



ORIGINAL ARTICLE

Phenotypic homogeneity of two intertidal snails across a wave exposure gradient in South Australia

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Abstract

Dislodgement by the large drag forces imparted by breaking waves is an important cause of mortality for intertidal snails. The risk of drag-induced dislodgement can be reduced with: (1) a smaller shell of lower maximum projected surface area (MPSA); (2) a streamlined shell shape characterized by a squatter shell; and/or (3) greater adhesive strength attained through a larger foot area or increased foot tenacity. Snails on exposed coasts tend to express traits that increase dislodgement resistance. Such habitat-specific differences could result from direct selection against poorly adapted phenotypes on exposed shores but may reflect gastropod adaptation to high wave action achieved through phenotypic plasticity or genetic polymorphism. With this in mind, we examined the size, shape and adhesive strength of populations of two gastropod species, *Austrocochlea constricta* (Lamarck) and *Nerita atramentosa* (Reeve), from two adjacent shores representing extremes in wave exposure. Over a 5 day period, maximum wave forces were more than 10 times greater on the exposed than sheltered shore. Size–frequency distributions indicate that a predator consuming snails within the 1.3–1.8 cm length range regulates sheltered shore populations of both snail species. Although morphological scaling considerations suggest that drag forces should not place physical limits on the size of these gastropods, exposed shore populations of both snails were small relative to the maximum size documented for these species. Therefore, selective forces at the exposed site might favour smaller individuals with increased access to microhabitat refuges. Unexpectedly, however, neither snail species exhibited between-shore differences in shape, foot area or foot tenacity, which are likely to have adaptive explanations. Hence, it is possible that these snails are incapable of adaptive developmental responses to high wave action. Instead, the homogeneous and wave-exposed nature of Australia's southern coastline may have favoured the evolution of generalist strategies in these species.

Key words: *Gastropod, phenotypic plasticity, wave energy*

Introduction

Tolerance of changing environmental conditions should be a natural outcome of organismal evolution (Pigliucci 1996). An important goal of evolutionary ecology is therefore to determine how organisms adapt to life in spatially and/or temporally variable habitats (Etter 1988; Scheiner & Lyman 1991; Via et al. 1995). There has consequently been much interest in the means by which organisms have adapted to life in one of the world's most heterogeneous environments, the rocky intertidal zone.

Spatial and temporal variation in wave exposure have probably exerted considerable influence over the evolutionary strategies of intertidal organisms. Breaking waves commonly generate water velocities of over

10 ms^{-1} and water accelerations in excess of 100 ms^{-2} (Denny 1985, 1988; Denny et al. 1985). These flows impart large hydrodynamic forces on intertidal organisms (Denny et al. 1985; Gaylord et al. 1994) whose survival is therefore partly determined by their ability to resist damage or dislodgement by waves (Trussell et al. 1993; Bell & Gosline 1997). Wave exposure has been shown to restrict the distributions of many intertidal organisms, including macroalgae (Carrington 1990; Shaughnessy et al. 1996), mussels (Bell & Gosline 1996, 1997) and crabs (Menge 1978; Palmer 1985) and clearly may have profound effects on intertidal community dynamics (Denny 1985, 1987a; Gaines & Denny 1993).

Many organisms exhibit adaptations to the hydrodynamic forces of drag, lift and acceleration reaction

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Published in collaboration with the University of Bergen and the Institute of Marine Research, Norway, and the Marine Biological Laboratory, University of Copenhagen, Denmark

(Accepted 1 June 2004; Printed 14 July 2005)

ISSN 1745-1000 print/ISSN 1745-1019 online © 2005 Taylor & Francis
DOI: 10.1080/17451000510018999

that are imparted by wave-induced flows (Vogel 1981; Denny 1988). Macroalgal flexibility allows deformation in the direction of water flow, thus minimizing drag and lowering the probability of dislodgement from the substratum (Denny 1988; Carrington 1990; Shaughnessy et al. 1996; reviewed by Koehl 1996). Similarly, animals have shapes that reduce lift (Branch & Marsh 1978; Denny 1989) or behaviours that minimize the effects of drag and acceleration reaction forces (Bell & Gosline 1997).

Phenotypic plasticity, the ability of a single genotype to express different phenotypes in different environments, is a common response to spatial variation in wave exposure. For example, in high wave energy environments, sponges produce stronger skeletons (Palumbi 1984) and mussel attachment strength is increased (Witman & Suchanek 1984). Similarly, the subtidal macroalga *Nereocystis luetkeana* exhibits wide blades with ruffled edges and increased photosynthetic ability at sheltered sites but narrow, flat blades that can collapse into streamlined bundles at exposed sites (Koehl & Alberte 1988).

Gastropods are ubiquitous organisms on rocky intertidal shores and are ideal for experimentation. The hydrodynamic force most likely to effect dislodgement of intertidal gastropods is drag (Denny et al. 1985; Trussell et al. 1993). Drag forces act in the direction of flow and are a function of organism shape and proportional to the square of the water velocity and to organism projected surface area (Denny 1987a). For intertidal snails, a reduction in the magnitude of drag forces experienced or an increase in adhesive ability can lower the probability of dislodgement. Drag minimization may be achieved through: (1) reduced shell size and thus maximum projected surface area (MPSA); and (2) a streamlined shape characterized by a squatter shell (Trussell et al. 1993). Improved adhesive strength may be afforded by: (1) larger surface area of the muscular foot; and (2) increased foot tenacity achieved by changing the properties of the pedal mucus (Grenon & Walker 1981; Denny 1984).

