2016

Dislodgement force and shell morphology vary according to wave exposure in a tropical gastropod (Cittarium pica)

Graham E. Forrester
University of Rhode Island, gforrester@uri.edu

Reuben J.A. Macfarlan
University of Rhode Island

Allison J. Holevoet
University of Rhode Island

Sarah Merolla
University of Rhode Island

Citation/Publisher Attribution

Forrester, G. E., Macfarlan, R. J.A., Holevoet, A. J., & Merolla, S. (2016). Dislodgement force and shell morphology vary according to wave exposure in a tropical gastropod (*Cittarium pica*), *Marine Biology Research*, *12*(9), 986-992. https://doi.org/10.1080/17451000.2016.1225956 Available at: https://doi.org/10.1080/17451000.2016.1225956

Dislodgement force and shell morphology vary according to wave exposure in a tropical gastropod (*Cittarium pica*)

GRAHAM E. FORRESTER[1,*], REUBEN J. A. MACFARLAN[1], ALLISON J. HOLEVOET[2], SARAH MEROLLA[2],

[1]*Department of Natural Resources Science, University of Rhode Island, Kingston, RI, USA*

[2]*Department of Biological Sciences, University of Rhode Island, Kingston, RI, USA*

*Corresponding author: Graham E. Forrester, Department of Natural Resources Science, University of Rhode Island, Kingston, RI 02881, US

E-mail:gforrester@uri.edu, Tel:401-874-7054

Running head: wave exposure and snail morphology

Abstract

Wave exposure has strong influences on population density, morphology and behaviour of intertidal species in temperate zones, but little is known about how intertidal organisms in tropical regions respond to gradients in wave exposure. We tested whether dislodgement force and shell shape of a tropical gastropod, *Cittarium pica*, differs among shores that vary in wave exposure. After adjusting for body size, we found that *C. pica* from exposed shores required greater dislodgement force to remove them from the shore, had slightly larger opercula (the closure to the shell aperture), and were slightly squatter in shape (reduced in shell height relative to shell width) than *C. pica* from sheltered shores. These morphological adjustments are consistent with those observed in temperate gastropods, which are argued to represent adaptive responses to the risk of mortality associated with dislodgement.

Keywords: adaptation, intertidal, shell shape, topshell

Introduction

Rocky shores have been an excellent venue for testing hypotheses about organismal responses to gradients in physical conditions. Differences between shores in wave exposure influence the distribution and abundance of intertidal species, and also induce changes in their morphology and behaviour (Denny 2006; Menge & Sutherland 1987, 1976). These adjustments may be either direct responses to the risk of dislodgement by waves, or indirect responses to other factors that covary with wave exposure, such as predation (Boulding 1990; Boulding et al. 1999).

Research on temperate gastropods provides some of the best evidence for morphological changes across gradients of wave exposure. In several species, gastropods from exposed shores have shells that are squatter (reduced height for a given length) than those on sheltered shores, which is postulated to be a direct response to wave forces because it reduces the projected surface area perpendicular to the shore (Trussell et al. 1993) and so reduces the drag forces experienced when waves wash across the shore (Hollander & Butlin 2010; Trussell & Etter 2001). Populations on exposed shores also have a larger foot muscle and a larger aperture (the opening in the shell through which the foot protrudes) for a given body size than those on sheltered shores (Hollander & Butlin 2010; Trussell & Etter 2001). A larger foot muscle is also argued to be a direct response to wave exposure because it is one of the factors that increases the wave force required to dislodge the snail from the shore (Trussell 1997a). Indirect responses include morphological adjustments to the risk of predation for example crab predation has been found to covary with wave exposure (Palmer 1990; Seeley 1986). Crabs typically consume snails by using their claws to crush or break the snail's shell, so snails on sheltered shores often have shells that are thicker and differ in shape from those on exposed shores (Boulding, et al. 1999; Good 2004; Hollander & Butlin 2010; Kitching & Lockwood 1974; Trussell & Etter 2001; Trussell, et al. 1993).

