

## Habitat Partitioning in Two Intertidal Limpets, *Siphonaria guamensis* (Heterobranchia) and *Patelloida saccharina* (Patellogastropoda), from Southern Thailand

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Mobile intertidal animals exhibit various strategies during emersion to mediate the impact of heat and desiccation, including behavioural adaptations such as moving to lower tidal levels and seeking thermal refuges which can result in spatial partitioning between species within the intertidal environment. We tested whether the limpets, *Siphonaria guamensis* (Heterobranchia) and *Patelloida saccharina* (Patellogastropoda), exhibited differential habitat use during tidal emersion by quantifying their abundance and size distribution in various habitats on two rocky shores on the west coast of Thailand. *S. guamensis* inhabited higher shore levels with hotter average rock temperatures when emersed as compared to *P. saccharina*. On one of the shores, large *S. guamensis* lived at higher tidal levels than smaller individuals, whereas large *P. saccharina* showed the reverse pattern, being found lower on the shore than smaller individuals. The abundance of *S. guamensis* was positively related to the shore slope, with more individuals found on vertical than horizontal rocks, while *P. saccharina* showed a negative relationship between abundance and algal cover. At the heights where they were most abundant, both species were more often found in bare rock habitats as opposed to crevices and areas dominated by oyster shells, despite the fact that bare rock was as hot as, or even hotter than other microhabitats. The exact resting locations of the two species were, however, cooler than the mean temperature of the bare rock. In general, limpets did not exhibit a strong preference for any particular rock orientation but *S. guamensis* on one shore was more abundant on east-facing rocks as compared to other aspects. As a result, although thermal stress appears to be a driver for habitat partitioning between species (occupying different tidal heights), temperature alone is unable to explain distribution patterns within species as limpets were

not adopting to thermal refuges during tidal emersion. Variations in the physical environments adopted may be mediated by species-specific morphological and/or physiological adaptations which determine the distribution of different limpet species on western Thailand rocky shores.

**Key words:** Behavioural adaptations, Vcal distribution, Termal stress, Topical rocky shore, Hitat selection

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## BACKGROUND

Studies from temperate shores reveal that intertidal organisms are strongly influenced by environmental factors that change throughout the tidal cycle, particularly temperature during daytime low tides which can often approach species' physiological tolerances (Chapman and Underwood 1996; Mislán et al. 2009; Hayford et al. 2015). Such high environmental temperatures can induce excessive water loss, change haemolymph concentrations, and perturb cellular enzymes and protein stability (Davies 1969; Marshall and McQuaid 1992; Hochachka and Somero 2014). As a result, physical stress, primarily temperature, has traditionally been proposed to be a major determinant of the upper limits of species' vertical distribution on temperate rocky shores (*e.g.*, barnacles, Connell 1961a b 1972 and algae, Schonbeck and Norton 1978). Several studies have, for example, demonstrated that species occupying different tidal levels on the shore exhibit dissimilar thermal tolerances, with tolerances generally increasing with shore height at both the intra- and interspecific levels (Broekhuysen 1940; Evans 1948; Gowenlock and Hayes 1926; Stillman and Somero, 1996). Many species also exhibit size gradients along the shore vertically (Vermeij 1972), often in relation to variation in shell morphology between small and large individuals (Harley et al. 2009), which can cause ontogenetic changes in distribution patterns (Marshall and Keough 1994).

Within shores the thermal environment experienced by species is highly heterogenous and affected by the aspect and topography of the shore (Williams and Morritt 1995; Helmuth and Hofmann 2001; Harley 2008). For example, in northern latitudes, south-facing surfaces are generally warmer than those facing north (Harley and Helmuth 2003; Denny and Gaines 2007; Firth et al. 2016), and on most shores vertical rock surfaces are typically cooler than horizontal ones (Williams and Morritt 1995; Lathlean et al. 2014). On the other hand, surface roughness or complexity (such as cracks and crevices) can protect intertidal species from direct sunlight (Leviten

and Kohn 1980; Garrity 1984; McAfee et al. 2022), leading to a mosaic of thermal environments on rocky shores even at the same tidal heights (Helmuth et al. 2006), which are often reflected by the patchy distribution of species as they utilize these habitats as refuges from thermal stress (Williams and Morritt 1995; Meager et al. 2011).

Although not as extensively studied as in temperate regions, temperatures on some tropical shores are extreme and can regularly exceed 50°C, reaching the lethal limits for many species (Lewis 1963; Williams 1993; Hui et al. 2020). As a consequence, mass mortalities frequently occur when animals are exposed to such extreme thermal stress in air during low tides (Levings and Garrity 1983; Tsuchiya 1983; Williams 1993; Liu and Morton 1994; Chan et al. 2006), posing a very strong selection pressure on the tidal heights and habitats these species occupy. Accordingly, many mobile species reside in cooler habitats within these mosaic thermal environments to help ameliorate thermal stress (Garrity 1984; Williams and Morritt 1995; reviewed by Ng et al. 2017). The chiton, *Liolophura (Acanthopleura) japonica*, for example, takes refuge in cracks and crevices to mitigate heat and desiccation stresses during low tides (Harper and Williams 2001) and littorinid snails, *Echinolittorina malaccana*, and *E. vidua*, actively shelter in patches of empty barnacle tests during summer (Cartwright and Williams 2012). Apart from habitat use, some coiled gastropods can exhibit other thermoregulatory behaviours such as isolating themselves by retracting their foot into the shell (Ng et al. 2017). Constrained by their body plan, limpets cannot retract their foot and always remain attached to the rock substrate (Vermeij 1973; Hodgson 1999), which gives them a limited ability to exhibit these thermoregulatory behaviours. Consequently, limpets are susceptible to thermal and desiccation stress during prolonged emersion and, as such, habitat selection such as residing in specific tidal levels and habitats is a key behavioural strategy for their survival in hot environments (Lewis 1954; Williams and Morritt 1995; Virgin and Schiel 2023).

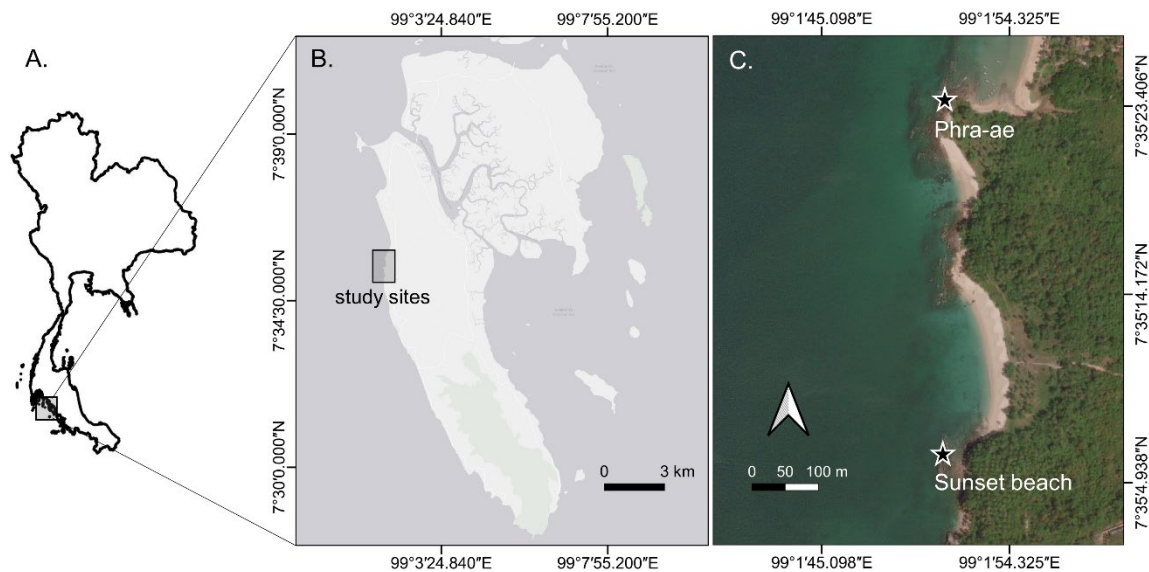
Both true- (patellogastropods) and false- (pulmonates) limpets are common on tropical rocky shores where they often co-exist (Morton and Morton 1983; Hodgson 1999). While some studies note that the difference in respiratory modes (primarily using the gill and mantle cavity for gaseous exchange in true- and false-limpets respectively) affects the thermal tolerance of these two groups of limpets (Marshall and McQuaid 1989 1992), others suggest that differences in thermal tolerances are probably species-specific (Kankondi et al. 2018). Observations on rocky shores along the coast of the Andaman Sea, Thailand reveal that the pulmonate limpet *Siphonaria guamensis* Quoy and Gaimard, 1833, and the patellogastropod *Patelloida saccharina* Linnaeus, 1758 are abundant, co-occurring grazers (Wangkulangkul and Promdam 2018). *S. guamensis* occupies higher levels on shore, below the littorinid snails, while *P. saccharina* is found lower, above the algal band. Unlike other tropical limpets (e.g., *Cellana grata*, Williams and Morritt 1995; Hutchinson and Williams 2001), *S. guamensis* and *P. saccharina* do not display substantial movements up and down

the shore to forage when awash by the tides but feed at similar tidal levels that they occupy during low tides (Sangphueak S., personal observations) and both exhibit “homing” behaviour (returning to the same exact location after feeding, Wangkulangkul K., unpublished data). In this study, we hypothesized that the distribution of these two species would exhibit both inter- and intraspecific variations in association with the thermal regime they experience on tropical Thailand shores. Firstly, we tested for interspecific differences in within-shore vertical distribution patterns between the two species in relation to the physical and biological conditions they experience. Given their body plan and limited behavioural capacity for thermal regulation, we further hypothesized that both species would exhibit intraspecific habitat selection to minimize thermal stress within the tidal levels they inhabit.