The dislodgement of snails by waves is a probable cause of mortality and may also reduce foraging efficiencies and reproductive success (Denny et al. 1985; Etter 1989; Trussell et al. 1993). Consequently, we might expect gastropods on exposed coasts to express traits that lower dislodgement risk. Such trends have previously been reported and can result from direct selection against poorly adapted phenotypes on exposed shores (e.g. Trussell 1997b), within-generation developmental responses (phenotypic plasticity) (e.g. Etter 1988; Trussell 1997a), or the evolution of genetically differentiated and locally adapted populations (genetic polymorphism) (e.g. Parsons 1997a,b).

The intertidal snails *Austrocochlea constricta* (Lamarck) and *Nerita atramentosa* (Reeve) occur sympatrically along much of the southern Australian coastline. Both species disperse by means of a planktonic larval stage that should have prevented the accumulation of genetic differences over smaller spatial scales, which is required for local adaptation. Instead, we might expect these snails to have evolved adaptive plastic responses to spatial variation in wave exposure. With this in mind, we searched for habitat-specific differences in both species by comparing the size, shape, foot area and foot tenacity of snail populations from two South Australian shores chosen to represent extremes in wave exposure. We asked two questions: (1) Are there between-shore differences in snail traits that affect the risk of drag-induced dislodgement?; (2) If so, are these differences likely to have adaptive explanations?

Methods

Gastropod species

Austrocochlea constricta and *Nerita atramentosa* are common on shores of low to moderate wave action along the coasts of the southern half of Australia (Edgar 1997). *Austrocochlea constricta* (family Trochidae) grows to a height of 2.5 cm and has separate sexes that release gametes into the water column for fertilization. *Nerita atramentosa* (family Neritidae) reaches a height of 2.8 cm and also has separate sexes, but fertilization is internal and egg capsules from which larvae are eventually liberated are laid on rocks or shells. The larvae of both species are planktonic and remain in the water column for approximately 1 week (Anderson 1962; Underwood 1974).

Study sites and timing

One exposed and one sheltered shore were selected for study on the basis of three criteria: (1) presence of suitable gastropod populations; (2) extreme difference in wave exposure, while still providing manageable and safe working conditions; and (3) extreme proximity, so that differences in other biotic and abiotic factors between sites were minimized and so that snail populations on each could be assumed to have arisen from the same genetic stocks. The shores selected are located on either side of Cape Donnington, South Australia (135°59'E 34°43'S), and separated by approximately 400 m (Figure 1). The exposed, high-energy shore is subjected to the wave forces of the Southern Ocean, whereas the sheltered, low-energy shore is not (Figure 1).

Only two shores were considered because the southern Australian coastline is extremely homogeneous as the surrounding terrestrial ecosystem is

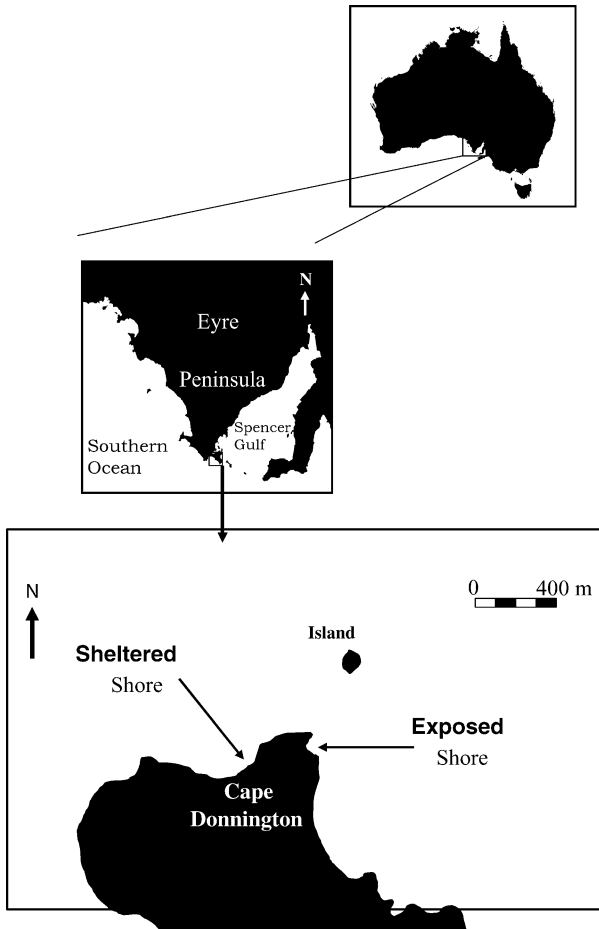


Figure 1. Maps indicating the location of the study sites on either side of Cape Donnington, South Australia.

desert. Ultimately, there are no rivers, streams or creeks to create embayments (El-Sabh et al. 1997). Additionally, the remoteness of the region results in a lack of infrastructure (i.e. roads) providing access to the coastline, and helicopter drops along the southern coasts are considered unsafe. Therefore, it is difficult to locate pairs of sites that meet the criteria listed above. Snail populations on each shore were examined by randomly sampling individuals of both species in early December, 1998, during the Austral summer when wave forces are at a minimum. The extreme conditions of the Southern Ocean prevent sampling of the intertidal during the winter months (Short 2001).

