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Population size and movement ecology of intertidal gastropods on rocky shores and seawalls in Singapore

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ABSTRACT

Increasing coastal development and global warming have resulted in large-scale habitat changes, with artificial coastal structures replacing extensive tracts of natural shores. In Singapore, for example, more than 63% of the natural coastline has been replaced by seawalls. Multiple studies from both temperate and tropical regions have compared species diversity supported by these artificial structures with natural rocky shores. Few, however, have estimated and compared the population size and movement of common intertidal species between these two habitat types. Using mark–recapture techniques, this study investigated: (1) the population size of three common gastropod genera (*Nerita* spp., *Trochus* spp. and *Turbo* spp.) and (2) differences in displacement of *Nerita* spp. and *Trochus* spp., two common species found on natural rocky shores and seawalls in Singapore. The results of our mark–recapture surveys indicated that seawalls supported large densities of *Nerita* spp.—more than 50 times greater than that on adjacent rocky shores. The mark–recapture data also revealed that movement of the gastropod species differed between the two habitats, with individuals on seawalls generally travelling longer distances.

INTRODUCTION

Growing human population numbers (Bloom, 2011; Gerland *et al.*, 2014), rising sea levels and increasing storm frequency due to climate change are driving the current expansion of coastal cities and shoreline defences worldwide (Creel, 2003; Sengupta, Chen & Meadows, 2018). Artificial defence structures, such as seawalls, breakwaters and groynes, are fast replacing natural habitats, leading to major changes in environmental conditions that have significant impacts on ecological communities and their connectivity (Bulleri & Chapman, 2015; Loke, Heery & Todd, 2019). Previous studies have shown that, compared with natural rocky shores, seawalls generally support lower species diversity and compositionally different assemblages (Chapman & Bulleri, 2003; Bulleri & Chapman, 2004; Moschella *et al.*, 2005; Chapman, 2006; Gacia, Satta & Martín, 2007; Lai *et al.*, 2018). Lower diversity on seawalls has often been attributed to differences in slope angle and substrate type (Chapman & Bulleri, 2003), as well as lower structural complexity and a concomitant reduction in important microhabitats for intertidal organisms (Chapman, 2003; Moschella *et al.*, 2005; Loke *et al.*, 2015). However, by contrast, little research has compared other responses such as the population size and movement of common intertidal species found in the two habitat types, with none being performed in the tropics.

One common problem with many field studies comparing rocky shores and seawalls is their tendency to present only a single snapshot of local species abundances, even though they are known to be highly variable across space and time (Underwood & Chapman, 1996; Olabarria & Chapman, 2001, 2002; Chapman & Underwood, 2008). Insufficient replication and the use of inappropriate spatial scales in collecting abundance and density data from quadrat surveys could result in misleading interpretations regarding the ecological role of artificial structures in the marine environment. In addition, estimates of motile organism abundance may be inaccurate due to dispersal, double counting and animals being hidden from view, especially at certain times of the diel and tidal cycles. For instance, ungrouted riprap seawalls may have deep crevices where certain organisms can hide (Pister, 2009; H.H.J. Yeo, personal observation), making them difficult to survey.

Mark–recapture techniques have been applied extensively in wildlife ecology studies for many taxa (Lincoln, 1930; Seber, 1962; Edwards & Eberhardt, 1967; Otis *et al.*, 1978; Cain, Cook & Currey, 1990; Pollock *et al.*, 1990; Alexander, Slade & Kettle, 1997; Kleewein, 1999; Mowat & Strobeck, 2000; Henry & Jarne, 2007; Carey *et al.*, 2019) and may be used to overcome some of the obstacles listed above. Here, we applied mark–recapture techniques to intertidal gastropods on seawalls and rocky shores to estimate their population size via the Schumacher–Eschmeyer technique for closed populations. Specifically, this involved marking the shells of snails with number labels and recording individual recapture history over a 31 day period. This is the first time that such a study has been conducted in Singapore or in tropical Southeast Asia (SEA). We expect our findings to provide an important baseline for long-term monitoring and can be used to inform conservation and eco-engineering of artificial coastal structures.

Besides estimating population size, mark–recapture methods can also be used to track the movement and dispersal of animals. Motile animals generally move through heterogeneous landscapes, travelling across suitable and unsuitable habitats in response to their needs (Bowler & Benton, 2005). Examples include responding to temperature or foraging in resource-rich patches, before returning to habitats that offer refuge from predators (Barraquand & Benhamou, 2008). Movement patterns therefore can result from animal–environment interactions that may reflect the response of animals to spatial distribution of resources (Levin, Cohen & Hastings, 1984; Johnson *et al.*, 1992; With, 1994; Schick *et al.*, 2008) and/or species interactions. Information on animal movement in heterogeneous habitats is central to developing a better understanding of habitat utilization, spatiotemporal distribution and community dynamics (Chapman, 2000a; Chapperon & Seuront, 2013).