## MATERIALS AND METHODS

### Study sites and location

The abundance and distribution of *Siphonaria guamensis* and *Patelloida saccharina* were quantified at low tides on two rocky shores (Phra-ae: 7°35'24.0"N, 99°01'51.1"E; Sunset beach: 7°35'06.2"N, 99°01'51.1"E, separated by approx. 400 m) on Lanta Island (Fig. 1) on the west coast of Thailand, in January 2021. January is among the year's hottest months, with maximum rock temperatures over 50°C recorded on the high shore (~2.5–3 m above C.D., unpublished data). Tides are semidiurnal with a tidal range of ~2.5 m and low tide occurs in the early morning and late afternoon. Both shores are wave-exposed and characterized by large boulders and rock platforms with similar inclinations. On both shores, the two limpet species are found to co-exist with other sessile species such as barnacles (*Chthamalus malayensis* and *Amphibalanus amphitrite*), oysters (*Saccostrea cucullata*), algae (*Sargassum* sp., *Padina* sp., *Turbinaria* sp.), and mobile species such as limpets (*Cellana* sp.) and snails (*Echinolittorina* sp., *Nerita* sp.; Coppejans et al. 2017; Wangkulangkul and Promdam 2018).



**Fig. 1.** Map of the study sites. (A) map of Thailand; (B) Lanta Island which is located on the west coast of Thailand; (C). The two shores at Phra-ae and Sunset beach (Google Maps, 2016).

### Vertical distribution patterns of the limpets

Abundance and size distribution of the limpets were assessed along the tidal gradient and related to the physical (slope, rock aspect, surface roughness and rock temperature) and biological (mobile and sessile species) conditions of the shores. Each shore was divided into six sections of 30 cm vertical heights (1.0–1.3 m, 1.3–1.6 m, 1.6–1.9 m, 1.9–2.2 m, 2.2–2.5 m, and 2.5–2.8 m above C.D. from low to high shore) covering the tidal range where the two limpets were present. In each section, ten random quadrats (30 × 30 cm) were placed along a 21 m horizontal transect to measure the abundance and size (maximum length using vernier callipers,  $\pm 0.1$  mm) of the two limpet species. Within each quadrat, to assess comparative spatial variations between habitats at different tidal levels, a snapshot measure of rock temperature was recorded from the quadrat centre using a GS LCD laser digital infrared thermometer. Slope was measured in the middle of the quadrat using a clinometer ( $\pm 1^\circ$ ) while aspect was measured by a mobile phone compass application (ColorOS Compass 7.2.1, OPPO F7). Surface roughness was quantified using the chain method (Beck 1998; Aguilera et al. 2014). Specifically, the chain (link size = 7 mm) was placed following the topography of the rock across the 30 cm quadrat length in the middle of the quadrat, and the actual length of the chain was measured (where longer length indicates greater roughness). A photo (Coolpix W300, Nikon) of each quadrat was taken to quantify percentage covers of sessile organisms and numbers of other mobile species.

Difference in the abundances of *S. guamensis* and *P. saccharina* between shores and tidal levels was tested using a generalized linear model (GzLM) fitted with a negative binomial distribution in the MASS package in R (Venables and Ripley 2002). The model was fitted using shore (fixed, two levels), tidal height (fixed, six levels) and their interaction as explanatory variables. To test for variations in limpets' size between shores and tidal heights, a general linear model (GLM) was used with natural log transformed size as the response variable and shore (fixed, two levels), tidal level (fixed, two levels for *S. guamensis* and three levels for *P. saccharina*, as tidal levels with less than 5 individuals were excluded from the analyses) and their interaction as the explanatory variables. Both models were followed by an analysis of deviance (for the GzLM)/variance (for the GLM) and *post-hoc* comparisons for significant explanatory variables (using the *car* and *emmeans* packages in R).

A stepwise regression was further constructed to identify physical (shore, temperature, aspect, slope, and roughness) and biological factors (the percentage covers of oysters, barnacles, crustose algae, and thalli algae) which best explained the distribution pattern of each limpet species. Rock aspect was firstly converted into linear measures of 'eastness' and 'northness' by sine and cosine transformations (to obtain projections along the east-west and north-south directions respectively), hereafter denoted as aspect E-W and aspect N-S (Olaya 2009; Barbosa et al. 2021). A generalized linear model with negative binomial distribution was used with forward selection to identify explanatory variables that best explain the number of limpets. All analyses were performed in R version 4.2.0 (R Core Team 2022).

### **Thermal environment at the limpets' most abundant shore heights**

To determine long term variation in rock temperatures experienced by the two species, the thermal environments of the shore heights where both *S. guamensis* and *P. saccharina* were most abundant were monitored at Phra-ae from November 2021 to February 2022 (89 days), encompassing the hottest time of the year. Three temperature loggers (27 mm Envlogger v2.4, ElectricBlue) were deployed using Z-Spar epoxy resin (A-788 Splash Zone Compound, Kop-Coat Inc.) at 2.5 m (for *S. guamensis*) and 1.6 m (for *P. saccharina*) above C.D. respectively to record rock surface temperatures at hourly intervals (sampling resolution: 0.1°C, after Lima and Wetthey 2009).

The temperature time series recorded were firstly aligned with predicted tidal heights from a nearby tidal station (8°02'38"N, 98°54'32"E, Hydrographic Department, Thailand 2021). Temperatures of the hottest days of spring (between 15<sup>th</sup>–21<sup>st</sup> January 2022) and neap tides (22<sup>nd</sup>–28<sup>th</sup> January 2022) were extracted to estimate the maximum thermal stress animals experienced.

Spring and neap tides were classified into morning and afternoon low tides with night time temperatures between 7 pm–6 am excluded to determine the emersion period when the loggers were exposed to air during the day (following Hui et al. 2020). Mean duration of emersion during daytime, daily mean, maximum, minimum, range and coefficient of variation of rock temperature (see Table S1) were calculated for all loggers ( $n = 3$  at each tidal height).

### Habitats available and occupied by the limpets

On the two shores, potential habitats for limpets could be broadly categorized into three types: bare rock, crevices and oyster-modified habitat. To quantify the availability of these three major habitat types, fifty random quadrats ( $10 \times 10$  cm) were placed along a 21 m horizontal transect within the 30 cm band where each limpet species was most abundant at each of the shores (1.6–1.9 m at both sites for *P. saccharina*; 2.2–2.5 m at Phra-ae and 1.9–2.2 m at Sunset beach for *S. guamensis*). Each quadrat was assigned into one of the three habitat types as: bare rock = areas with > 50% bare rock surface without cracks or oysters; crevices = areas where > 50% of the surface was composed of cracks or crevices (2.5 to < 5 cm at the widest opening) and oyster-modified habitats = areas where > 50% of the surface was occupied by the oysters, *Saccostrea* spp.

To examine the overall physical characteristics of available habitats on the two shores, one hundred random quadrats ( $10 \times 10$  cm) were placed at the same tidal levels. Habitat type, slope, temperature, and aspect were measured for each quadrat (using the same methods as described above). To assess whether the limpets occupied different habitats, one hundred individuals (at 2.5 m and 1.6 m above C.D. for *S. guamensis* and *P. saccharina*, respectively) were haphazardly chosen and a  $10 \times 10$  cm quadrat was placed over the chosen limpets, and the habitat type, slope, temperature, and aspect of the limpets' resting locations were measured as above.