Most studies testing how intertidal organisms respond to gradients in physical conditions have been done in temperate locations (Bertness 1981; Good 2004). Early work on wave exposure on tropical shorelines was influenced by the assumption that these are physically benign environments (Brosnan 1992; Menge & Lubchenco 1981) and, perhaps for that reason, little is known about how intertidal organisms in tropical regions respond to gradients in wave exposure (Vermeij 1973). We tested effects of wave exposure on a large herbivorous intertidal gastropod, *Cittarium pica* (Linnaeus, 1758), the West Indian topshell. *Cittarium pica* occurs on rocky shores throughout the Caribbean (Clench & Abbott 1943; Robertson 2003), and populations differ in density, size-distribution, growth and survival across wave exposure gradients (Debrot

1990a,b). There are thus potentially direct effects of wave exposure on shell morphology, plus indirect responses to a suite of human and natural predators (Debrot 1990a). *Cittarium pica* is collected extensively by humans for food, and fishing pressure covaries with wave exposure because of the increased difficulty and danger of collecting on wave-exposed shores. The potential effect of differing selective pressures on exposed and protected shores depends in part on the extent of migration and genetic exchange between populations. Potential effects should be greatest for those gastropods with direct development and lowest for those species with a long pelagic larval stage that increases the potential for the intermixing of offspring among geographically separated populations. *Cittarium pica* produces larvae that are pelagic for only a few days (Bell 1992), so although larval exchange among sites occurs and DNA sequence variation indicates some connectivity among populations a few hundred kilometres apart (Díaz-Ferguson et al. 2010), the potential for local adaption in *C. pica* is perhaps greater than for species with a long pelagic stage.

We tested the general hypothesis that dislodgement force and shell shape of *C. pica* differs among shores that vary in wave exposure. If wave exposure in the tropics has effects on snail morphology similar to those reported on temperate shores, we expect snails on exposed shores to have features likely to reduce drag and increase the force required to dislodge them. We therefore predicted that, after adjusting for body size, *C. pica* from exposed shores would have: (1) greater dislodgement force, (2) larger opercula (the closure to the shell aperture, a proxy for foot size), and (3) reduced shell height relative to *C. pica* from sheltered shores.

Methods

Study sites

We studied *Cittarium pica* on nine shores around Guana Island, British Virgin Islands (BVI), plus two other BVI sites (Carval Rock and Brandywine Bay). These sites were selected because they provide a strong gradient in wave exposure while being relatively inaccessible to fishing (Table I, Fig. 1). We combined several pieces of information to classify shores in terms of relative wave exposure (Ballantine 1961). We assumed that exposure to waves was a function of fetch, prevailing wind direction, and nearshore topographical features that affect wave forces (shoreline curvature, water depth and slope of the seabed) (Denny 1995; Helmuth & Denny 2003). Our classification was based on prevailing conditions, including the winter period of elevated wave heights, but does not account for intermittent summer hurricanes whose directional pattern of impacts is little known. The four exposed shores are all steep rocky walls, adjacent to deep water, with high fetch length and face the prevailing winds. The two intermediate shores also have high fetch length and are exposed to prevailing winds, but are shallower in slope and adjacent to shallow reefs that dissipate wave energy. The three sheltered shores are shallow in slope, adjacent to shallow water and are in leeward-facing bays.

On five shores, we also installed maximum wave force dynamometers (n = 4 per shore) for 30 days in each of July 2000 and July 2004 (Carrington Bell & Denny 1994). Because the expected range of applied wave force was unknown, the dynamometers at each site were fitted with two types of spring that required differing amounts of force to maximally extend the spring (2 low-force, and 2 high-force dynamometers per site). We found that the wave forces measured were in accord with our exposure classification (Table I), and with wave forces measured at some of the same sites by Good (2004).

Measuring dislodgement force and shell shape

To measure the force required to dislodge *Cittarium pica* from the shore, we sampled individuals greater than 20 mm in shell width that were encountered during daytime low tides, and were positioned on bare rock above water (Table I). Suitable *C. pica* were approached carefully and first tapped on the shell, because this caused them to visibly withdraw their mantle and move their shell towards the substratum, so presumably standardizing their attachment (Etter 1988; Prowse & Pile 2005; Trussell 1997a; Trussell, et al. 1993). We used spring scales to measure dislodgement force to the nearest 1 N (Arbor Scientific, 10N, 20N or 50N Push-Pull Spring Scales). The spring was attached to a line (3 mm diam.) with a sliding loop at its end, so that the loop tightened when pulled. The loop was placed over the shell and pulled snug around the base of the shell where it met the substratum. The scale was then pulled upward in a direction roughly 45° to the shore, and we recorded the scale reading (N) when the *C. pica* became detached (Miller 1974; Prowse & Pile 2005).