Despite the extensive past research quantifying the differences in diversity and community composition between seawalls and rocky shores, to our knowledge, only one study to date (i.e. Bulleri, Chapman & Underwood, 2004), conducted in a temperate Australia, has directly compared the behavioural response of motile organisms (i.e. intertidal gastropods) between these two habitats. The movement of key consumers such as gastropod grazers can have direct and indirect influences on the abundance and distribution of intertidal organisms (Benedetti-Cecchi *et al.*, 2001) and may explain why different assemblages are often found on artificial structures. Furthermore, there is substantial evidence that the behaviour of intertidal species varies spatially and temporally in relation to various environmental factors. Several studies have shown that environmental and biotic factors such as water and algal cover, surface complexity, predation risk, prey availability and the presence of other sessile invertebrates can influence the movement patterns of intertidal gastropods (e.g. Branch, 1975; Garrity, 1984; Hazlett, 1984; Fairweather, 1988; Underwood & Chapman, 1989; Chapman & Underwood, 1994; Takada, 1996; Minchinton & Ross, 1999; Chapman, 2000a; Lauzon-Guay & Scheibling, 2009; Chapperon & Seuront, 2013). Movement of animals has important consequences for the degree of mixing and spatial structure within a population and interactions between individuals of different species (Morales *et al.*, 2010). Understanding the extent of movement can be used to guide the type and scale of management actions needed, such as planning and designing reserves or habitats that facilitate movement and maintain connectivity. For example, installing ecological engineered structures (i.e. habitat tiles) at species-appropriate scales can help managers create a more permeable matrix and improve connectivity in the seawall landscape (see Loke, Chisholm & Todd, 2019).

This study examined the three common genera of gastropods commonly found on seawalls and rocky shores. To provide key baseline data that can help inform the management of intertidal hard shores in Singapore, we (1) estimated gastropod population sizes and (2) compared their dispersal distances, among sites, habitats and common genera.

MATERIAL AND METHODS

Study area and study species

Singapore is a small tropical island city–state located at the tip of southern Peninsular Malaysia. Over 63% of its natural coastline has been modified and replaced by seawalls (Lai *et al.*, 2015; Tan *et al.*, 2023). Natural rocky shores are limited to a 300-m stretch on the mainland, along the southern shore, and several locations in the Southern Islands (Todd & Chou, 2005; Lai *et al.*, 2015). Our study was conducted at two island sites south of mainland Singapore: Sentosa Island (1°15′28″N, 103°48′30″E) and St John's Island (1°13′23″N, 103°50′42″E) (Fig. 1). At each site, seawall and the adjacent rocky shore, spaced *c.* 300 m apart and separated by sandy beaches, were surveyed during low tides between June and August 2017. In general, the rocky shore plots were gently sloping with a variety of rock sizes while seawalls plots were steeply sloping riprap with crevices between large granite boulders.

For seawalls, we established a permanent quadrat that ran 3 m up the sloping wall from the middle shore level (i.e. 0.6–0.9 m above chart datum) and 3 m laterally along the wall was marked out so that the same 9-m^2 plot could be surveyed on all subsequent visits. The same was done for rocky shore habitats, except in this case the horizontal length along the shore was increased to 10 m, creating a 30-m^2 quadrat. The length of sampling area for seawall (3 m) and rocky shore (10 m) was chosen due to the large difference (greater than two orders of magnitude) in the densities of gastropods in the two habitats; specifically, 10 m was needed to achieve a reasonable sample size on rocky shores, but on seawalls 10 m resulted in >1,000 snails, far too many to mark within a 3-h low-tide period.

Due to the time constraints in the field, we identified gastropods to genus level only (i.e. *Nerita*, *Trochus* and *Turbo*) in this study. Species covered in this study included *Nerita undata*, *N. albicilla*, *N. chamaeleon*, *N. histro* (previously known as *N. squamulata*), *Trochus maculatus*, *Turbo intercostalis* and *Turbo bruneus*. None of these species are known to exhibit homing behaviour, nor have we observed any instances of this. We did not include individuals that were less than 7 mm as the labels used for tagging (see the next section) were 5 mm in diameter.