To test whether the two limpets exhibited a bias in their habitat occupation, the frequency count of habitat availability between the three habitat types was tested against the frequency count of habitats the limpets occupied using Fisher's exact test in the *stats* package in R version 4.2.0. based on data from fifty quadrats placed in each species' band. Principal Component Analysis (PCA) in Past (Paleontological Statistics) 4.06 (Hammer et al. 2001) was performed to elucidate the key physical characteristics (rock temperature, rock slope, and rock aspect) explaining the variation in the limpets' resting location. Temperature and aspect, two key physical factors as identified by the PCA (see Results), were further analysed. A GLM was performed to examine whether temperatures varied between sites (fixed, two levels), zones (*S. guamensis* and *P. saccharina* zones, fixed, two levels), and habitats (bare rock, crevice, oyster-modified habitat and limpet resting locations; fixed, four levels). *Post-hoc* multiple comparisons for significant factors were then

investigated using the emmeans package in R version 4.2.0. Rayleigh’s tests (Zar 2010) were used to determine whether aspects of the rock surface where limpets were found, and the aspects of the rock surface that were available on the shores, differed from a random orientation. When both aspects were non-randomly distributed, Watson-Williams tests were used to determine the difference between the mean aspects of the limpets’ resting location and the mean angle of the rock aspect available on the shores (Zar 2010).

RESULTS

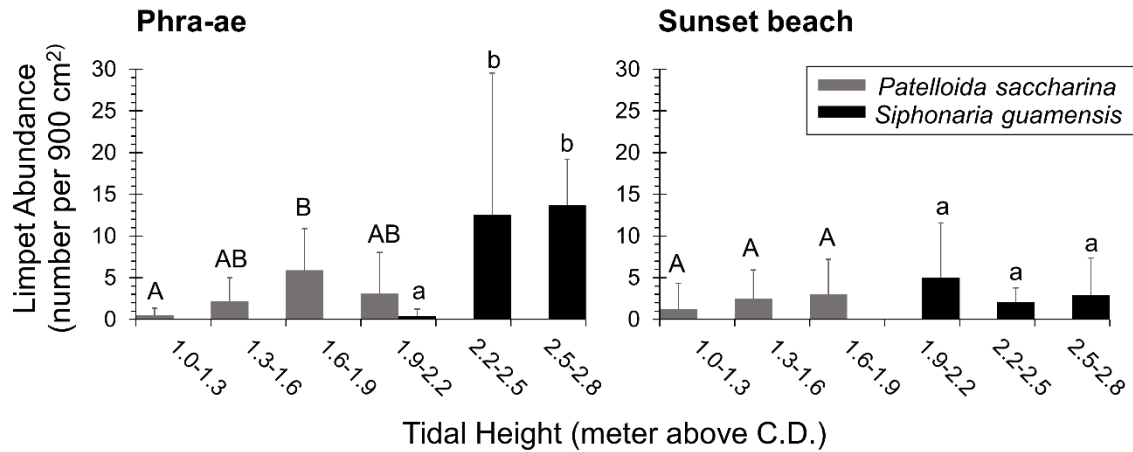
Vertical distribution patterns of the limpets

*Siphonaria guamensis* was found higher on the shore at both sites (1.9–2.8 m above C.D.) than *Patelloida saccharina* (1.0–2.2 m at Phra-ae and 1.0–1.9 m above C.D. at Sunset, Fig. 1). At Phra-ae, the highest density of *S. guamensis* was observed at 2.2–2.8 m above C.D., and at 1.6–1.9 m above C.D. for *P. saccharina*. At Sunset beach, however, both limpet species were distributed evenly across the tidal heights (Fig. 1, Table 1). In terms of size, large individuals of *S. guamensis* inhabited higher levels than small ones at Phra-ae while this difference was not found at Sunset beach where they were less abundant (Fig. 2, Table 2). Large individuals of *P. saccharina* inhabited lower levels than small individuals at Phra-ae, but the reverse pattern was observed at Sunset beach (Fig. 3, Table 2). The environmental factors which best explained the distribution pattern of *S. guamensis* were shore and slope, while the presence of both thallose and crustose algae best explained distributions of *P. saccharina* (Table 3). *S. guamensis* were more abundant at Phra-ae as compared to Sunset beach and in areas with greater slope; whereas *P. saccharina* had higher abundance in areas with low cover of algae.

**Table 1.** Analysis of deviance on the negative binomial generalized linear models to investigate the effects of tidal level, shore and their interaction on the abundances of *Siphonaria guamensis* and *Patelloida saccharina*. Asterisks indicate significant effects ( $P < 0.05$ ). *Post-hoc* comparisons of significant factors are shown in figure 2

Source of variation	$\chi^2$	d.f.	P
<i>Siphonaria guamensis</i>			
Shore	4.11	1	< 0.05*
Tidal level	191.10	5	< 0.001*
Shore × Tidal level	32.63	5	< 0.001*
<i>Patelloida saccharina</i>			
Shore	2.35	1	0.13
Tidal level	77.45	5	< 0.001*
Shore × Tidal level	17.80	5	< 0.01*

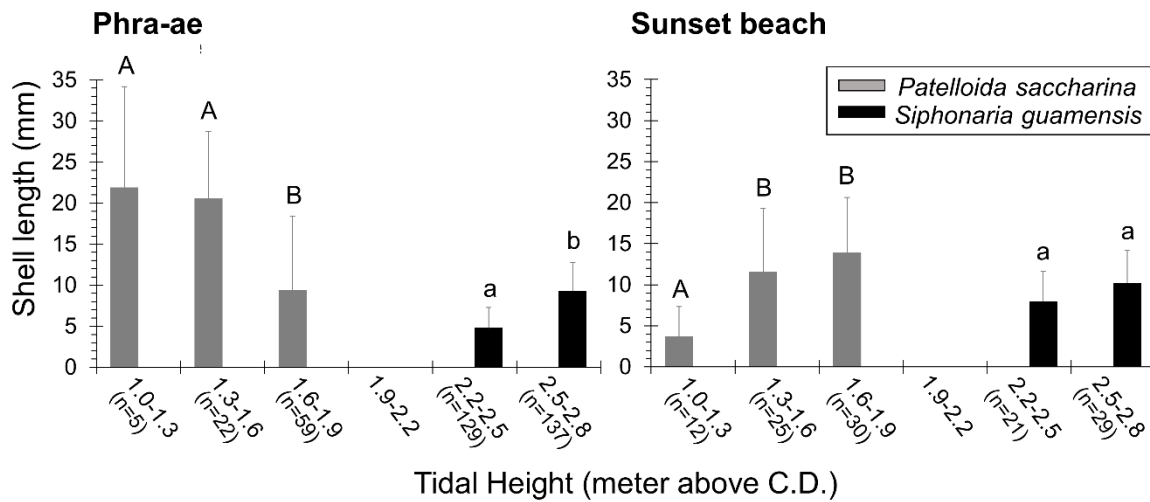




**Fig. 2.** The abundances of *Patelloida saccharina* and *Siphonaria guamensis* (mean + S.D.,  $n = 10$ ) measured during low tide along the vertical gradient (divided into six sections of 30 cm of vertical height) in Phra-ae and Sunset beach. Different letters indicate significant variation in abundance across tidal heights (uppercase for *P. saccharina* and lowercase for *S. guamensis*). Results were retrieved from *post-hoc* comparisons ( $P < 0.05$ ).

**Table 2.** Analysis of variance on the general linear models to investigate the effects of shore, tidal level and their interaction on size (shell lengths) of *Siphonaria guamensis* and *Patelloida saccharina*. Asterisks indicate significant effects ( $P < 0.05$ ). *Post-hoc* comparisons of significant factors are shown in figure 3

Source of variation	Sum of Square	d.f.	F	P
<i>Siphonaria guamensis</i>				
Shore	2.95	1	14.24	< 0.001*
Tidal level	28.56	1	137.83	< 0.001*
Shore $\times$ Tidal level	1.86	1	8.99	< 0.01*
Residuals	63.82	308		
<i>Patelloida saccharina</i>				
Shore	0.44	1	0.67	0.41
Tidal level	12.97	2	9.97	< 0.001*
Shore $\times$ Tidal level	28.46	2	21.87	< 0.001*
Residuals	95.64	147		



**Fig. 3.** Shell lengths of *Patelloida saccharina* and *Siphonaria guamensis* (mean + S.D.) measured during low tide along the tidal gradient in Phra-ae and Sunset beach. Sample sizes at each tidal height are shown in the x-axis. Different letters indicate significant variation in shell length between tidal levels (uppercase for *P. saccharina* and lowercase for *S. guamensis*). Results were retrieved from *post-hoc* comparisons ( $P < 0.05$ ).