To assess differences in shell shape among shores, we measured three shell dimensions using callipers: shell length, shell height (sensu Trussell et al. 1993), and operculum length (sensu Chiu et al. 2002). Operculum length was measured as a rough proxy for foot area (Supplementary material: Fig. SI). We originally intended to measure foot area directly, but *C. pica* are slow to extend their foot when picked up for measurement, making it too time-consuming to obtain a large sample of foot size measurements in the field (Fig. SI). Shell length, shell height, and operculum length were measured using *C. pica* that were removed to measure dislodgment force, and by making additional collections. Additional collections were made on foot at low tide and on snorkel at high tide, during both day and night, to obtain samples of *C. pica* spanning the size-range present (Table I).

Statistical analysis

We used ANCOVA to test whether dislodgement force and shell shape varied among sites, after confirming that data met the assumptions of normality and homoscedasticity. Our analysis focused on how dislodgement force, shell height and operculum length changed relative to shell length (a measure of absolute body size). The full ANCOVA model included terms for the effect of (1) wave exposure - a fixed categorical factor with 3 levels (protected, intermediate, and exposed), (2) site - a random categorical factor nested within wave exposure, (3) shell length - a covariate in order to control for the effect of overall body size, and (4) the interaction between wave exposure and shell length. When differences between sites, and the interaction between exposure and shell length, were non-significant ($p > 0.1$) they were removed from the model to allow more powerful tests for the main effect of exposure (Quinn & Keough 2002).

Results

Dislodgement force changes with wave exposure

The ANCOVA revealed a significant exposure by shell length interaction (ANCOVA, F (2,103) = 5.20, P = 0.0007; Table SI). Inspection of the data suggests that the interaction arose because the relationship between body size and dislodgement force was steepest on exposed shores, shallowest on protected shores, and intermediate on shores that were intermediate in wave exposure (Fig. 2a). The magnitude of difference in dislodgement force between sheltered and exposed shores thus increased with increasing body size and, for larger *Cittarium pica,* was substantial (e.g. at 60 mm in shell length, whelks from exposed shores took more than twice as much force to dislodge as those from sheltered shores; Fig. 2a)

Operculum length changes with wave exposure

The slope of the relationship between shell length and operculum length was unaffected by wave exposure (ANCOVA, F (2,214) = 1.04, P = 0.964), and did not differ among sites (ANCOVA, F (4,214) = 3.53, P = 0.181) (Table SII). With these non-significant terms removed, the ANCOVA indicated that operculum length varied according to wave exposure (ANCOVA, F (2,220) = 6.84, P = 0.001). *Cittarium pica* from exposed shores had larger opercula than those from both other types of shore (marginal mean ± 95%CI: exposed = 24.1 ± 0.4 mm; intermediate = 23.0 ± 0.5 mm; sheltered = 23.2 ± 0.3 mm; Fig. 2b). The difference in operculum length between sheltered and exposed shores was, however, slight (mean operculum length differed by a factor of 1.1; Fig. 2b).

Shell height changes with wave exposure

After removing the non-significant interaction term (ANCOVA, F (2,426) = 1.58, P = 0.149), the ANCOVA revealed that *Cittarium pica* varied in shell height depending on wave exposure (ANCOVA, F (2,426) = 7.85, P < 0.0004; Fig. 2c; Table SIII). Within each wave exposure category, shell height also differed among individual shores (ANCOVA, F (5,428) = 5.83, P < 0.001; Table S3). Comparison of marginal mean shell heights showed that average shell height progressively increased with decreasing exposure (marginal mean ± 95%CI: exposed = 30.2 ± 0.6 mm; intermediate = 31.9 ± 0.7 mm; sheltered = 33.2 ± 0.4 mm), but the difference in shell height between sheltered and exposed shores was slight (mean shell height differed by a factor of 0.96; Fig. 2c).

Discussion

Our results suggest that *Cittarium pica* displays a combination of features that are correlated with wave exposure in a manner qualitatively similar to correlations previously described for several temperate species. For example, like *C. pica*, *Littorina obtusata* (Linnaeus, 1758) and *Nucella lapillus* (Linnaeus, 1758) from exposed shores were harder to dislodge than those from sheltered shores (Etter 1988; Kitching et al. 1966; Trussell 1997a), which may reduce the probability of being ripped from the shore by the high water velocities and acceleration experienced on wave-exposed shores (Trussell 1997b). However for *C. pica*, the magnitude of difference in dislodgement force between sheltered and exposed shores increased with increasing body size. Larger *C. pica* are thus disproportionately affected by wave forces which is in contrast to studies of *N. lapillus* or *L. obtusata* which have shown isometric scaling of body-size and dislodgement forces (Etter 1988; Kitching, et al. 1966; Trussell 1997a).