Mark and recapture field surveys

Surveys were conducted daily during low spring tides over a period of 1 month in June 2017. At each site, rocky shores and seawalls were surveyed on the same day during daytime low tides and nonrainy weather conditions. To account for the differences in plot sizes, total search efforts were standardized by the number of researchers searching the plots for 1 min/m^2 (i.e. 30 min for rocky shore plots and 9 min for seawall plots). All snails found within the plot (with a shell length >7 mm) were collected, identified, measured with a Vernier calliper and marked with a circular number label (5 mm in diameter), which was glued to the shell with clear epoxy (Araldite Rapid 5 Minutes, Huntsman Advanced Materials LLC, Belgium). Previous studies employing similar marking techniques have shown that this results in little disturbance to gastropods (e.g. Chapman, 1986, 2000a; but see Chapman, 2000b). We also checked that there was no disturbance caused by our handling protocol, which may potentially alter their movement on the first day (see details in Supplementary Material Appendix S1.1, Table S1). Marked snails were subsequently released to random points within the plot (following Underwood & Chapman, 1985), and we recorded their positions relative to the top and bottom corners of the plot (Fig. 2). On seven consecutive sampling trips per site, after a time interval of 1, 2, 3, 28, 29, 30 and 31 days after the first day of marking (day 0), the plots were surveyed again for marked and unmarked (i.e. new) snails within the focal area. Position of previously marked snails found at each time point was recorded *in situ* without disturbance, by taking the distance from the two fixed points (top and bottom, Fig. 2). Meanwhile new snails found were measured, marked and released back into the plot. As snails could travel outside the fixed plot, we also searched a boundary strip of 5 m in length on both sides of the focal plots during each survey to record tagged snails' displacement. Multiple sampling occasions and distinct marking allowed for recording of individuals'

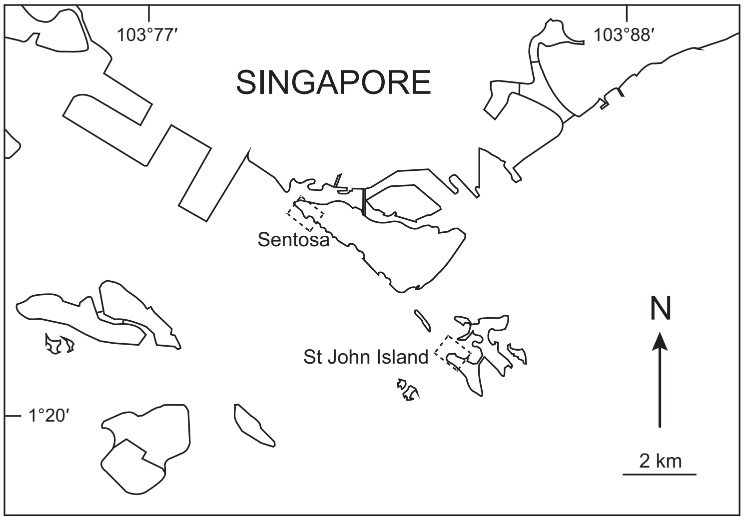

Figure 1. Locations of the survey sites on Sentosa and St John's Island. At each site, seawall and natural rocky shore habitats were sampled.

displacement and capture history patterns, ranging from 1 day (two tidal cycles) to 1 month.

Population estimation

Estimates of population size were obtained from individual capture history for all sampling occasions. Close population size estimation for multiple census mark–recapture was carried out with the Schumacher & Eschmeyer (1943) method (De Lury, 1958) in R using the *FSA* package v. 0.9.4 (Ogle, 2017). Owing to differences in sample size and the tendency of intertidal snails to cluster or stratify, De Lury (1958) suggested using the 'Schumacher–Eschmeyer (1943) method', which involves weighting by sample size, over the 'Schnabel (1938) method', which weights according to proportion of marked individuals. To account for differences in plot size, we calculated population density per square metre by dividing the population size estimate (N) by the respective plot area for seawall (9 m^2) and rocky shore (30 m^2) habitats at each site.

Snail displacement

The coordinate's position (x, y) of each marked snail was calculated by coordinate geometry following Underwood (1977), using two fixed corners of the plot (Fig. 2; Supplementary Material Appendix S1.2). The position of all recaptured individuals within the 31 day period in each habitat was joined together to create a movement pathway, and the mean displacement was obtained from all recorded linear displacement distance (d_i) travelled by each individual (Fig. 2). This process involved summing the displacements between consecutive days—for example, adding the displacement from day x to $x + 1$ (Fig. 2; d_1), from day $x + 1$ to $x + 2$ (Fig. 2; d_2) and from day $x + 2$ to $x + 3$ (Fig. 2; d_3), and so forth (see Supplementary Material Appendix S1.2 for more details). The average displacement for each individual was determined, followed by calculating the average distances displaced for each genus. This approach avoided double counting and allowed us to obtain a better estimate and compare the total and average distances moved by gastropods over a period of 31 days in both types of habitats. However, we acknowledge that this method also has its limitations; for instance, it underestimates the absolute distance travelled by snails.