The rocky intertidal of the southern coast line of Australia is dominated by a variety of molluscs (Wormersley & Thomas 1976). Typically three species of gastropod, *Austrocochlea constricta*, *Nerita atramentosa*, and *Bembicium nanum*, roam among a smattering of barnacles or the serpulid worm *Galeolaria capisotosa*. The community does not have much algae except for small patches of the

brown algae *Hormosira bankassi* and a variety of filamentous blue green algae.

Maximum wave force

Maximum rather than mean water velocities provide more information about the probability of gastropod dislodgement (Gaines & Denny 1993; Bell & Denny 1994). Wave exposure differences between the two shores were quantified with maximum velocity recorders (Bell & Denny 1994) deployed on horizontal rock platforms in the low intertidal zone. The maximum extension of the spring component of these wave gauges was recorded at low tide every 24 h for 5 days and converted to units of force (N) using Hooke's law.

Shell size and shape

Snails were collected from haphazardly placed 0.25 m² quadrants along the rock platforms. The size of the snails was quantified using the shell height, length and width of *Austrocochlea constricta* (exposed shore n = 20; sheltered shore n = 18) and *Nerita atramentosa* (exposed shore n = 19; sheltered shore n = 20) individuals measured to the nearest 0.5 mm with callipers. The greatest height and width were measured as either perpendicular (height) or parallel (length and width) to the substrate during the snail's attachment. The MPSA of snail shells, a general indicator of shell shape, was estimated as shell height by length.

Dislodgement force, foot area and tenacity

A length of monofilament line was attached to the apex of each of the aforementioned snails with cyanoacrylic glue. After an interval of approximately 1 h in situ, the snails were tapped to induce maximum adhesion to the substratum (Etter 1988). Recording spring scales (Pesola) were hooked through a loop in the monofilament line and used to dislodge snails vertically (Denny 1987b), thus providing the normal dislodgement force. Although drag imposes shear rather than normal forces on gastropod shells, the normal dislodgement force measured can still be used to reveal differences in the ability of individual gastropods to resist dislodgement. In the laboratory, the same snails were placed on a glass platform in flowing salt water to encourage foot extension and then tapped. Digital photographs of the foot were taken and foot areas (cm²) determined using NIH Image (Scion). Tenacity was calculated as the dislodgement force per unit foot area (N m⁻²).

Size–frequency distributions

The shell length of additional snails of each species ($n = 80$) collected randomly from both shores was measured in order to allow better consideration of the size structure of the different populations. Three quadrants (0.25 m^2) were placed across the rock platform and all the snails in the quadrants were collected and measured.

Statistical analyses

Prior to analyses, data were examined with Levene's test ($P > 0.05$) and $\log(x+1)$ transformed as necessary to maintain homogeneity of variance. We examined the allometry between: (1) each of the linear shell dimensions (height, width and length); (2) foot area and shell MPSA; and (3) dislodgement force and foot area. Scaling coefficients were quantified by determining the slope of log–log plots (Trussell et al. 1993). ANOVA, ANCOVA, t-tests and linear regression analyses were performed using SPSS 10.0 for Windows software. t-tests were used to compare the slopes of log–log plots to a line with a slope of 1.0. Size–frequency histograms of snail lengths accommodated normal curves, with the exception of data from the *Austrocochlea constricta* sheltered shore population, which was analysed using a best-fit model (Real 1977).

Results

Maximum wave force

Maximum wave forces on the exposed shore (mean = $7.46 \pm 0.39 \text{ N}$) were more than 10 times greater than those at the sheltered site (mean = $0.670 \pm 0.19 \text{ N}$; ANOVA: $F_{(1,54)} = 285.9$, $P < 0.001$). We may, therefore, assume that the magnitude of drag forces acting on gastropods is significantly greater on the exposed shore.

Shell shape and size

At both sites, the linear dimensions (height, width and length) of *Austrocochlea constricta* shells scaled isometrically (b was not significantly different to 1.0; all b between 0.94 and 1.11; all t_{16} or $t_{18} < 1.62$, all $P > 0.05$; Figure 2). Furthermore, this species was the same shape on both shores (ANCOVA, Table I; Figure 2). Notably, however, *Austrocochlea constricta* on the exposed shore had a smaller mean size (mean MPSA = 1.87 cm^2) than those on the sheltered shore (mean MPSA = 3.19 cm^2 ; ANOVA: $F_{(1,36)} = 15.4$, $P < 0.001$).

At the sheltered site, the linear dimensions of *Nerita atramentosa* shells scaled isometrically (b was