Like *C. pica*, several temperate gastropods have squatter shells on exposed shores than on protected shores, which can reduce drag (Branch & Marsh 1978; Grenon & Walker 1981; Kitching & Lockwood 1974; Trussell 1997b; Trussell, et al. 1993; Warburton 1976). Increased operculum length on exposed shores is also a possible response to wave forces because the size of the operculum, and the aperture it covers (Chiu, et al. 2002), are both proxies for foot size (Atkinson & Newbury 1984; Etter 1988; Heller 1976; Kitching 1976) and relative foot size is one of the factors controlling dislodgement force in temperate gastropods (Trussell 1997a). Future analyses should thus test directly whether the changes in dislodgement force and shell shape we documented actually reduce the magnitude of drag forces experienced and lower *C. pica*'s probability of dislodgement in nature.

Greater dislodgement force of *C. pica* on wave exposed shores is plausibly a direct response to the higher wave forces experienced at those sites, but is also a potential adaptation to reduce the risk of capture by two of its many predators - humans and octopuses. In some temperate systems, predatory crabs are excluded from wave exposed shores and so prey morphology is influenced by the combination of high wave forces on exposed shores and high predation risk on sheltered shores (Palmer 1990; Seeley 1986). Humans have been preying on *C. pica* for at least 1,000 years, and fishing activity is concentrated on sheltered shores because of the difficulty and danger associated with collecting amidst breaking waves. Although *C. pica* are much more likely to encounter human predators on sheltered shores, the difficulty of fishing amidst crashing waves means that large *C. pica* are more likely to survive attempts to pull them free of the shore at wave exposed sites (based on our own experience, and interviews with over 100 *C. pica* collectors). Octopuses must also pull *C. pica* from the rock surface to consume them, but how wave exposure affects the density, size-distribution, and foraging activity of octopuses is largely unknown. Human predation is thus a possible agent of selection for increased dislodgement force on wave exposed shores, but the effect of octopus predation remains to be determined.

Whether the impacts of *C. pica's* other predators covary with wave exposure is largely unstudied. *Cittarium pica* is consumed by a diverse group of predators, including dog whelks, octopuses, oystercatchers, lobsters and various fishes (Robertson 2003). The density of predatory dog whelks was not associated with wave exposure on Guana Island (Good 2004), but in the Bahamas was highest on exposed shores (Debrot 1990a; Debrot 1990b), so generalizations about their distribution require further study. We know little about how the distribution and foraging of other *C. pica* predators, such as oystercatchers, lobsters and fishes, varies with wave exposure on tropical shores. It would thus be valuable to test whether the combined densities of *C. pica*'s predators follows gradients in wave exposure in a predictable fashion and might exert selective pressures on shell shape. We can then test whether the influence of predators has a different pattern of covariation with wave exposure to that reported on temperate shores.

Although preliminary, our work casts doubt on early assumptions that tropical intertidal habitats are physically benign, and suggests further analysis of tropical gastropods is warranted. In order to develop a better understanding of differences between temperate and tropical shores, future analyses should aim towards replicated phylogenetically controlled comparisons (e.g.Vermeij & Williams 2007) of the magnitude of wave forces, and associated morphological changes, experienced by tropical and temperate species.

Acknowledgements

Funding was provided by the University of Puerto Rico Sea Grant College Program and the Falconwood Foundation. Student co-authors were supported by the URI Cobb Endowment Independent Study Award (Allison Holevoet.), URI Undergraduate Research Initiative Award (Allison Holevoet), and the URI EPSCoR SURF Fellowship (Allison Holevoet and Sarah Merolla). Thanks to Lianna Jarecki and the Guana Island staff for help with logistics, and to Maggie Chan, Dennis Conetta, Russell Dauksis, Linda Forrester, Fiona Forrester, Katherine Forrester, and Alicia Siravo for help with field work.

References:

Atkinson WD, Newbury SF. 1984. The adaptations of the rough winkle, *Littorina rudis*, to desiccation and to dislodgement by wind and waves. Journal of Animal Ecology 53:93-105.

Ballantine WJ. 1961. A biologically-defined exposure scale for the comparative description of rocky shores. Field Studies Journal 1:1-19.

Bell LJ. 1992. Reproduction and larval development of the West Indian topshell, *Cittarium pica* (Trochidae), in the Bahamas. Bulletin of Marine Science 51:250-66.