Given that no *Turbo* spp. were found on seawall plots in this study, they were not compared with *Nerita* spp. and *Trochus* spp. For the latter two genera, we fitted linear mixed-effects models (LMEs) with site, habitat and genus as fixed effects with random slopes (shell size) and random intercepts (day marked nested within the identities of unique individuals). The random intercepts accounted for unequal sampling occasions and nonindependence amongst recapture events for individuals. We also found that shell height, width and length were highly correlated (variance inflation factor > 5) with one another and with genus, so we proceeded with using shell width as a parameter for shell size in our statistical model. Shell height was first removed from the model because it was strongly influenced by genus shell morphometrics (i.e. *Trochus* spp. have a much higher shell height than *Nerita* spp.). The choice between using shell width or length in the model determined via a principal component analysis (PCA) to identify which shell measurement contributed the most to PC1 for both genera (see Supplementary Material Tables S2, S3). Since there were more than two data points (i.e. recapture events) for each individual, we specified appropriate residual variance structures to account for the unequal variance in the residuals of our full model (Zuur *et al.*, 2009). Akaike information criterion corrected for small sample sizes (AICc) was then used to compare models with and without residual variance structures. We used the *varIndent* function for constant variance structure to account for the unequal variance between time points (i.e. number of days in between two time points), which improved model fit (see Supplementary Material Table S4). We evaluated the linear mixed-effects models by fitting every combination of variables, using the R package *nlme* v. 3.1.157 (Pinheiro *et al.*, 2018). Model selection was achieved by creating a top model set that comprised all models with 2 ΔAICc of the best model (Supplementary Material Table S5), using the package *MuMIn* v. 1.47.1 (Bartoń, 2013). Following the protocol in Zuur, Ieno & Elphick (2010), assumptions of normality and homogeneity of variance were evaluated graphically for all models retained in the top model set. Based on visual inspection, residual plots for all of the models did not reveal any nonnormality or heteroscedasticity. *Post hoc* test was done using the pairwise argument in the *emmeans* v. 1.8.2 function and package (Lenth *et al.*, 2023) with Bonferroni adjustment.

RESULTS

In total, 741 individuals of three gastropod genera were marked in this study (Table 1). The majority of snails found and marked were *Nerita* spp. (527 individuals), followed by *Trochus* spp.