**Table 3.** Stepwise regression to determine the environmental factors (including shore, temperature, aspect, slope, roughness, the percentage covers of oysters, barnacles, crustose algae, and thalli algae) best explaining limpet abundances via forward selection procedures. Only explanatory variables retained in the final model are shown. Asterisks indicate significant effects

	Estimate	Standard Error	z value	P
<i>Siphonaria guamensis</i>				
Shore	-1.76	0.35	-5.09	< 0.001*
Slope	0.01	0.01	2.20	< 0.05*
<i>Patelloida saccharina</i>				
Thalli algae	-0.02	0.01	-2.80	< 0.01*
Crustose algae	-0.03	0.01	-2.50	< 0.05*

### Thermal environment at the limpets' most abundant shore heights

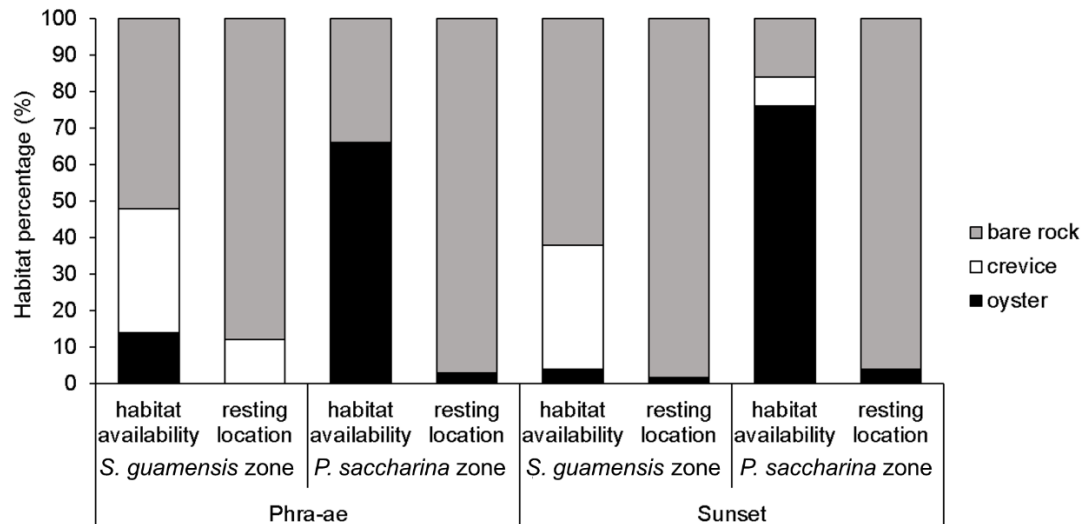
On spring tides, emersion periods were longer in the afternoon than in the morning, with the reverse pattern for neap tides (Table 4, Figs. S1, S2). The longest emersion duration at 2.5 m (*S. guamensis*'s most abundant shore height) was ~7 hours in the afternoon on spring tides, whereas at 1.6 m (*P. saccharina*'s most abundant shore height), it was ~4 hours in the afternoon on spring tides and in the morning on neap tides (Table 4). The average daily maximum rock temperatures on the afternoon low tide were greater than in the morning low tide for both spring and neap tides and also at 2.5 m (max. 47.8°C) than 1.6 m (max. 42.5°C, on afternoon neap tides, Table 4).

**Table 4.** Summary metrics of emersion durations (hour) and daily maximum rock temperature (°C,  $n = 3$ , Envloggers) during spring (15<sup>th</sup>–21<sup>st</sup> January 2022) and neap tides (22<sup>nd</sup>–28<sup>th</sup> January 2022) recorded at 1.6 and 2.5 m above C.D. for *Patelloida saccharina* and *Siphonaria guamensis* respectively at Phra-ae

Tide	Parameters	2.5 m above C.D.				1.6 m above C.D.			
		Average	SD	Max.	Min.	Average	SD	Max.	Min.
Spring	Morning low tide								
	Duration of emersion	3.0	0.8	4.0	2.0	2.0	0.8	3.0	1.0
	Daily maximum temperature	31.9	4.0	39.8	24.9	25.8	1.7	29.6	23.5
	Afternoon low tide								
	Duration of emersion	5.3	1.5	7.0	3.0	3.0	0.8	4.0	2.0
	Daily maximum temperature	38.6	3.2	44.2	30.3	32.4	2.0	38.9	28.4
Neap	Morning low tide								
	Duration of emersion	5.0	0.0	5.0	5.0	3.3	0.8	4.0	2.0
	Daily maximum temperature	37.8	2.4	43.8	29.8	31.0	1.9	38.4	26.9
	Afternoon low tide								
	Duration of emersion	3.3	1.4	6.0	2.0	1.7	1.2	3.0	1.0
	Daily maximum temperature	39.4	6.3	47.8	29.5	33.5	5.4	42.5	27.6

### Habitats available and occupied by the limpets

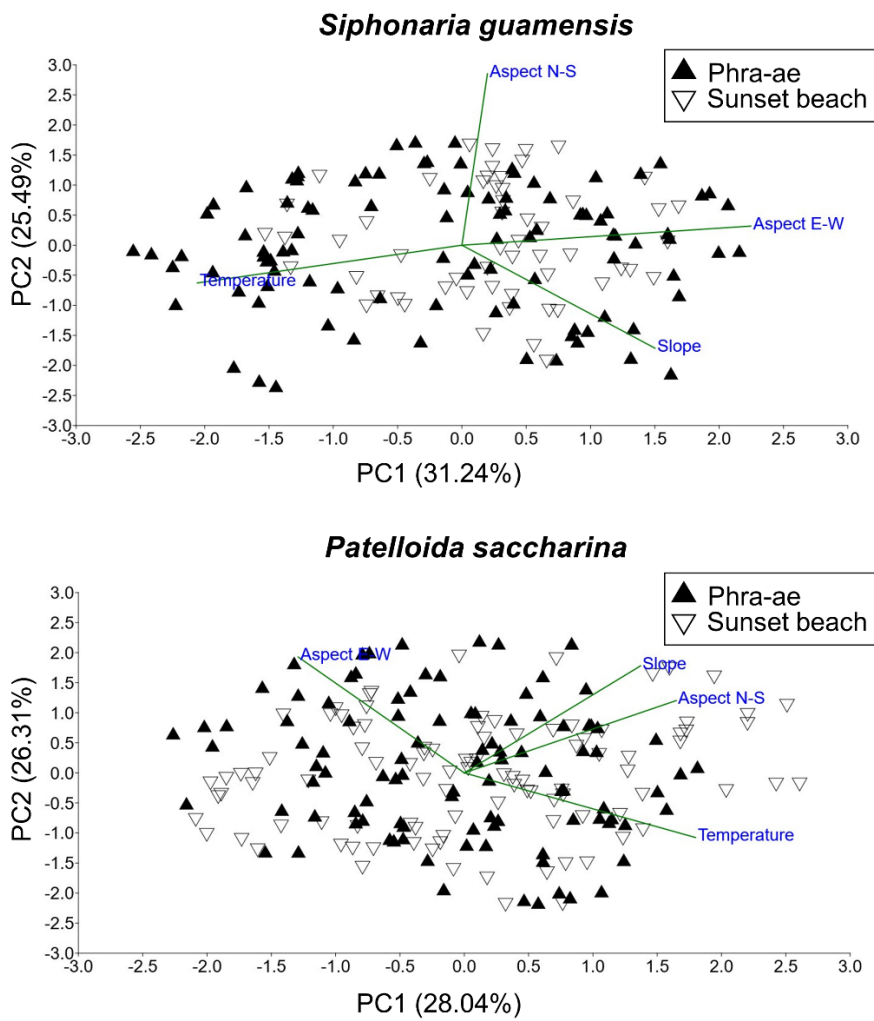
Both limpet species were mostly found on bare rock rather than crevice or oyster-modified habitats at both sites (Fig. 4; Fisher's exact test,  $p < 0.001$ ). PCA analysis indicated that 56.72 % of the total variance of *S. guamensis* resting locations at the two sites could be explained by the first two principal components, whereas for *P. saccharina* the two principal components explained 54.35%. Temperature and aspect showed relatively strong loading values for both species (Fig. 5). Mean temperature of *S. guamensis*' resting locations were lower than bare rock and crevice habitats at Phra-ae and lower than the bare rock at Sunset beach (Fig. 6, Table 5). The temperatures of *P. saccharina* resting locations at Phra-ae were also lower than bare rock whereas there was no difference among habitats at Sunset beach (Fig. 6, Table 5). In most cases, temperatures of crevices and oyster-modified habitat did not differ from bare rock (Fig. 6). Aspects of available rock surfaces at the most abundant heights occupied by *S. guamensis* at Phra-ae and *P. saccharina* at Sunset beach were non-random (Rayleigh's tests, mean angles = 295° and 58° from the north, respectively, Fig. 7A) as were the aspects of limpets' resting locations of *S. guamensis* at both sites (mean angles = 317° in and 98° from the north in Phra-ae and Sunset beach, respectively, Fig. 7B). The aspect of resting locations of *P. saccharina* were, however, random at both sites (Fig. 7B). The mean aspects of the rock surface that were available on the shores and the resting locations of *S. guamensis* at Phra-ae were similar (Watson-William's test,  $F = 2.526$ ,  $n = 100$ ,  $P > 0.05$ ).