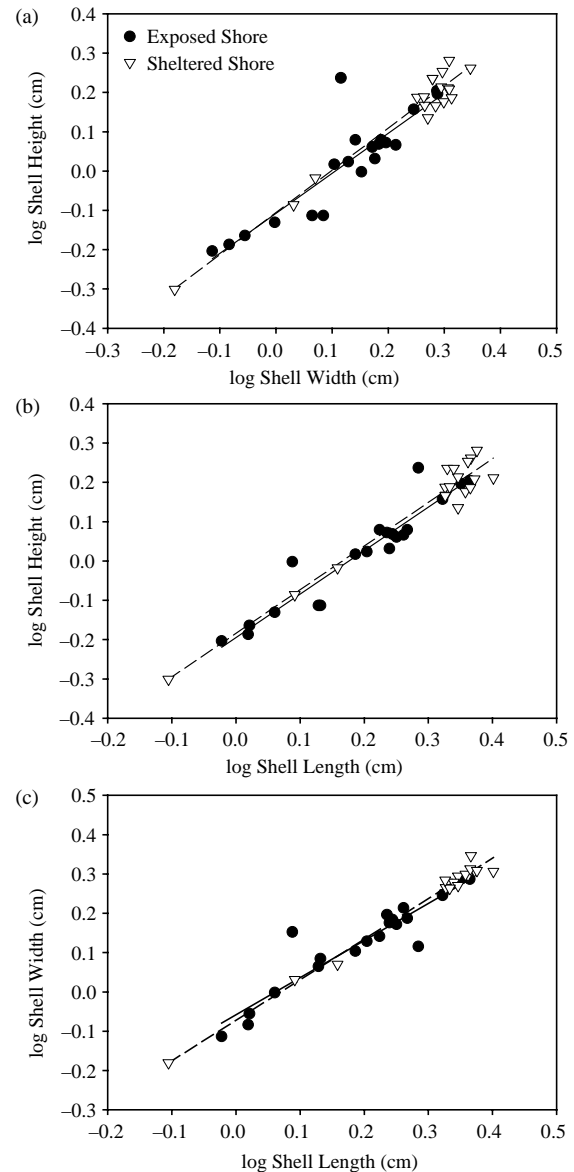


Figure 2. *Austrocochlea constricta*. Log–log plots of (a) shell height versus shell width, (b) shell height versus shell length and (c) shell width versus shell length for snails from the exposed (solid circles, solid line) and sheltered (open inverse triangle, dotted line) shores. Lines represent least-squared regressions for data from each site. Within each plot neither the slopes nor the elevation of the lines differs significantly (see Table I for linear regression and ANCOVA statistics).

not significantly different to 1.0; all b between 0.95 and 1.10; all $t_{18} < 1.49$, all $P > 0.05$; Figure 3). As *Nerita atramentosa* from the exposed shore increased in size, however, shell height increased more rapidly than shell length or width (both $b > 1$; both $t_{17} > 6.73$, both $P < 0.001$). Additionally, shell width increased less quickly than shell length ($b < 1$, $t_{17} = -2.16$, $P < 0.05$). Relative to the sheltered shore population, therefore, snails on the exposed shore became taller as they grew (ANCOVA, Table I; Figure 3). In contrast to *Austrocochlea constricta*,

Table I. Results of log (Y) – log (X) regression analyses for relationships between various snail traits for *Austrocochlea constricta* (exposed shore, n = 20; sheltered shore, n = 18) and *Nerita atramentosa* (exposed shore, n = 19; sheltered shore, n = 20). Also shown are the results of an ANCOVA that compares the slopes and elevations of regression lines for the exposed and sheltered shore snail populations. The E versus S column indicates the direction of any significant difference.

Regression Equation	ANCOVA		
	r ²	F	E versus S
<i>Austrocochlea constricta</i>			
Log shell height versus log shell width (Figure 3a)			
E: log Y = 1.02 log X – 0.11	0.99***	Slope: 0.00	E = S
S: log Y = 1.07 log X – 0.11	0.93***	Elevation: 0.65	E = S
Log shell height versus log shell length (Figure 3b)			
E: log Y = 1.11 log X – 0.19	0.89***	Slope: 0.00	E = S
S: log Y = 1.11 log X – 0.18	0.94***	Elevation: 0.65	E = S
Log shell width versus log shell length (Figure 3c)			
E: log Y = 0.94 log X – 0.06	0.87***	Slope: 0.92	E = S
S: log Y = 1.03 log X – 0.07	0.98***	Elevation: 0.36	E = S
Log foot area versus log shell MPSA (Figure 5a)			
E: log Y = 0.75 log X – 0.41	0.31*	Slope: 0.59	E = S
S: log Y = 0.97 log X – 0.36	0.81***	Elevation: 2.16	E = S
Log dislodgement force versus log foot area (Figure 6a)			
E: log Y = 0.84 log X – 0.84	0.23*	Slope: 0.23	E = S
S: log Y = 1.05 log X – 0.55	0.70***	Elevation: 3.57	E = S
<i>Nerita atramentosa</i>			
Log shell height versus log shell width (Figure 4a)			
E: log Y = 1.30 log X – 0.21	0.98***	Slope: 5.29	E > S
S: log Y = 0.95 log X – 0.08	0.95***	Elevation: n/a	n/a
Log shell height versus log shell length (Figure 4b)			
E: log Y = 1.24 log X – 0.32	0.99***	Slope: 5.54*	E > S
S: log Y = 1.08 log X – 0.31	0.95***	Elevation: n/a	n/a
Log shell width versus log shell length (Figure 4c)			
E: log Y = 0.95 log X – 0.08	0.99***	Slope: 0.00	E = S
S: log Y = 1.10 log X – 0.22	0.93***	Elevation: 0.49	E = S
Log foot area versus log shell MPSA (Figure 5b)			
E: log Y = 0.81 log X – 0.21	0.81***	Slope: 0.29	E = S
S: log Y = 0.68 log X – 0.19	0.31*	Elevation: 2.17	E = S
Log dislodgement force versus log foot area (Figure 6b)			
E: log Y = 1.19 log X – 0.66	0.28*	Slope: 1.68	E = S
S: log Y = 0.08 log X – 1.31	0.00	Elevation: 1.09	E = S

E, exposed shore; S, sheltered shore; MPSA, maximum projected surface area.