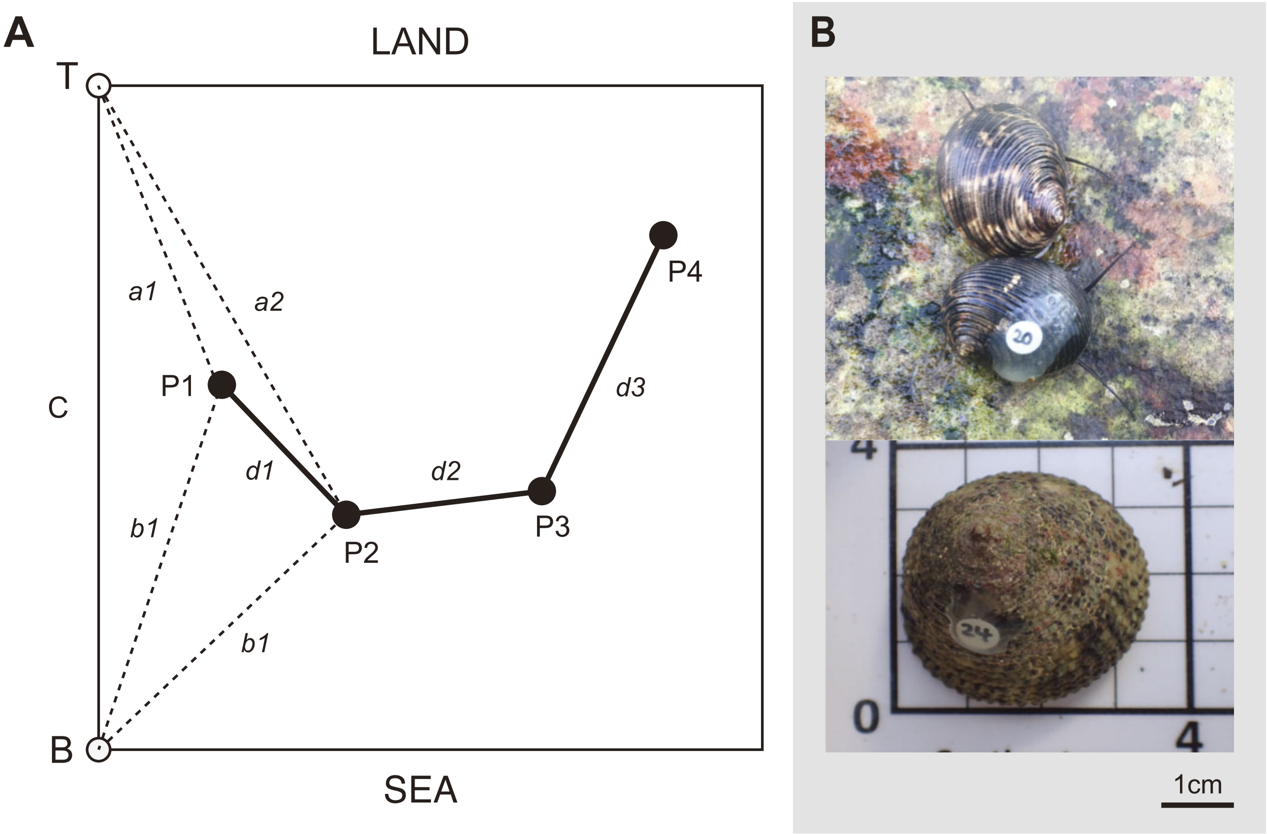

Figure 2. A. Coordinate geometry method for calculating distance displaced (adapted from Underwood, 1977). The distance (m) of C represents the height of plot from point T (top left corner of plot) to point B (bottom left corner of plot). The distance displaced (d_1) by each snail from P1 to P2 was calculated using *in situ* field measurement of the distance a_1, b_1, a_2 and b_2 (Supplementary Material Appendix S1.2). Average displacement was calculated by averaging the total distance travelled by an individual snail (i.e. d_1, d_2 and d_3). **B.** Marked *Nerita* sp. (top panel) and *Trochus* sp. (bottom panel) with circular number labels attached with clear epoxy.

(113 individuals) and *Turbo* spp. (101 individuals). *Turbo* spp. were only found and marked on the rocky shores at Sentosa and St John's Island. Over a period of 31 days (i.e. seven recapture occasions), we had a total of 265 recapture events across both sites and habitat pairs (Table 1).

Mark and recapture population size estimates

The population density estimates for *Nerita* spp. were greater for seawalls than for rocky shores (Fig. 3), with *c.* 52 (51.89 *vs* 1.10) and 57 (36.33 *vs* 0.63) times more individuals per square metre on seawalls than rocky shores at Sentosa and St John's Island sites, respectively (Table 2). The population density estimates of *Trochus* spp. were similar for rocky shores and seawalls (Fig. 3, Table 2). Population density estimates of *Turbo* spp. per square metre were 1.94 at Sentosa and 1.60 at St John's Island (Table 2). However, since no *Turbo* spp. were found in the seawall plots, it was not possible to compare genus-level population sizes between these habitats.

Mean distance displaced

Generally, there were differences in displacement distances between seawalls and rocky shores for all species (Table 3). Across all sites and habitats, *Nerita* spp. displayed the greatest mean displacement (1.69 ± 0.09 m), followed by *Turbo* spp. (1.05 ± 0.13 m) and *Trochus* spp. (1.05 ± 0.12 m) (Table 3). Overall, gastropods moved significantly greater distances on seawalls than on rocky shores ($P = 0.018$) (Tables 3, 4), particularly for *Nerita* spp. and *Trochus* spp. at Sentosa ($P = 0.016$) (Fig. 4, Supplementary Material Table S6). There was a weaker effect of genus ($P = 0.068$) across both sites and habitat, and distance displaced by *Nerita* spp. ($n = 149$) was higher than that by *Trochus* spp. ($n = 58$) (Fig. 4, Table 3). There was no significant interaction between genus and site ($P = 0.242$) for mean displacement (Table 4). Snails displaced shorter distances on seawalls at St John's Island compared with the same habitat type at Sentosa (Fig. 4).

DISCUSSION

Baseline data regarding the ecology of organisms on intertidal rocky shores and seawalls are essential for environmental management and conservation (Engle & Davis, 2000; Bulleri, Chapman & Underwood, 2005). Here, we obtained population density estimates, assuming closed populations of key common species in both habitats, and tracked their movement using mark–recapture techniques. Other studies have used mark–recapture to assess populations or movement patterns of gastropods on rocky shores (e.g. Underwood, 1977; Barnes, 1998; Bulleri, Chapman & Underwood, 2004), but the current study is the first to use this approach on tropical shores to estimate and compare these parameters between natural rocky shores and artificial structures. Our comparisons showed that population density estimates of *Trochus* spp. were similar between the two habitats but that the densities of nerites on seawalls were much greater than those on natural rocky shores. We also found that snails moved significantly greater distances on seawalls.

Table 1. Number of individuals of each genus marked and recaptured at respective sites, habitats and sampling days (D_0 = day 0, first day of marking with no recapture sampling).

			Mark								Recapture						
Site	Habitat	Genus	D_0	D_1	D_2	D_3	D_{28}	D_{29}	D_{30}	D_{31}	D_1	D_2	D_3	D_{28}	D_{29}	D_{30}	D_{31}
Sentosa	Rocky shore	*Nerita*	13	9	5	5	8	6	1	0	3	3	3	5	7	6	1
Sentosa	Rocky shore	*Trochus*	14	8	12	5	9	4	7	2	3	4	9	3	3	5	1
Sentosa	Rocky shore	*Turbo*	3	16	6	6	11	4	5	7	0	6	11	2	4	3	0
Sentosa	Seawall	*Nerita*	65	74	39	42	27	28	18	15	4	6	14	7	24	22	0
Sentosa	Seawall	*Trochus*	0	1	1	9	2	4	3	3	0	0	0	0	0	3	1
SJI	Rocky shore	*Nerita*	8	2	3	2	9	1	0	0	1	1	2	2	5	3	6
SJI	Rocky shore	*Trochus*	8	1	3	7	7	2	0	1	1	2	2	4	4	6	6
SJI	Rocky shore	*Turbo*	10	6	7	1	4	5	7	0	2	2	1	1	0	5	9
SJI	Seawall	*Nerita*	49	13	5	14	26	22	8	10	7	0	1	11	5	6	6
SJI	Seawall	*Turbo*	1	0	1	0	0	0	1	0	1	0	0	0	0	0	0
		Total	**171**	**130**	**82**	**91**	**103**	**76**	**50**	**38**	**22**	**24**	**43**	**35**	**52**	**59**	**30**

Mark, refers to the number of new snails marked on that day. For seawalls, snails were collected from 9 m^2, and rocky shores snails were collected from 30 m^2 (see the 'Material and Methods' section).

