bertness et al., 1981), and desiccation (Cook, 1969), which are key evolutionary drivers to limpet behaviour (Chelazzi & Vannini, 1988; Little, 1989). Additionally, Branch & Cherry (1985) noted that food availability, wave action, and osmotic stress can also influence these movement patterns. Given that most limpet species reported are of marine origin, Little (1989) emphasised that desiccation is more important in limiting the behavioural plasticity of limpets. However, Branch (1981) argued that if desiccation is the motivation for preference of movement while submerged, why was there no movement during daytime submergence?

The scope of the current study may not be able to determine whether *P. saccharina* movement is driven by competition, predation, or food availability. However, it is probable that *P. saccharina* limpets thriving on the horizontal surface of the high intertidal zone may experience hotter conditions and higher rates of water loss, similar to the reported habitat partitioning in the tropical *Cellana grata* (Gould, 1859) population in Hong Kong (Williams & Morritt, 1995). Moreover, the combination of nocturnal activity and homing habit appears to be a favourable response by *P. saccharina* limpets to persist on the tropical rocky intertidal shores of Samal Island. It should be noted that different movement patterns may be observed in other areas (e.g., Villarta et al., 2019), depending on the habitat type and corresponding environmental gradients (Branch, 1981). Similar studies may be conducted on other limpet species in Samal Island to enrich our understanding of the dynamics of the tropical intertidal environment.

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