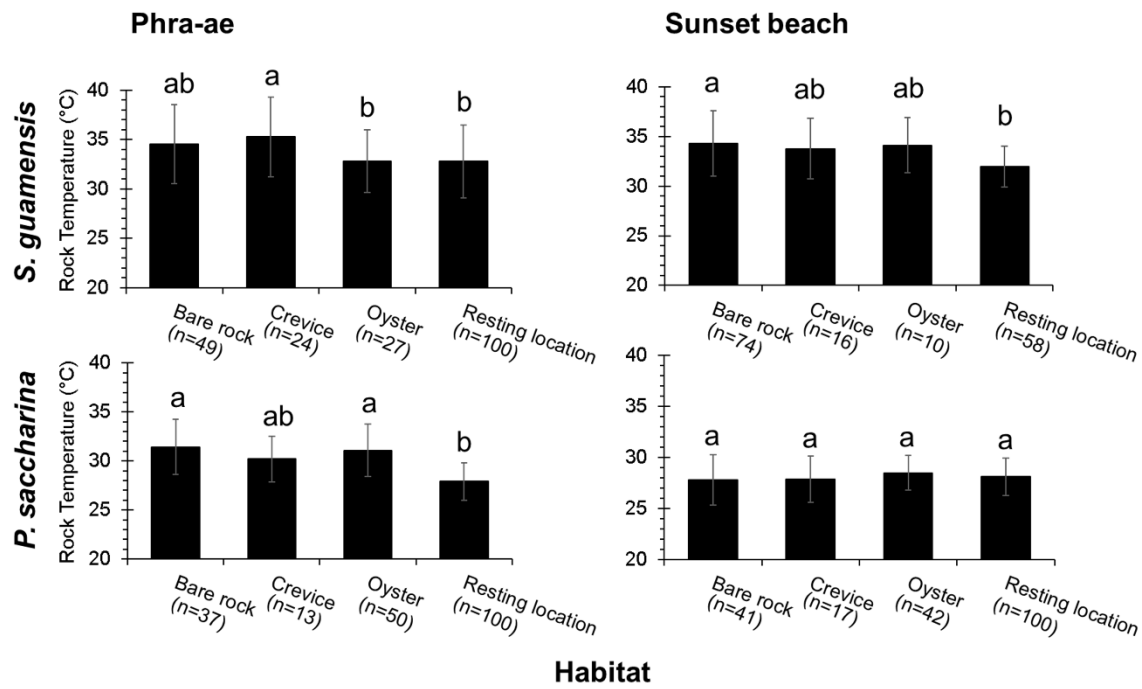
**Fig. 4.** Relative percentage availability of the three habitat types (bare rock, crevice and oyster) and resting habitat locations of the limpets at levels where they were most abundant at each shore ( $n = 58$  individuals for *S. guamensis* at Sunset beach and  $n = 100$  individuals in all others).

**Table 5.** Analysis of variance on the general linear model to investigate temperature variation between shores (Phra-ae and Sunset beach), tidal levels where the two limpets were most abundant (denoted as limpet zone, two levels), habitat types (bare rock, crevice and oyster habitat) and their interaction. Asterisks indicate significant effects ( $P < 0.05$ ). *Post-hoc* comparisons of significant factors are shown in figure 6

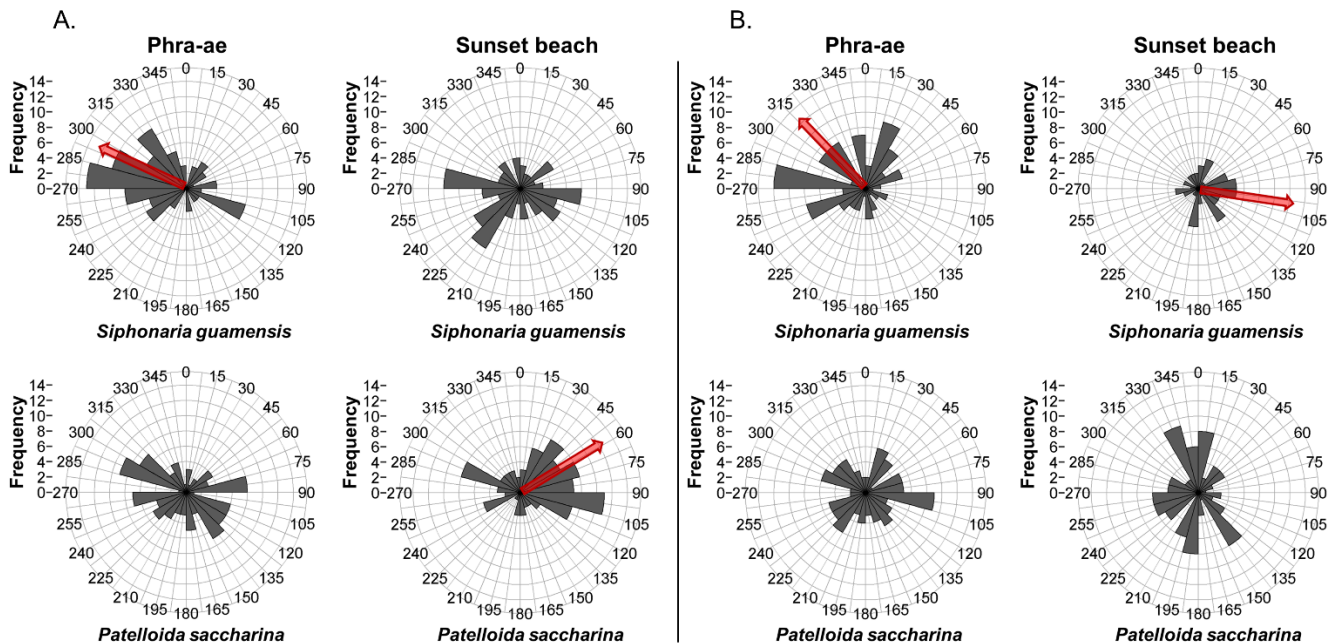
Source	Sum of Square	d.f.	F	P
Shore	171.80	1	21.89	< 0.001*
Limpet zone	3535.80	1	450.39	< 0.001*
Habitat type	524.70	2	22.28	< 0.001*
Shore × Limpet zone	44.70	1	5.70	< 0.05*
Shore × Habitat type	103.80	3	4.41	< 0.01*
Limpet zone × Habitat type	71.50	3	3.04	< 0.05*
Shore × Limpet zone × Habitat type	201.80	3	8.57	< 0.001*
Residuals	5825.00	742		



**Fig. 5.** Ordinations from Principal Component Analysis (PCA) on physical factors measured at limpets' resting locations, including temperature, slope, aspects N-S and E-W. Directions of the vectors represent their strengths of correlation with the principal components (higher correlation when more aligned with the axes).



**Fig. 6.** Comparative measurements of rock temperatures measured using an infrared thermometer (mean  $\pm$  S.D., n values given in brackets)) during a low spring tide at limpets' resting locations and three habitat types (bare rock, crevice, and oyster) within the tidal height where the limpets were most abundant. Sample sizes at each tidal height are shown in the x-axis. Different letters indicate significant variation in rock temperature between four habitat types (bare rock, crevice, oyster, and limpets' resting location). Results were retrieved from *post-hoc* comparisons ( $P < 0.05$ ).



**Fig. 7.** Frequency distributions of rock aspects in areas where limpets were not present (A) and at limpets' resting locations (B), at the same tidal height. Arrows indicate significant deviation from random orientation, Rayleigh's Test).  $n = 58$  for *S. guamensis* resting locations at Sunset and  $n = 100$  for all others.