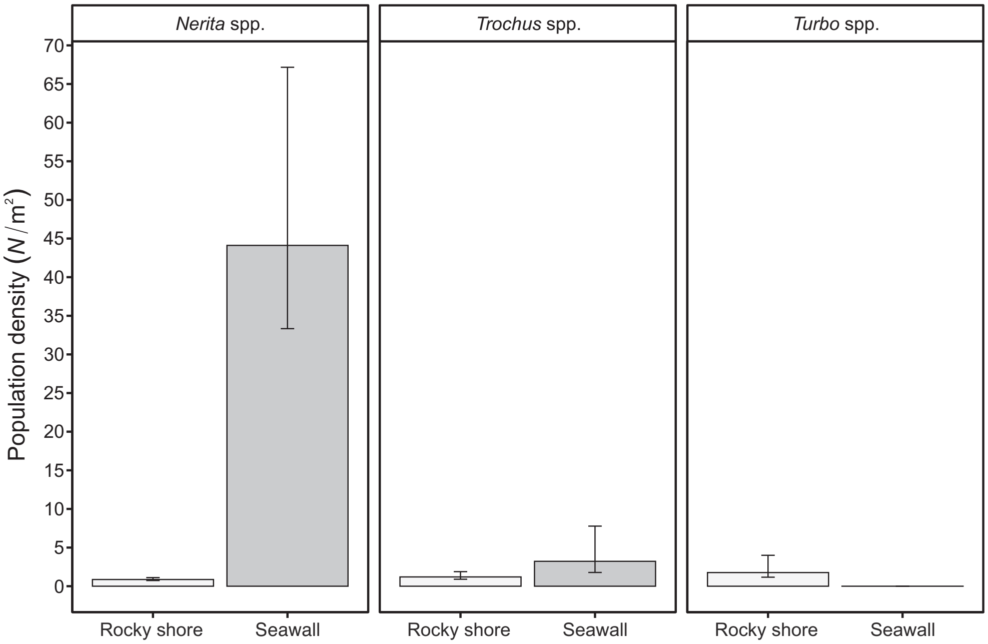

Figure 3. Mean population density estimate (N/m^2) with lower and upper 95% confidence interval on seawalls and rocky shores was calculated using the Schumacher–Eschmeyer (1943) method (using the *FSA* package; Ogle, 2017).

While seawalls in Singapore generally exhibit lower species richness compared with rocky shores, as indicated by Lai *et al.* (2018), our examination of population density estimates reveals a remarkable statistic: these seawalls harbour 50 times more *Nerita* spp. at the respective sites. The methodology employed in this study, known as the Schumacher–Eschmeyer method, is tailored for closed populations characterized by no recruitment or losses, no tag loss and an equal likelihood of capturing every individual during each sampling occasion. Given the brief time frame of 1 month, it is highly unlikely that there would be a significant level of immigration or emigration by adult individuals from the delimited area in this study. Furthermore, owing to our comprehensive search across the entire plot, each snail stood an equal chance of being captured.

Neritid species recorded in Singapore can be found in a wide range of habitats (e.g. brackish to fully marine) and have colonized artificial coastal habitats (Tan & Clements, 2008; Lai *et al.*, 2018; Tan *et al.*, 2018). *Nerita undata* was particularly common and represented most of the population of *Nerita* spp. found on seawalls in this study. This species often occupies middle to upper intertidal zones (Hughes, 1971; Ruwa & Jaccarini, 1986, 1988; Tan & Clements, 2008), which are usually characterized by relatively harsh environmental conditions (i.e. greater exposure to high temperatures and desiccation risk). Similar to other tropical intertidal snails, *N. undata* uses behavioural thermoregulation to cope with high seawall temperatures in the upper intertidal zone that can reach 57.6 °C in Singapore (Chan *et al.*, 2022). One possible explanation for the large *Nerita* populations on seawalls could be a lack of natural predators (top-down regulation) or high primary productivity (bottom-up regulation). However, further investigations are necessary to test these hypotheses on

Table 2. Population size estimate (N) with 95% confidence intervals and population density per square metre for three gastropod genera on seawalls and rocky shores at Sentosa and St John's Island.