Bertness MD. 1981. Predation, physical stress, and the organization of a tropical rocky inter-tidal hermit crab community. Ecology 62:411-25.

Boulding EG. 1990. Are the opposing selection pressures on exposed and protected shores sufficient to maintain genetic differentiation between gastropod populations with high intermigration rates? Hydrobiologia 193:41-52.

Boulding EG, Holst M, Pilon V. 1999. Changes in selection on gastropod shell size and thickness with wave-exposure on northeastern pacific shores. Journal of Experimental Marine Biology and Ecology 232:217-39.

Branch GM, Marsh AC. 1978. Tenacity and shell shape in six *Patella* species: Adaptive features. Journal of Experimental Marine Biology and Ecology 34:111-30.

Brosnan DM. 1992. Ecology of tropical rocky shores: plant-animal interactions in tropical and temperate latitudes. In: John D M, Hawkins S J, Price J H, editors. Plant Animal interactions in the marine benthos. Oxford: Clarendon Press, p 101–31.

Carrington Bell E, Denny MW. 1994. Quantifying "wave exposure": a simple device for recording maximum velocity and results of its use at several field sites. Journal of Experimental Marine Biology and Ecology 181:9-29.

Chiu Y-W, Chen H-C, Lee S-C, Chen CA. 2002. Morphometric analysis of shell and operculum variations in the viviparid snail, *Cipangopaludina chinensis* (Mollusca: Gastropoda), in Taiwan. Zoological Studies-Taipei 41:321-31.

Clench WJ, Abbott RT. 1943. The genera *Gaza* and *Livona* in the western Atlantic. Johnsonia: Monographs of the marine mollusks of the Western Atlantic 1:1-12.

Debrot AO. 1990a. Survival, growth, and fecundity of the West Indian topshell, *Cittarium pica* (Linnaeus), in various rocky intertidal habitats of the Exuma Cays, Bahamas. The Veliger 33:363-71.

Debrot AO. 1990b. Temporal aspects of population dynamics and dispersal behavior of the West Indian topshell, *Cittarium pica* (L.), at selected sites in the Exuma Cays, Bahamas. Bulletin of Marine Science 47:431-47.

Denny M. 1995. Predicting Physical Disturbance: Mechanistic Approaches to the Study of Survivorship on Wave-Swept Shores. Ecological Monographs 65:371-418.

Denny MW. 2006. Ocean waves, nearshore ecology, and natural selection. Aquatic Ecology 40:439-61.

Díaz-Ferguson E, Haney R, Wares J, Silliman B. 2010. Population Genetics of a Trochid Gastropod Broadens Picture of Caribbean Sea Connectivity. PLoS ONE 5:e12675. 8 pages.

Etter RJ. 1988. Asymmetrical developmental plasticity in an intertidal snail. Evolution:322-34.

Good TP. 2004. Distribution and Abundance Patterns in Caribbean Rocky Intertidal Zones. Bulletin of Marine Science 74:459-68.

Grenon JF, Walker G. 1981. The tenacity of the limpet, *Patella vulgata* L.: An experimental approach. Journal of Experimental Marine Biology and Ecology 54:277-308.

Heller J. 1976. The effects of exposure and predation on the shell of two British winkles. Journal of Zoology 179:201-13.

Helmuth B, Denny MW. 2003. Predicting wave exposure in the rocky intertidal zone: Do bigger waves always lead to larger forces-9. Limnology and Oceanography 48:1338-45.

Hollander J, Butlin RK. 2010. The adaptive value of phenotypic plasticity in two ecotypes of a marine gastropod. Bmc Evolutionary Biology 10:333. 7 pages.

Kitching JA. 1976. Distribution and changes in shell form of *Thais* spp.(Gastropoda) near Bamfield, BC. Journal of Experimental Marine Biology and Ecology 23:109-26.

Kitching JA, Lockwood J. 1974. Observations on shell form and its ecological significance in thaisid gastropods of the genus *Lepsiella* in New Zealand. Marine Biology 28:131-44.

Kitching JA, Muntz L, Ebling FJ. 1966. The Ecology of Lough Ine. XV. The Ecological Significance of Shell and Body Forms in *Nucella*. The Journal of Animal Ecology 35:113-26.