## DISCUSSION

## Vertical distribution patterns of the limpets

*Siphonaria guamensis* and *Patelloida saccharina* showed clear interspecific differences in their vertical distribution ranges on the two shores on the west coast of Thailand. *S. guamensis* inhabited higher tidal levels than *P. saccharina* and so experienced longer emersion periods and higher average maximum temperatures. These patterns appear to match literature records for the genera, as limpets in the genus *Siphonaria* are known to have a diverse vertical distribution range from the lower to upper littoral zone (see review by Hodgson 1999), and some species can be found in tide pools (Branch and Cherry 1985; Lombardo et al. 2013). *S. guamensis* has been recorded on seawalls in Singapore with a wide vertical tidal range (0.5–2.8 m above C.D. with the highest density in the mid-littoral zone at 1.2–2.2 m above C.D., Chim and Tan 2009). Marshall and McQuaid (1992) noted that *Siphonaria oculus* maintained a higher vertical distribution than the patellid *Scutellastra* (= *Patella*) *granularis* on South African shores as a result of its ability to withstand water loss and longer periods of aerial exposure. Previous studies have shown that *P. saccharina* occupies low and mid-levels (1.25–1.75 m above C.D.) in Hong Kong (Liu and Morton 1998; Lam et al. 2009) and low shore levels in the Philippines (0.25–0.50 m above C.D., Villarta et al. 2017). Villarta et al. (2017) suggested that these levels are suitable resting areas for *P. saccharina* because limpets are exposed to short durations of sunlight and experience reduced levels of desiccation. On both shores in the present study, *S. guamensis* appears to be more tolerant of aerial exposure as compared to *P. saccharina* as it was exposed in air for approximately twice as long as *P. saccharina* and experienced higher rock temperatures, particularly during afternoon low tides when the shore experiences its maximum temperature.

At Phra-ae, large individuals of *S. guamensis* were mainly found at higher levels than small ones, but this pattern was reversed for *P. saccharina*. This observation conforms to Vermeij's (1972) model of intraspecific size distribution of gastropods across tidal levels. In this model Vermeij proposed a difference in size gradients between high shore and lower shore species with physical stress and biological factors as the dominant driving forces respectively. Vermeij suggested that the size of high shore species tends to increase up the shore, as large individuals with reduced surface area:volume ratios will be less susceptible to physical stress; whereas in contrast, the size of species inhabiting lower levels often increase down shore as large individuals can better withstand predation and competition. These interpretations seem logical and have been supported by evidence from a number of rocky shore species (Connell 1972; Wolcott 1973; Miller et al. 2009; Stickle et al. 2017) including other siphonariid species exhibiting larger sizes higher on the shore (Vermeij 1972;

Olivier and Penchaszadeh 1968; Marcus and Marcus 1960). Large individuals of *S. guamensis* in the present study probably have a higher tolerance to prolonged aerial exposure as compared to small individuals, consequently enabling them to occupy higher shore levels. As for the lower shore *P. saccharina*, whilst there were no further records found for *Patelloida* species, a similar pattern of mean size increasing down shore has been noted in other limpet species living at similar shore levels (*A. pelta* in Oregon, Shotwell 1950; *A. testudinalis testudinalis* in Nova Scotia, Stephenson and Stephenson 1954; *A. scutum* in Oregon, Shotwell 1950 and *A. noronhensis* in Brazil, Vermeij 1972 and *P. argenvillei* in west South Africa, Stephenson et al. 1940 and *P. intermedia* in Senegal, Vermeij 1972).

Across the tidal gradient, variation in slope and abundance of algae on the shores also contributed to the distribution patterns of *S. guamensis* and *P. saccharina*, respectively. The abundance of *S. guamensis* was positively related to the slope of rock with more individuals found on vertical than horizontal bare rocks over the tidal gradient, which may be a consequence of the limpets seeking cooler areas to occupy during low tides as rock temperatures on vertical surfaces are usually lower than on horizontal surfaces (e.g., Garrity 1984; Williams and Morritt 1995; Chan et al. 2006; Harley 2008). Amnuaypon and Wangkulangkul (2018) found that *S. guamensis* on bare rock was more abundant and had larger shells than those found on oyster shells. The limpets may avoid areas covered by oysters but whether this drives them to reside on bare rock has yet to be tested. As compared to *S. guamensis*, *P. saccharina* were more abundant low on the shore where crustose and thallose algae were present, although their abundance was negatively associated with coverage of these algae. In the areas covered by dense algae, *P. saccharina* was sparse or absent which may be a result of the macroalgae fragmenting the habitat available for the limpets to feed on, as limpets tend to avoid moving over irregular surfaces (Erlandsson et al. 1999). *Cellana tramoserica*, for example, does not move or feed effectively over dense beds of foliose algae and was constrained from moving downwards by the algae lower down the shore (Underwood and Jernakoff 1981).

### **Habitat selection of the limpet species**

Both species were found more frequently on bare rock as compared to crevices or oyster-modified areas, which contradicts previous studies showing species residing in shaded microhabitats such as cracks, crevices, or biogenically modified habitats during low tides, especially in the tropics (e.g., limpets in Branch 1976; Williams and Morritt 1995; Gray and Hodgson 2004, littorinid snails in Cartwright and Williams 2012, chitons in Harper and Williams 2001; Aguilera and Navarrete 2007, and nerites in Hui et al. 2022). In the present study, the overall



rock surface temperatures between habitat types (bare rock, crevices and oyster-modified habitat) were similar, which might explain why the limpets did not actively take refuge in shaded areas. The temperatures of the limpets' resting positions were, however, generally lower than the average temperature of any available habitat types on the shores, including bare rock. Limpets appear, therefore, to be adopting resting locations on cool bare rock surfaces. This is supported by the fact that on one shore (Sunset beach), the aspect of the rock surface where most *S. guamensis* was found, was east-facing. On both shores, the thermally stressful low tides occur in the afternoon, when west-facing rock surfaces heat up more than east-facing surfaces. Such selection with regard to aspect was not, however, evident at Phra-ae or for *P. saccharina*, suggesting that whilst species-specific physiological adaptations of *S. guamensis* and *P. saccharina* to cope with thermal stress may determine their overall patterns of distribution (occupying different tidal heights), local environmental heterogeneity is another key component modifying distribution patterns within species and shores.

## CONCLUSIONS

*S. guamensis* and *P. saccharina* show species-specific vertical partitioning along the tidal gradient on the west coast of Thailand both in terms of abundance and size distribution, which can be associated with species-specific responses (such as morphology and physiology) to thermal stress higher on the shore, as noted for many temperate rocky shore mobile molluscs. Within the heights occupied by the two species, their resting locations were found on bare rock surfaces which were, in general, cooler than any unoccupied habitats of various types, and provide the limpets with areas free from algae or oyster habitats to feed on. The patterns of distribution and habitat use in these tropical species highlight the importance of species-specific responses and local scale variations in determining larger scale patterns (in terms of vertical distribution) and habitat selection by the limpets.

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## REFERENCES

- Aguilera MA, Broitman BR, Thiel M. 2014. Spatial variability in community composition on a granite breakwater versus natural rocky shores: Lack of microhabitats suppresses intertidal biodiversity. *Mar Pollut Bull* **87**:257–268. doi:10.1016/j.marpolbul.2014.07.046.
- Aguilera MA, Navarrete SA. 2007. Effects of *Chiton granosus* (Frembly, 1827) and other molluscan grazers on algal succession in wave exposed mid-intertidal rocky shores of central Chile. *J Exp Marine Biol Ecol* **349**:84–98. doi:10.1016/j.jembe.2007.05.002.
- Amnuaypon P, Wangkulangkul K. 2018. Influence of habitat modification by rock oysters and barnacles on small-scale distribution of the tropical pulmonate limpet *Siphonaria guamensis*. *Zoology and Ecology* **28**: 292–299. doi:10.1080/21658005.2018.1520023.
- Barbosa RV, Bacher C, Jean F, Thomas Y. 2021. Linking individual and population patterns of rocky-shore mussels. *PeerJ* **9**:e12550. doi:10.7717/peerj.12550.
- Beck MW. 1998. Comparison of the measurement and effects of habitat structure on gastropods in rocky intertidal and mangrove habitats. *Mar Ecol Prog Ser* **169**:165–178. doi:10.3354/meps169165.
- Branch GM. 1976. Interspecific competition experienced by South African *Patella* species. *The J Anim Ecol* **45**:507–529. doi:10.2307/3888.
- Branch GM, Cherry MI. 1985. Activity rhythms of the pulmonate limpet *Siphonaria capensis* Q. & G. as an adaptation to osmotic stress, predation and wave action. *J Exp Marine Biol Ecol*

**87**:153–168. doi:10.1016/0022-0981(85)90088-7.

Broekhuysen, G. J. 1940. A preliminary investigation of the importance of desiccation, temperature, and salinity as factors controlling the vertical distribution of certain intertidal marine gastropods in False Bay, South Africa. T Roy Soc S Afr **28**: 255–292.

doi:10.1080/00359194009520016.