Site	Habitat	Genus	N	95% Confidence interval		Density/m^2
				Lower	Upper	
Sentosa	Seawall	*Nerita*	467	373	625	51.89
Sentosa	Rocky shore	*Nerita*	33	28	42	1.10
Sentosa	Seawall	*Trochus*	52	32	140	5.78
Sentosa	Rocky shore	*Trochus*	57	41	94	1.90
Sentosa	Rocky shore	*Turbo*	58	36	159	1.94
SJI	Seawall	*Nerita*	327	227	584	36.33
SJI	Rocky shore	*Nerita*	19	16	25	0.63
SJI	Seawall	*Trochus*	6	N/A	N/A	0.67
SJI	Rocky shore	*Trochus*	15	13	19	0.50
SJI	Rocky shore	*Turbo*	48	34	81	1.60

N/A, species not present; SJI, St John's Island.

Table 3. Average distance displaced (metre) with standard error for each species over a 31 day period, across all sites (Sentosa and St John's Island).

Genera	Seawall	Rocky shore	Average
Nerita	1.76 ± 0.10	1.55 ± 0.19	1.69 ± 0.09
Trochus	1.53 ± 0.38	1.01 ± 0.13	1.05 ± 0.12
Turbo	N/A	1.05 ± 0.13	1.05 ± 0.13

N/A, species not present.

Table 4. Estimated parameters, standard errors, z-values and P-values of the LME fitted for average distance displaced.

Variables	Estimate	SE	Adjusted SE	z-value	P-value
(Intercept)	1.404	0.162	0.161	8.652	<2e-16***
Genus (*Trochus*)	−0.366	0.200	0.199	1.827	0.068
Habitat (seawall)	0.443	0.186	0.187	2.371	0.018*
Site (SJI)	−0.230	0.270	0.272	0.847	0.397
Genus:site	−0.438	0.372	0.374	1.171	0.242
Habitat:site	−0.452	0.344	0.342	1.314	0.189

SJI, St John's Island; * $P < 0.05$, *** $P < 0.001$.

resource availability and species interactions such as competition and predation (see Yeo *et al.*, 2024).

Overall, our results suggest that seawalls are viable habitats for, and may even benefit, certain groups of gastropod species. This phenomenon of animals, such as birds and mammals successfully colonizing urban environments, known as 'synurbization', is common worldwide (Gliwicz, Goszczyński Luniak, 1994; Luniak, 2004). Synurbic populations are characterized by increased population densities (Luniak, 2004; Parker Nilon, 2012) and shifts in behaviour, such as dispersal, and migratory and activity patterns (Luniak, 2004). While synurbization has not been used to describe marine gastropods, results from the current study show preliminary evidence of *N. undata* on seawalls as possibly a synurbic population, with much higher densities compared with those on natural rocky shores. Future work could examine *N. undata* between rural and urban populations for relevant adaptations to these distinct environments.

Although we had limited plot replication in our study, estimated parameters on rocky shores were comparable with those reported in previous studies conducted in temperate regions (Bulleri *et al.*, 2004). For example, intertidal gastropods on artificial structures tended to disperse over longer distances; in our system, *Nerita* spp. and *Trochus* spp. travelled further (on average) on seawalls compared with rocky shores at Sentosa Island. This could be due to the difference in topographic complexity of the two habitats. Previous research has shown that, on more complex surfaces, the movement of snails is shorter and more directionally random (Underwood & Chapman, 1985, 1989; Chapman, 2000a). Thus, the lower displacement we observed on natural rocky shores could be due to it being more topographically complex than seawalls at scales relevant to our study species (Chapman, 2003; Moschella *et al.*, 2005; Loke *et al.*, 2015). Microhabitats could have limited gastropod displacement by providing refuges from predation, desiccation or enhancing food availability, allowing gastropods to travel less when foraging. By contrast, the smoother, larger and relatively more homogeneous granite boulders used for the construction of riprap seawalls in Singapore could potentially drive these gastropods to travel further to forage or take refuge from predators. This may even be exacerbated by high intraspecific competition for food and space due to their large population size on seawalls, as shown earlier in this study.

It is important to highlight that, on St John's Island, the distance displaced by *Nerita* spp. (excluding *Trochus* spp.) was in contrast to the observed pattern at Sentosa Island. Greater displacement was observed on natural rocky shores instead, possibly influenced by slight temperature variations between the two sites. For instance, during this study, the Sentosa site was possibly cooler as it receives more southwest monsoon wind between the months of June and July. Meanwhile, the sites on St John's Island face northeast and receive limited wind during those months. Granite seawalls have high solar absorption and thermal conductivity and this, coupled with the limited wind at St John's during the period of this study (Zhao *et al.*, 2019), could have resulted in an overall hotter environment there. Intertidal gastropods generally cope with higher substratum temperature by reducing activity patterns and displaying certain behaviour that helps to reduce desiccation or heat stress (see Garrity, 1984). This may be especially so for nerites, as they are usually found higher up the shore compared with *Trochus*.