*P < 0.05; **P < 0.01; ***P < 0.001.

Nerita atramentosa on the exposed shore had a larger mean size (mean MPSA = 0.83 cm²) than those on the sheltered shore (mean MPSA = 0.45 cm²; ANOVA: F_(1,37) = 5.41, P < 0.05).

Foot area

For all snail populations, the scaling coefficient describing the relationship between foot area and

Table II. Summary of morphological differences between shores for both species of snails. Differences between means were determined by ANOVA and are reported in the text.

Snail	MPSA	Foot area	Dislodgement force
<i>Austrocochlea constricta</i>	E < S	E < S	E < S
<i>Nerita atramentosa</i>	E > S	E = S	E = S

MPSA, maximum projected surface area; E, exposed shore; S, sheltered shore.

MPSA was not significantly different to 1.0 (all b between 0.75 and 0.97; all t_{16,17 or 18} < -0.30, all P > 0.05; Figure 4). For both species, snails of a given size had the same foot area regardless of their habitat (ANCOVA, Table I; Figure 4). *Austrocochlea constricta* on the exposed shore had a smaller mean foot area (0.70 cm²) than those on the sheltered shore (1.37 cm²; ANOVA: F_(1,36) = 16.59, P < 0.001), whereas the foot area of *Nerita atramentosa* did not differ significantly between shores (ANOVA: F_(1,37) = 0.89, P > 0.05).

Dislodgement force and foot tenacity

For both species, the force required to dislodge a snail scaled isometrically with foot area on both shores (all b between 0.08 and 1.05; all t_{16,17 or 18} < 0.4, all P > 0.05; Figure 5). These results suggest that tenacity (dislodgement force per unit foot area)

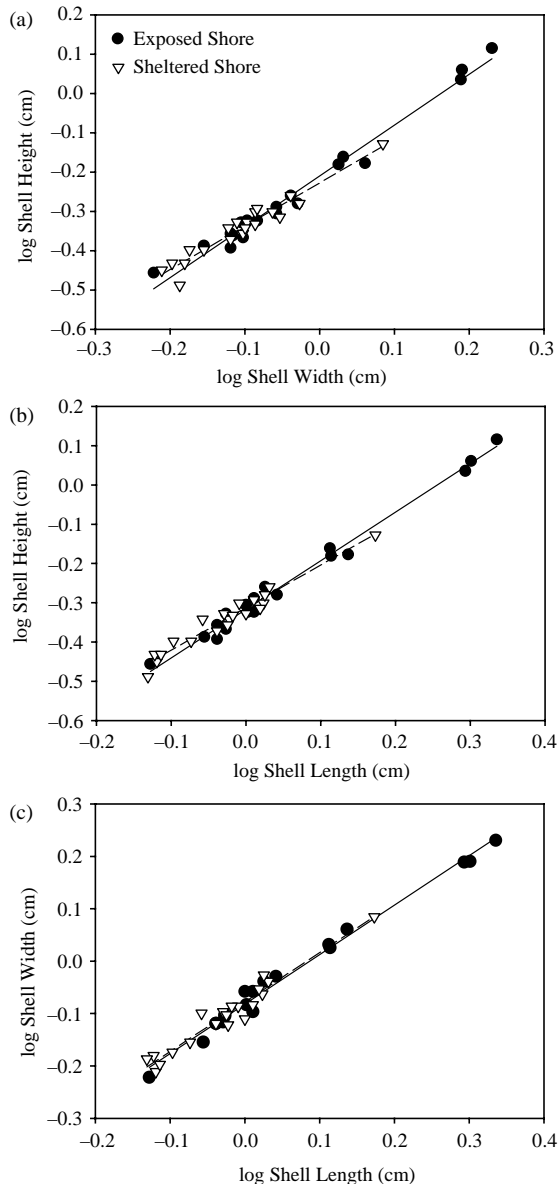


Figure 3. *Nerita atramentosa*. Log-log plots of (a) shell height versus shell width, (b) shell height versus shell length and (c) shell width versus shell length for snails from the exposed (solid circle, solid line) and sheltered (open inverse triangle, dotted line) shores. Lines represent least-squared regressions for data from each site. Within plots (a) and (b) the slopes of the lines are significantly different, being greater for the wave-exposed population (see Table I for linear regression and ANCOVA statistics).

is independent of foot area, as expected (Trussell et al. 1993). The dislodgement force for a snail of a given foot area did not differ significantly between shores for either species (ANCOVA, Table I; Figure 5). The mean dislodgement force of *Austrocochlea constricta* was significantly lower on the exposed (0.16 N) than sheltered shore (0.41 N; ANOVA: $F_{(1,36)} = 21.01$, $P < 0.001$), reflecting the larger foot area of this species at the latter site. However, the force required to dislodge *Nerita atramentosa* was not