Cartwright SR, Williams GA. 2012. Seasonal variation in utilization of biogenic microhabitats by littorinid snails on tropical rocky shores. Mar Biol **159**:2323–2332. doi:10.1007/s00227-012-2017-3.

Chan BKK, Morritt D, De Pirro M, Leung KMY, Williams GA. 2006. Summer mortality: Effects on the distribution and abundance of the acorn barnacle *Tetraclita japonica* on tropical shores.

Mar Ecol Prog Ser **328**:195–204. doi:10.3354/meps328195.

Chapman MG, Underwood AJ. 1996. Influences of tidal conditions, temperature and desiccation on patterns of aggregation of the high-shore periwinkle, *Littorina unifasciata*, in New South Wales, Australia. J Exp Marine Biol Ecol **196**:213–237. doi:10.1016/0022-0981(95)00131-X.

Chim CK, Tan KS. 2009. Vertical distribution, spawning and recruitment of *Siphonaria Guamensis* (Gastropoda : Pulmonata) on a seawall in Singapore. Raffles Bulletin of Zoology Supplement **22**:269–278.

Connell JH. 1961a. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. Ecol Monogr **31**:61–104.

doi:10.2307/1950746.

Connell JH. 1961b. The Influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus Stellatus*. Ecology **42**:710–723. doi:10.2307/1933500.

Connell JH. 1972. Community interactions on marine rocky intertidal shores. Ann Rev Ecol Syst **3**:169–192. doi:10.1146/annurev.es.03.110172.001125.

Coppejans E, Prathep A, Lewmanomont K, Hayashizaki K, De Clerck O, Leliart F, Terada R. 2017. Seaweeds and seagrasses of the southern Andaman sea coast of Thailand. Kagoshima university museum, Kagoshima.

Davies PS. 1969. Physiological ecology of *Patella*. III. dsiccation effects. J Mar Biol Assoc UK **49**:291–304. doi:10.1017/S0025315400035918.

Denny M, Gaines SD. 2007. Encyclopedia of tidepools and rocky shores. University of California Press, Berkeley CA.

Erlandsson, J., V. Kostylev, and G. A. Williams. 1999. A field technique for estimating the influence of surface complexity on movement tortuosity in the tropical limpet *Cellana grata* Gould.

Ophelia **50**: 215–224. doi:10.1080/00785326.1999.10409396.

Evans RG. 1948. The lethal temperatures of some common British littoral molluscs. J Anim Ecol

**17**:165-173. doi:10.2307/1480

- Firth LB, White FJ, Schofield M, Hanley ME, Burrows MT, Thompson RC, Skov MW, Evans AJ, Moore PJ, Hawkins SJ. 2016. Facing the future: The importance of substratum features for ecological engineering of artificial habitats in the rocky intertidal. *Mar Freshwater Res* **67**:31–143. doi:10.1071/MF14163.
- Garritty SD. 1984. Some adaptations of gastropods to physical stress on a tropical rocky shore. *Ecology* **65**:559–574. doi:10.2307/1941418.
- Gowenlock JN, Hayes FR. 1926. Contributions to the study of marine gastropods. I. The physical factors, behavior, and intertidal life of *Littorina*. *Contributions to Canadian Biology and Fisheries* **3**:133-166.
- Gray DR, Hodgson AN. 2004. The importance of a crevice environment to the limpet *Helcion pectunculus* (Patellidae). *J Mollu Stud* **70**:67–72. doi:10.1093/mollus/70.1.67.
- Hammer Ø, Harper DAT, Ryan, PD. 2001. Paleontological statistics software package for education and data analysis. *Palaeontol Electron* **4**:1–9.
- Harley CDG. 2008. Tidal dynamics, topographic orientation, and temperature-mediated mass mortalities on rocky shores. *Mar Ecol Prog Ser* **371**:37–46. doi:10.3354/meps07711.
- Harley CDG, Denny MW, Mach KJ, Miller LP. 2009. Thermal stress and morphological adaptations in limpets. *Funct Ecol* **23**:292-301. doi:10.1111/j.1365-2435.2008.01496.x.
- Harley CDG, Helmuth BST. 2003. Local- and regional-scale effects of wave exposure, thermal stress, and absolute versus effective shore level on patterns of intertidal zonation. *Limnol Oceanogr* **48**:1498–1508. doi:10.4319/lo.2003.48.4.1498.
- Harper KD, Williams GA. 2001. Variation in abundance and distribution of the chiton *Acanthopleura japonica* and associated molluscs on a seasonal, tropical, rocky shore. *J Zool* **253**:293–300. doi:10.1017/S0952836901000279.
- Hayford HA, Gilman SE, Carrington E. 2015. Foraging behavior minimizes heat exposure in a complex thermal landscape. *Mar Ecol Prog Ser* **518**:165–175. doi:10.3354/meps11053.
- Helmuth BST, Broitman BB, Blanchette CA, Gilman S, Halpin P, Harley CDG, O' Donnell MJ, Hofmann GE, Menge B, Strickland D. 2006. Mosaic patterns of thermal stress in the rocky intertidal zone: implications for climate change. *Ecol Monogr* **76**:461–479. doi:10.1890/0012-9615(2006)076[0461:MPOTSI]2.0.CO;2.
- Helmuth BST, Hofmann GE. 2001. Microhabitats, thermal heterogeneity, and patterns of physiological stress in the rocky intertidal zone. *Biol Bull* **201**:374–384. doi:10.2307/1543615.
- Hochachka PW, Somero GN. 2014. Biochemical adaptation: mechanism and process in physiological evolution. Oxford university press, New York.
- Hodgson AN. 1999. The biology of siphonariid limpets (Gastropoda: Pulmonata). *Oceanogr Mar*

Biol **37**:245–314.

- Hui TY, Crickenberger S, Lau JW, Williams GA. 2022. Why are ‘suboptimal’ temperatures preferred in a tropical intertidal ectotherm?. J Anim Ecol **91**:1400–1415. doi:10.1111/1365-2656.13690.
- Hui TY, Dong Y-W, Han G-D, Lau SLY, Cheng MCF, Meepoka C, Ganmanee M, Williams GA. 2020. Timing metabolic depression: Predicting thermal stress in extreme intertidal environments. Am Nat **196**:501–511. doi:10.1086/710339.
- Hutchinson N, Williams GA. 2001. Spatio-temporal variation in recruitment on a seasonal, tropical rocky shore: the importance of local versus non-local processes. Mar Ecol Prog Ser **215**:57–68. doi:10.3354/meps215057.
- Kankondi SL, McQuaid CD, Tagliarolo M. 2018. Influence of respiratory mode on the thermal tolerance of intertidal limpets. PLoS ONE **13**:1–15. doi:10.1371/journal.pone.0203555.
- Lam NWY, Huang R, Chan BKK. 2009. Variations in intertidal assemblages and zonation patterns between vertical artificial seawalls and natural rocky shores: A case study from Victoria Harbour, Hong Kong. Zool Stud **48**:184–195.
- Lathlean JA, Ayre DJ, Coleman RA, Minchinton TE. 2014. Using biomimetic loggers to measure interspecific and microhabitat variation in body temperatures of rocky intertidal invertebrates. Mar Freshwater Res **66**:86–94. doi:10.1071/MF13287.
- Levings SC, Garrity SD. 1983. Diel and tidal movement of two co-occurring neritid snails; differences in grazing patterns on a tropical rocky shore. J Exp Mar Biol Ecol **67**:261–278. doi:10.1016/0022-0981(83)90043-6.
- Leviten PJ, Kohn AJ. 1980. Microhabitat resource use, activity patterns, and episodic catastrophe: *Conus* on tropical intertidal reef rock benches. Ecological Society of America **50**:55–75. doi:10.2307/2937246.
- Lewis JB. 1963. Environmental and tissue temperatures of some tropical intertidal marine animals. The Biological Bulletin **124**:277–284.
- Lewis JR. 1954. Observations on a high-level population of limpets. J Anim Ecol **23**:85–100. doi:10.2307/1661.
- Lima FP, Wetthey DS. 2009. Robolimpets: measuring intertidal body temperatures using biomimetic loggers. Limnol Oceanogr-Meth **7**:347–353. doi:10.4319/lom.2009.7.347.
- Liu JH, Morton B. 1994. The temperature tolerances of *Tetraclita squamosa* (Crustacea: Cirripedia) and *Septifer virgatus* (Bivalvia: Mytilidae) on a sub-tropical rocky shore in Hong Kong. J Zool **234**:325–339. doi:10.1111/j.1469-7998.1994.tb06078.x.
- Liu JH, Morton B. 1998. The impacts of pollution on the growth, reproduction and population structure of Hong Kong limpets. Mar Pollut Bull **36**:152–158. doi:10.1016/S0025-

326X(97)00175-6.