Nerite snails exhibited greater displacement than *Trochus* spp., regardless of whether surfaces were natural or artificial (Fig. 4). Snails from these two genera are both grazers (Maboloc & Mingoa-Licuanan, 2013; Lai *et al.*, 2018) and were present within our rocky shore and seawall plots. Species that are present in the same habitat and have similar diet and trophic level may vary in displacement distances due to morphological differences in radula and feeding efficiency, which affects the distance travelled during feeding excursions (Underwood, 1977). While snails from both the genera *Nerita* and *Trochus* possess rhipidoglossan radulae (Underwood, 1977; Hawkins *et al.*, 1989; Eisapour, Seyfabadi & Daghooghi, 2015), it is possible that the better ability of trochids to remove diatoms

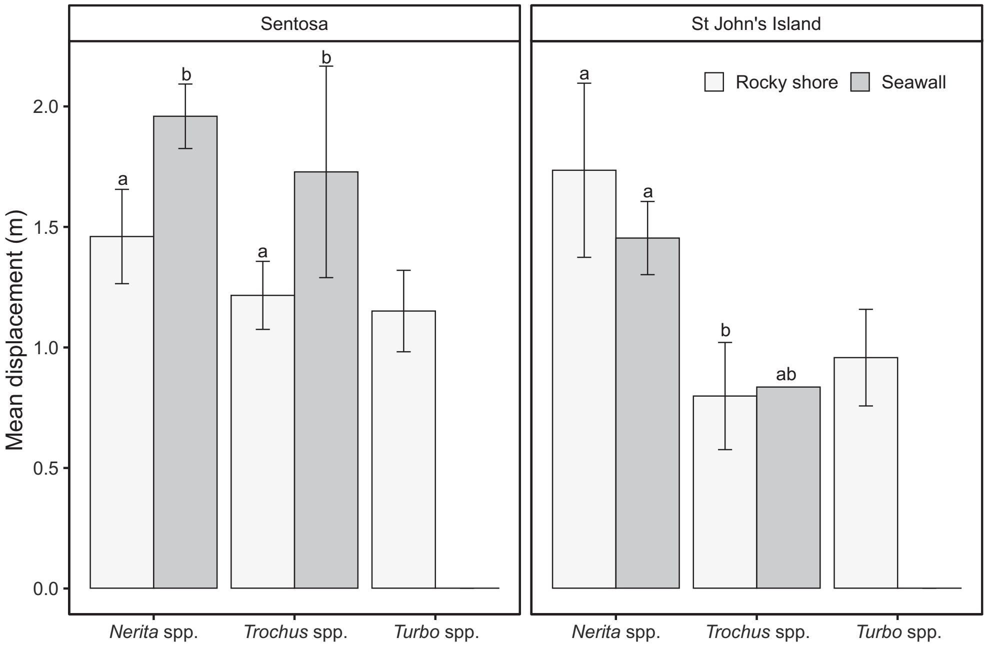

Figure 4. Average distance displaced (±SE) by individuals of each genus at respective sites and habitats over a 31 day period. Letters denote statistical significance between seawalls and rocky shores at Sentosa and St John's Island for the genera *Nerita* and *Trochus*.

(Hawkins *et al.*, 1989) resulted in *Trochus* spp. needing to travel shorter distances to extract sufficient food. Although not explicitly quantified in the present study, most tagged *Trochus* spp. returned to large boulders in the rocky shore plots (H.H.J. Yeo, personal observation), and this may limit how far they can travel during foraging excursions. In addition, many species of *Trochus* (e.g. *Trochus maculatus*) are mostly found in the lower intertidal zone and may be restricted by environmental conditions from travelling higher up the shore. Conversely, the species of *Nerita* in the current study can occupy the low to high intertidal zone and hence are more likely to travel greater distances when migrating vertically with falling and rising tides (Levings & Garrity, 1983).

The mark and recapture survey performed in this study provides evidence that artificial structures can support high abundances of nerite snails. Furthermore, dispersal patterns of adult snails significantly differed between seawalls and natural rocky shores. Given the trophic importance of grazing gastropods, quantifying the changes in behaviour or habitat utilization resulting from habitat changes (e.g. replacement of natural rocky shores by seawalls) will be valuable for teasing apart drivers behind the different distribution and community assemblages on natural and artificial structures. As the natural intertidal environment undergoes rapid conversion into artificial habitats as a result of urbanization and coastal defence (Bulleri & Chapman, 2010; Lai *et al.*, 2015; Todd *et al.*, 2019), understanding the population ecology and changes in movement behaviour of key invertebrates is essential in order to manage and enhance the ecological roles that these novel artificial structures provide.

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SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

AUTHOR CONTRIBUTIONS

H.H.J.Y.: conceptualization, methodology, data analysis, writing and original draft preparation. L.H.L.L.: conceptualization, methodology, supervision, writing, reviewing and editing. P.A.T.: funding acquisition, supervision, writing, reviewing and editing.

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