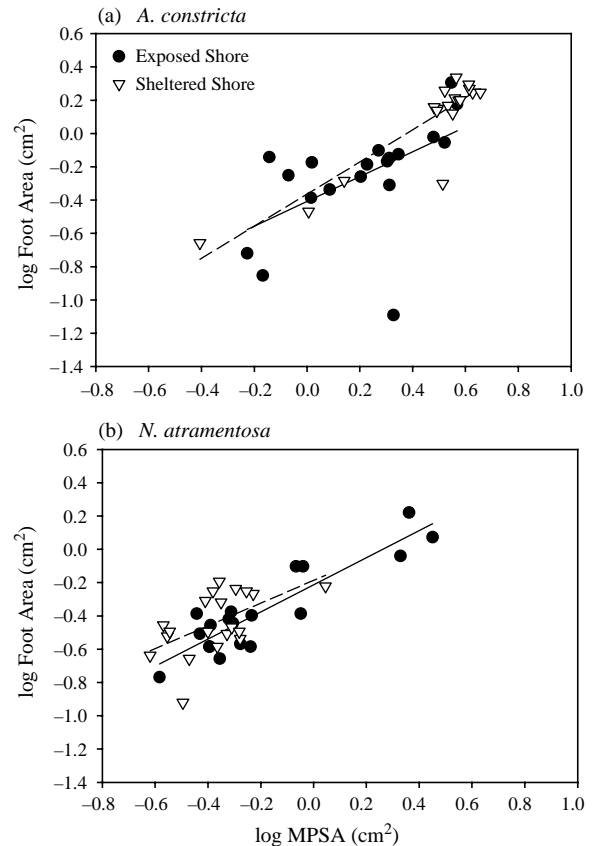


Figure 4. Log-log plots of foot area as a function of shell maximum projected surface area (MPSA) for (a) *Austrocochlea constricta* and (b) *Nerita atramentosa* from the exposed (solid circle, solid line) and sheltered (open inverse triangle, dotted line) shores. Lines represent least-squared regressions for data from each site. Within each plot neither the slopes nor the elevation of the lines differs significantly (see Table I for linear regression and ANCOVA statistics).

significantly different between shores (ANOVA: $F_{(1,37)} = 1.73$, $P > 0.05$). The mean foot tenacity at the two sites was statistically the same for both *Austrocochlea constricta* (exposed = 0.29 ± 0.09 Nm^{-2} ; sheltered = 0.32 ± 0.04 Nm^{-2} ; ANOVA: $F_{(1,36)} = 0.04$, $P > 0.05$) and *Nerita atramentosa* (exposed = 0.31 ± 0.06 Nm^{-2} ; sheltered = 0.23 ± 0.05 Nm^{-2} ; ANOVA: $F_{(1,37)} = 0.941$, $P > 0.05$).

Size-frequency distributions

The size structure of snail populations differed between shores for both species. On the sheltered shore, *Austrocochlea constricta* appeared to be able to approach their asymptotic growth limit, whereas this species exhibited a more normal distribution on the exposed shore (Figure 6a). Consistent with the previous results, large size classes of *Austrocochlea constricta* (length 2.0–2.5 cm) were dominant on the sheltered shore but relatively underrepresented at the exposed site. Consequently, this species was

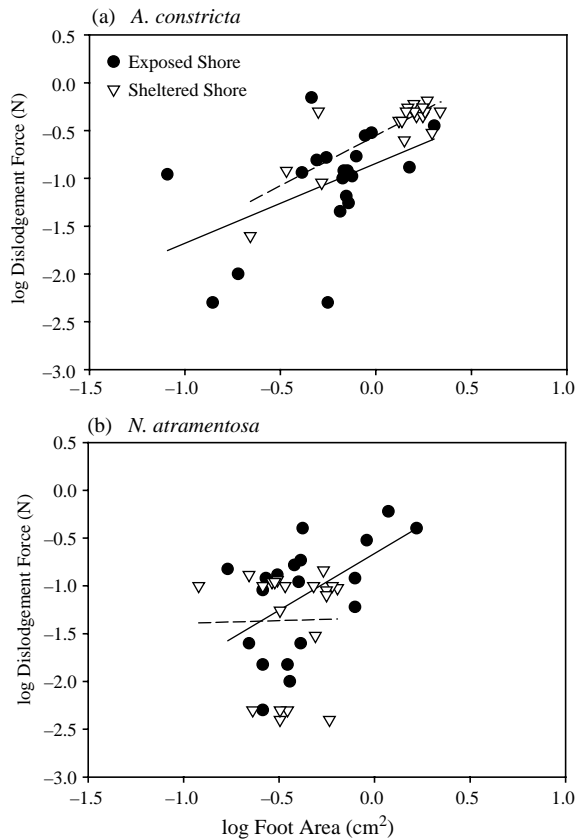


Figure 5. Log–log plots of dislodgement force as a function of foot area for (a) *Austrocochlea constricta* and (b) *Nerita atramentosa* from the exposed (solid circle, solid line) and sheltered (open inverse triangle, dotted line) shores. Lines represent least-squared regressions for data from each site. Within each plot neither the slopes nor the elevation of the lines differs significantly (see Table I for linear regression and ANCOVA statistics).

significantly longer on the sheltered (mean = 2.11 cm) than exposed shore (mean = 1.84 cm; ANOVA: $F_{(1,158)} = 28.54$, $P < 0.001$; Figure 6a). As before, the reverse was true for *Nerita atramentosa*, which were longer on the exposed (mean = 1.53 cm) than sheltered shore (mean = 1.06 cm; ANOVA: $F_{(1,158)} = 96.07$, $P < 0.001$; Figure 6b). Snails of both species of length 1.3–1.8 cm were comparatively rare on the sheltered shore (Figure 6).

