

2016

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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>

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

3

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14 Running head: wave exposure and snail morphology

15

1

2 **Abstract**

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

15 Keywords: adaptation, intertidal, shell shape, topshell

16 **Introduction**

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

23 Research on temperate gastropods provides some of the best evidence for morphological changes
24 across gradients of wave exposure. In several species, gastropods from exposed shores have

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

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

1 1990a,b). There are thus potentially direct effects of wave exposure on shell morphology, plus
2 indirect responses to a suite of human and natural predators (Debrot 1990a). *Cittarium pica* is
3 collected extensively by humans for food, and fishing pressure covaries with wave exposure
4 because of the increased difficulty and danger of collecting on wave-exposed shores.
5 The potential effect of differing selective pressures on exposed and protected shores depends in
6 part on the extent of migration and genetic exchange between populations. Potential effects
7 should be greatest for those gastropods with direct development and lowest for those species
8 with a long pelagic larval stage that increases the potential for the intermixing of offspring
9 among geographically separated populations. *Cittarium pica* produces larvae that are pelagic for
10 only a few days (Bell 1992), so although larval exchange among sites occurs and DNA sequence
11 variation indicates some connectivity among populations a few hundred kilometres apart (Díaz-
12 Ferguson et al. 2010), the potential for local adaptation in *C. pica* is perhaps greater than for
13 species with a long pelagic stage.

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

1 **Methods**

2 *Study sites*

3 We studied *Cittarium pica* on nine shores around Guana Island, British Virgin Islands (BVI),
4 plus two other BVI sites (Carval Rock and Brandywine Bay). These sites were selected because
5 they provide a strong gradient in wave exposure while being relatively inaccessible to fishing
6 (Table I, Fig. 1). We combined several pieces of information to classify shores in terms of
7 relative wave exposure (Ballantine 1961). We assumed that exposure to waves was a function of
8 fetch, prevailing wind direction, and nearshore topographical features that affect wave forces
9 (shoreline curvature, water depth and slope of the seabed) (Denny 1995; Helmuth & Denny
10 2003). Our classification was based on prevailing conditions, including the winter period of
11 elevated wave heights, but does not account for intermittent summer hurricanes whose
12 directional pattern of impacts is little known. The four exposed shores are all steep rocky walls,
13 adjacent to deep water, with high fetch length and face the prevailing winds. The two
14 intermediate shores also have high fetch length and are exposed to prevailing winds, but are
15 shallower in slope and adjacent to shallow reefs that dissipate wave energy. The three sheltered
16 shores are shallow in slope, adjacent to shallow water and are in leeward-facing bays.

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

1 *Measuring dislodgement force and shell shape*

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

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

1 *Statistical analysis*

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

12 **Results**

13 *Dislodgement force changes with wave exposure*

14 The ANCOVA revealed a significant exposure by shell length interaction (ANCOVA, $F(2,103)$
15 $= 5.20$, $P = 0.0007$; Table SI). Inspection of the data suggests that the interaction arose because
16 the relationship between body size and dislodgement force was steepest on exposed shores,
17 shallowest on protected shores, and intermediate on shores that were intermediate in wave
18 exposure (Fig. 2a). The magnitude of difference in dislodgement force between sheltered and
19 exposed shores thus increased with increasing body size and, for larger *Cittarium pica*, was
20 substantial (e.g. at 60 mm in shell length, whelks from exposed shores took more than twice as
21 much force to dislodge as those from sheltered shores; Fig. 2a)

1 *Operculum length changes with wave exposure*

2 The slope of the relationship between shell length and operculum length was unaffected by wave
3 exposure (ANCOVA, $F(2,214) = 1.04, P = 0.964$), and did not differ among sites (ANCOVA, F
4 $(4,214) = 3.53, P = 0.181$) (Table SII). With these non-significant terms removed, the ANCOVA
5 indicated that operculum length varied according to wave exposure (ANCOVA, $F(2,220) =$
6 $6.84, P = 0.001$). *Cittarium pica* from exposed shores had larger opercula than those from both
7 other types of shore (marginal mean \pm 95%CI: exposed = 24.1 ± 0.4 mm; intermediate = $23.0 \pm$
8 0.5 mm; sheltered = 23.2 ± 0.3 mm; Fig. 2b). The difference in operculum length between
9 sheltered and exposed shores was, however, slight (mean operculum length differed by a factor
10 of 1.1; Fig. 2b).

11 *Shell height changes with wave exposure*

12 After removing the non-significant interaction term (ANCOVA, $F(2,426) = 1.58, P = 0.149$),
13 the ANCOVA revealed that *Cittarium pica* varied in shell height depending on wave exposure
14 (ANCOVA, $F(2,426) = 7.85, P < 0.0004$; Fig. 2c; Table SIII). Within each wave exposure
15 category, shell height also differed among individual shores (ANCOVA, $F(5,428) = 5.83, P <$
16 0.001 ; Table S3). Comparison of marginal mean shell heights showed that average shell height
17 progressively increased with decreasing exposure (marginal mean \pm 95%CI: exposed = $30.2 \pm$
18 0.6 mm; intermediate = 31.9 ± 0.7 mm; sheltered = 33.2 ± 0.4 mm), but the difference in shell
19 height between sheltered and exposed shores was slight (mean shell height differed by a factor of
20 0.96; Fig. 2c).

21 **Discussion**

22 Our results suggest that *Cittarium pica* displays a combination of features that are correlated with

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

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

21 Greater dislodgement force of *C. pica* on wave exposed shores is plausibly a direct response to
22 the higher wave forces experienced at those sites, but is also a potential adaptation to reduce the
23 risk of capture by two of its many predators - humans and octopuses. In some temperate

1 systems, predatory crabs are excluded from wave exposed shores and so prey morphology is
2 influenced by the combination of high wave forces on exposed shores and high predation risk on
3 sheltered shores (Palmer 1990; Seeley 1986). Humans have been preying on *C. pica* for at least
4 1,000 years, and fishing activity is concentrated on sheltered shores because of the difficulty and
5 danger associated with collecting amidst breaking waves. Although *C. pica* are much more
6 likely to encounter human predators on sheltered shores, the difficulty of fishing amidst crashing
7 waves means that large *C. pica* are more likely to survive attempts to pull them free of the shore
8 at wave exposed sites (based on our own experience, and interviews with over 100 *C. pica*
9 collectors). Octopuses must also pull *C. pica* from the rock surface to consume them, but how
10 wave exposure affects the density, size-distribution, and foraging activity of octopuses is largely
11 unknown. Human predation is thus a possible agent of selection for increased dislodgement force
12 on wave exposed shores, but the effect of octopus predation remains to be determined.

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

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

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9 **Acknowledgements**

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

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14 **Figure captions**

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

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

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14 Table I. List of study sites grouped by relative wave exposure. Site numbers correspond to the
 15 map of study sites (Fig. 1). Also shown are mean dynamometer readings for four sites (with
 16 standard errors) and the sample size by site for each of the response variables (dislodgement
 17 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

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

3

4

5 Supplementary material