- Lombardo RC, Christy JH, Cipriani R. 2013. The false limpet *Siphonaria gigas*, a simultaneous hermaphrodite, lives in pairs in rock fissures on the Pacific coast of Panama. *Mar Biol* **160**:729–735. doi:10.1007/s00227-012-2127-y.
- Marcus E, Marcus E. 1960. On *Siphonaria hispida*. Boletim da Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo. *Zoologia* **23**:107–139. doi:10.11606/issn.2526-3382.bffclzoologia.1960.120436.
- Marshall DJ, McQuaid CD. 1989. The influence of respiratory responses on the tolerance to sand inundation of the limpets *Patella granularis* L. (Prosobranchia) and *Siphonaria capensis* Q. et G. (Pulmonata). *J Exp Mar Biol Ecol* **128**:191–201. doi:10.1016/0022-0981(89)90027-0.
- Marshall DJ, McQuaid CD. 1992. Comparative aerial metabolism and water relations of the intertidal limpets *Patella granularis* L. (Mollusca: Prosobranchia) and *Siphonaria oculus* Kr. (Mollusca: Pulmonata). *Physiol Zool* **65**:1040–1056. doi:10.1086/physzool.65.5.30158558.
- Marshall PA, Keough MJ. 1994. Asymmetry in intraspecific competition in the limpet *Cellana tramoserica* (Sowerby). *J Exp Mar Biol Ecol* **177**: 121–138. doi:10.1016/0022-0981(94)90147-3
- McAfee D, Bishop MJ, Williams GA. 2022. Temperature-buffering by oyster habitat provides temporal stability for rocky shore communities. *Marine Environmental Research* **173**:105536. doi:10.1016/j.marenvres.2021.105536.
- Meager JJ, Schlacher TA, Green M. 2011. Topographic complexity and landscape temperature patterns create a dynamic habitat structure on a rocky intertidal shore. *Mar Ecol Prog Ser* **428**: 1–12. doi:10.3354/meps09124.
- Miller LP, Harley CDG, Denny MW. 2009. The role of temperature and desiccation stress in limiting the local-scale distribution of the owl limpet, *Lottia gigantea*. *Funct Ecol* **23**:756–767. doi:10.1111/j.1365-2435.2009.01567.x.
- Mislan KAS, Wetthey DS, Helmuth B. 2009. When to worry about the weather: role of tidal cycle in determining patterns of risk in intertidal ecosystems. *Glob Change Biol* **15**:3056–3065. doi:10.1111/j.1365-2486.2009.01936.x.
- Morton B, Morton J. 1983. The sea shore ecology of Hong Kong. Hong Kong University Press, Hong Kong.
- Ng TP, Lau SLY, Seuront L, Davies MS, Stafford R, Marshall DJ, Williams GA. 2017. Linking behaviour and climate change in intertidal ectotherms: insights from littorinid snails. *J Exp Mar Biol Ecol* **492**:121–131. doi:10.1016/j.jembe.2017.01.023.
- Olaya V. 2009. Basic land-surface parameters. *Dev Soil Sci* **33**:141–169. doi:10.1016/S0166-2481(08)00006-8.

- Olivier SR, Penchaszadeh PE. 1968. Observaciones sobre la ecología y biología de *Siphonaria* (*Pachysiphonaria*) *lessoni* (Blainville, 1824) en el litoral rocoso de Mar del Plata (Buenos Aires). *Cah Biol Mar* **9**:469-491.
- R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Schonbeck M, Norton TA. 1978. Factors controlling the upper limits of furoid algae on the shore. *J Exp Mar Biol Ecol* **31**:303–313. doi:10.1016/0022-0981(78)90065-5.
- Shotwell JA. 1950. Distribution of volume and relative linear measurement changes in *Acmaea*, the limpet. *Ecology* **31**:51–61. doi:10.2307/1931360.
- Stephenson TA, Stephenson A. 1954. Life between tide-marks in North America: III A. Nova Scotia and Prince Edward Island: description of the region. *J Ecol* **42**:14–45. doi:10.2307/2256978.
- Stephenson TA, Stephenson A, Day JH. 1940. The South African intertidal zone and its relation to ocean currents. VIII. Lamberts Bay and the west coast. *Annals of the Natal Museum* **9**:345–380.
- Stickle WB, Carrington E, Hayford H. 2017. Seasonal changes in the thermal regime and gastropod tolerance to temperature and desiccation stress in the rocky intertidal zone. *J Exp Mar Biol Ecol* **488**:83–91. doi:10.1016/j.jembe.2016.12.006.
- Stillman JH, Somero GN. 1996. Adaptation to temperature stress and aerial exposure in congeneric species of intertidal porcelain crabs (genus *Petrolisthes*): correlation of physiology, biochemistry and morphology with vertical distribution. *J Exp Biol* **199**:1845-1855. doi:10.1242/jeb.199.8.1845.
- Tsuchiya M. 1983. Mass mortality in a population of the mussel *Mytilus edulis* L. Caused by high temperature on rocky shores. *J Exp Mar Biol Ecol* **66**:101–111. doi:10.1016/0022-0981(83)90032-1.
- Underwood AJ, Jernakoff P. 1981. Effects of interactions between algae and grazing gastropods on the structure of a low-shore intertidal algal community. *Oecologia* **48**:221–233. doi:10.1007/BF00347968.
- Venables WN, Ripley BD. 2002. *Modern Applied Statistics with S*, Fourth edition. Springer, New York.
- Vermeij GJ. 1972. Intraspecific shore-level size gradients in intertidal molluscs. *Ecology* **53**:693–700. doi:10.2307/1934785.
- Vermeij GJ. 1973. Morphological patterns in high-intertidal gastropods: Adaptive strategies and their limitations. *Mar Biol* **20**:319–346. doi:10.1007/BF00354275.
- Villarta KA, Ontoy AFL, Villanueva IKD, Ybañez MAD. 2017. An initial exploration into the

population dynamics and reproduction of *Patelloida saccharina* on Rocky Shores in Taklong Island National Marine Reserve (TINMR), Southern Guimaras, Philippines. Philippine Journal of Natural Sciences **22**:48–60.

Virgin SD, Schiel DR. 2023. Behavioural thermoregulation and food availability drive fine-scale seasonal habitat partitioning in limpets. *Funct Ecol* **37**: 2687–2702. doi:10.1111/1365-2435.14421.

Wangkulangkul K, Promdam R. 2018. Spatial variability in the composition of macrofauna on intertidal rocky shores along the coast of the Andaman sea and the gulf of Thailand, Southern Thailand. *Plankton and Benthos Research* **13**:154–162. doi:10.3800/pbr.13.154.

Williams GA. 1993. Seasonal variation in algal species richness and abundance in the presence of molluscan herbivores on a tropical rocky shore. *J Exp Mar Biol Ecol* **167**:261–275. doi:10.1016/0022-0981(93)90034-L.

Williams GA, Morritt D. 1995. Habitat partitioning and thermal tolerance in a tropical limpet, *Cellana grata*. *Mar Ecol Prog Ser* **124**:89–103. doi:10.3354/meps124089.

Wolcott TG. 1973. Physiological ecology and intertidal zonation in limpets (*Acmaea*): a critical look at "limiting factors". *The Biological Bulletin* **145**:389–422. doi:10.2307/1540048.

Zar JH. 2010. Biostatistical analysis. Upper Saddle River, New Jersey.



## Supplementary materials

**Fig. S1.** Hourly temperatures recorded of Envloggers (n = 3) deployed at Phra-ae during the spring tide (15<sup>th</sup>–21<sup>st</sup> January 2022) were plotted against the predicted tide. Red lines indicate loggers' height, which is either the most abundant level of *S. guamensis* (A, at 2.5 m above C.D.) or *P. saccharina* (B, at 1.6 m above C.D.). The yellow highlighted blocks indicate daytime periods. (download)

**Fig. S2.** Hourly temperatures recorded of Envloggers (n = 3) deployed at Phra-ae during the neap tide (22<sup>nd</sup>–28<sup>th</sup> January 2022) were plotted against the predicted tide. Red lines indicate loggers' height, which is either the most abundant level of *S. guamensis* (A, at 2.5 m above C.D.) or *P. saccharina* (B, at 1.6 m above C.D.). The yellow highlighted blocks indicate daytime periods. (download)

**Table S1.** Summary daily metrics of rock temperature (°C) averaged across three Envloggers which were deployed at 2.5 m and 1.6 m above C.D., during spring and neap tides at Phra-ae between 15<sup>th</sup>–28<sup>th</sup> January 2022. (download)