Linnaeus C. 1758. Systema Naturae, Ed. 10, Vol. 1. Holmiae, Sweden: Laurentii Salvii. 824 pages. (in Latin)

Menge BA, Lubchenco J. 1981. Community Organization in Temperate and Tropical Rocky Intertidal Habitats: Prey Refuges in Relation to Consumer Pressure Gradients. Ecological Monographs 51:429-50.

Menge BA, Sutherland JP. 1976. Species Diversity Gradients: Synthesis of the Roles of Predation, Competition, and Temporal Heterogeneity. The American Naturalist 110:351-69.

Menge BA, Sutherland JP. 1987. Community Regulation: Variation in Disturbance, Competition, and Predation in Relation to Environmental Stress and Recruitment. The American Naturalist 130:730-57.

Miller SL. 1974. Adaptive design of locomotion and foot form in prosobranch gastropods. Journal of Experimental Marine Biology and Ecology 14:99-156.

Palmer AR. 1990. Effect of crab effluent and scent of damaged conspecifics on feeding, growth, and shell morphology of the Atlantic dogwhelk *Nucella lapillus* (L.). In: Progress in Littorinid and Muricid Biology. Netherlands: Springer, p 155-82.

Prowse TAA, Pile AJ. 2005. Phenotypic homogeneity of two intertidal snails across a wave exposure gradient in South Australia. Marine Biology Research 1:176-85.

Quinn GP, Keough MJ. 2002. Experimental design and data analysis for biologists: Cambridge: Cambridge University Press. 556 pages.

Robertson R. 2003. The edible West Indian "whelk" *Cittarium pica* (Gastropoda: Trochidae): Natural history with new observations. Proceedings of the Academy of Natural Sciences of Philadelphia 153:27-47.

Seeley RH. 1986. Intense natural selection caused a rapid morphological transition in a living marine snail. Proceedings of the National Academy of Sciences 83:6897-901.

Trussell GC. 1997a. Phenotypic plasticity in the foot size of an intertidal snail. Ecology 78:1033-48.

Trussell GC. 1997b. Phenotypic selection in an intertidal snail: effects of a catastrophic storm. Marine Ecology Progress Series 151:73-9.

Trussell GC, Etter RJ. 2001. Integrating genetic and environmental forces that shape the evolution of geographic variation in a marine snail. Genetica 112:321-37.

Trussell GC, Johnson AS, Rudolph SG, Gilfillan ES. 1993. Resistance to dislodgment-Habitat and size-specific differences in morphology and tenacity in an intertidal snail. Marine Ecology-Progress Series 100:135-44.

Vermeij G. 1973. Morphological patterns in high-intertidal gastropods: adaptive strategies and their limitations. Marine Biology 20:319-46.

Vermeij GJ, Williams ST. 2007. Predation and the geography of opercular thickness in turbinid gastropods. Journal of Molluscan Studies 73:67-73.

Warburton K. 1976. Shell form, behaviour, and tolerance to water movement in the limpet *Patina pellucida* (L.) (Gastropoda: Prosobranchia). Journal of Experimental Marine Biology and Ecology 23:307-25.

Figure captions

Fig. 1. Map of study sites. See Table 1 for site names that correspond to each site number.

Fig. 2. Relationships between *Cittarium pica* body size (shell length mm) and (a) force needed to dislodge individuals from the shore (N), (b) operculum length (mm) and (c) shell height (mm). *C. pica* are grouped by wave exposure at their site of origin and regression lines were fit to each group using ANCOVA.

Table I. List of study sites grouped by relative wave exposure. Site numbers correspond to the map of study sites (Fig. 1). Also shown are mean dynamometer readings for four sites (with standard errors) and the sample size by site for each of the response variables (dislodgement force, shell height and operculum length).

Wave exposure		Dynamometer force (N)		Dislodgement force (N)	Shell height (mm)	Operculum length (mm)
Site # and name		Mean	(SE)	Sample sizes (n)		
Exposed						
1	Long Point*	-	-	5	26	23
2	Grand Central	-	-	-	51	43

3	Carval Rock	-	-	-	63	-
4	Grand Ghut	-	-	10	-	-
Intermediate						
5	North Beach East	8	(1.5)	31	30	12
6	North Beach West	4.6	(0.9)	28	58	24
Sheltered						
7	Harris Ghut	3.9	(0.3)	14	33	12
8	White Bay	3.8	(0.2)	24	136	70
9	Brandywine Bay	-	-	-	40	40

* At Long Point, four dynamometers were installed but all disappeared. We suspect this occurred because the wave forces were too great for the dynamometer design used.

Supplementary material