Discussion

The ability of intertidal gastropods to survive on wave-exposed coasts is partially determined by their ability to resist dislodgement by breaking waves (Trussell et al. 1993). Snails on exposed shores typically exhibit traits that reduce the probability of dislodgement, potentially reflecting selection favouring well-adapted snail phenotypes. However, this pattern can also result from the ability of gastropods to adapt to high wave action through phenotypic plasticity or genetic polymorphism.

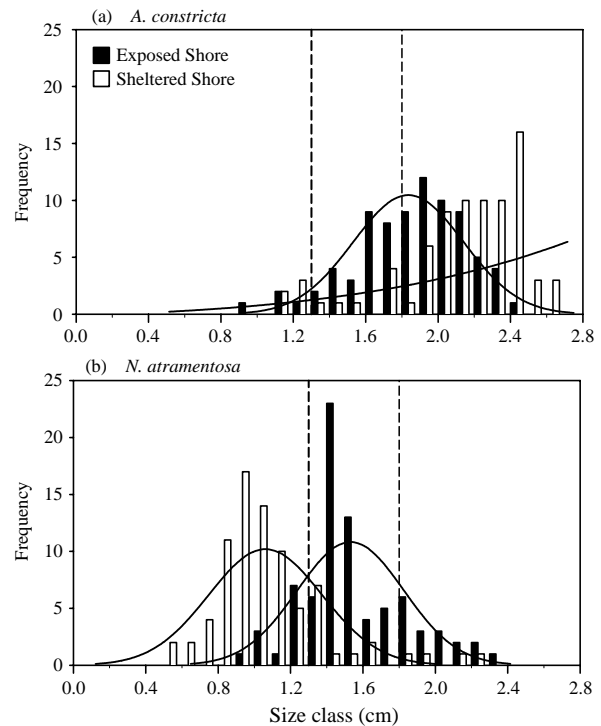


Figure 6. Size–frequency histograms of (a) *Austrocochlea constricta* and (b) *Nerita atramentosa* shell lengths from the exposed and sheltered shores ($n = 80$ for each population). Reference lines are drawn to highlight the shell length range of 1.3–1.8 cm, because snails of both species in this size range are comparatively rare on the sheltered shore. *Austrocochlea constricta* were significantly longer on the sheltered shore, but the reverse was true for *Nerita atramentosa* (see Results for statistics).

Both *Austrocochlea constricta* and *Nerita atramentosa* possess a planktonic larval stage. This dispersal mechanism should have prevented the evolution of genetic polymorphism over the small spatial scales pertinent to this study. However, the life histories and habitat of the two species might be expected to have favoured the evolution of adaptive phenotypic plasticity. Indeed, phenotypic modulation by hydrodynamic forces is known to allow gastropods developing on exposed shores to increase their ability to resist dislodgement relative to sheltered conspecifics (Etter 1988; Trussell 1997a).

Intertidal molluscs on wave-exposed shores are typically smaller and squatter than those at sheltered sites (Etter 1988; Sundberg 1988; Trussell et al. 1993; Trussell 1997a). In this study, *Austrocochlea constricta* shell size but not shape differed between the exposed and sheltered shore: this species achieved a greater mean size at the sheltered site. Atypically, *Nerita atramentosa* on the exposed shore had larger shells that actually became taller with increasing size (Table II).

Previously, studies using a combination of reciprocal transplant and laboratory flume experiments have shown that high flow environments induce

increases in the size-specific foot area of snails (Etter 1988; Trussell 1997a). However, there is no evidence to suggest that either *Austrocochlea constricta* or *Nerita atramentosa* is able to improve its ability to resist dislodgement through plastic changes in size-specific foot area (Table II). By the same token, the results are not indicative of any direct selection operating on the exposed shore against snails with smaller size-specific foot areas.

Foot tenacity did not differ between shores for either snail. Branch & Marsh (1978) reported that limpet tenacity increased with stronger wave action and Trussell et al. (1993) found the reverse in the snail *Littorina obtusata*, but these were atypical results. As in this study, tenacity has more commonly been reported to be constant across geographical gradients in wave exposure (Grenon & Walker 1981; Etter 1988; Trussell 1997a).

Dislodgement by hydrodynamic forces at exposed sites and predation by crabs at sheltered sites are generally believed to be the primary determinants of intertidal snail phenotypes (Menge 1978; Palmer 1985; Trussell 1997a,b). In this study, size–frequency distributions indicate that a predator consuming snails within the 1.3–1.8 cm length range regulates sheltered shore populations of both snail species (Figure 6). Chilton & Bull (1984) reported that the common shore crab, *Ozius truncatus*, preferentially consumes *Nerita atramentosa* of height 0.4–1.1 cm, which, from data obtained in this study, approximately translates into a 0.7–2.0 cm length range. This crab may, therefore, be an important snail predator at the sheltered site. In any case, the presence of a sheltered shore predator is likely to explain some of the results presented.

Nerita atramentosa at the exposed but not sheltered site became taller during ontogeny. This is unusual because we might have expected the reverse if the strength of hydrodynamic forces is an important factor in determining shell shape. Potentially, predator cues at the sheltered site have suppressed *Nerita atramentosa* growth rates by reducing grazing rates (Appleton & Palmer 1988; Palmer 1990) and resulted in squatter shells. However, slower growth tends to lead to taller shapes in other intertidal gastropods (Kemp & Bertness 1984; Vermeij 1993; Parsons 1997a). Because foraging behaviour reduces a snail's ability to adhere to the substratum (Miller 1974), intertidal gastropods may cease feeding in periods of high wave action and take refuge in microhabitats (Emson & Faller-Fritsch 1976; Raffaelli & Hughes 1978). Therefore, the between-shore difference in *Nerita atramentosa* shell shape may reflect slower growth rates on the exposed shore resulting from reduced food availability and/or

feeding efficiency at this site (Menge 1978; Denny et al. 1985; Brown & Quinn 1988).

Sheltered shore conditions appear to allow those *Austrocochlea constricta* that have achieved a size refuge from predation to approach their asymptotic size limit (Figure 6a). However, large size classes of this species were comparatively rare at the exposed site. *Nerita atramentosa* achieved greater size at the exposed site, which is probably due to a release from predation pressure (Figure 6b). Nevertheless, even exposed shore *Nerita atramentosa* were much smaller than the documented maximum size of this species (Edgar 1997). For both gastropods, foot area and shell MPSA scale isometrically, so drag forces should not directly place physical limits on their size (Koehl 1996). However, larger shells can limit the exploitation of sheltered microhabitats and render unavailable the reduction in experienced drag forces afforded by this behaviour (Raffaelli & Hughes 1978; Brown & Quinn 1988). Therefore, the small size of both species at the exposed site might reflect direct selection against larger individuals with reduced access to microhabitat refuges (Trussell 1997b).

Apart from between-shore differences in shell size, however, populations from the two habitats exhibited a surprising phenotypic homogeneity. There is no evidence to suggest that either *Austrocochlea constricta* or *Nerita atramentosa* has expressed adaptive developmental responses to stronger wave forces on the exposed shore. Before considering the implications of this result, it should first be noted that such plasticity may have been overlooked by this population-level study for several reasons.

First, adaptive plastic responses to high wave exposure may have been masked by other factors. In particular, snail phenotypes on the sheltered shore may primarily be determined by predation pressure. For example, high predator densities typically induce the expression of defensive phenotypes in intertidal molluscs (Palmer 1985, 1990; Appleton & Palmer 1988; Trussell 1996; Leonard et al. 1999; Trussell & Smith 2000). Second, this study was conducted during the summer and it has been suggested that habitat-specific differences in those snail traits affecting dislodgement risk may be more apparent in stormy seasons (Trussell 1997a). On the other hand, plastic adaptation to high wave forces is usually irreversible, probably because wave energies are temporally very unpredictable and loss of adaptive traits is an extremely risky strategy (Palumbi 1984; Etter 1988). Third, the measured difference in maximum wave forces between the exposed and sheltered shores (Figure 2) may not have been great enough to reveal an induced response. This is unlikely, however, because phenotypic modulation

by hydrodynamic forces has been shown to produce continuous responses to wave exposure (Etter 1988; Trussell 1997a).

At first glance, we might be surprised if neither *Austrocochlea constricta* nor *Nerita atramentosa* has utilized developmental responses to afford increased tolerance of conditions at the exposed site. For such intertidal snails, the physical and biological nature of the shore upon which a larva recruits is likely to be unpredictable. However, maximum water velocities experienced during ontogeny should be a good indicator of future conditions because gastropods are relatively territorial (Trussell 1997b). Given the likelihood that snail phenotypes that reduce drag and increase adhesive strength will incur energetic and reproductive costs, we might expect *Austrocochlea constricta* and *Nerita atramentosa* to leave the choice of phenotype to until after the adult habitat has been reached (Stearns 1989). However, this prediction is less plausible when the unusual habitat of these animals is taken into account.

With the exception of some anomalous geography (e.g. Spencer Gulf, Gulf St. Vincent, Port Phillip Bay), the southern Australian shoreline consists of a long stretch of extremely homogenous and wave-exposed coast (El-Sabh et al. 1997). In all probability, gastropod larvae will settle on a shore that is subject to high wave energies. The evolution of adaptive phenotypic plasticity, however, requires that the environment is sufficiently unpredictable over the spatial (and/or temporal) scales of individuals (Newman 1992). Therefore, we propose that the environment inhabited by *Austrocochlea constricta* and *Nerita atramentosa* is not sufficiently heterogeneous to have favoured the evolution of adaptive developmental responses to wave exposure. Instead, these species may employ a generalist strategy and constitutively express traits that reduce the risk of dislodgement by waves.

In conclusion, this was the first study to investigate the effects of spatial variation in wave exposure on the phenotypes expressed by the intertidal snails *Austrocochlea constricta* and *Nerita atramentosa*. The relatively small size of both species at the exposed site may reflect direct selection against larger snails that are unable to make effective use of microhabitat refuges. However, snails from the exposed and sheltered shores were remarkably similar in all other respects considered. Potentially, both species have evolved fixed phenotypes that are pre-adapted to high wave action. Future research should determine if this is indeed the case by: (1) performing common garden transplant experiments with juvenile snails; and (2) comparing phenotypic expression between snail populations along the exposed southern Aus-

tralian coastline and those within the more sheltered gulf systems.

Acknowledgements

We wish to thank Damien Allen and Michael Eliades for assistance in conducting this study during a FUSA Marine Biology Field Course, Jon Havenhand, Steve Hall and two anonymous reviewers for insightful comments regarding this work, Dick Edyvean for help with the construction of maximum velocity recorders and Lynne Giles for valuable statistical advice. Funding for this project was provided by FUSA Research Council to AJP.

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