Defense in shallow-water invertebrates at oceanic islands vs. the mainland coast

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ABSTRACT: Islands are often considered natural laboratories and thus excellent models for testing theories on adaptive radiation. To date, most studies have focused on terrestrial ecosystems. In a comparative study between island populations and their mainland counterparts, Vermeij (2004, Frontiers of biogeography, p 239–254), using published data, argued that shallow-water marine shelled molluscs are better defended against predation along continents than on oceanic islands, possibly due to a lower predation pressure on islands. Here we evaluate this hypothesis, using shallow-water marine gastropods from the Azores and the Portuguese mainland as models (the island species *Columbella adansoni* and the mainland species *C. rustica*, and populations of *Stramonita haemastoma* from both study areas). Pleistocene *S. haemastoma* fossils from the Azores were also analyzed. Specimens were measured for defense-related shell characteristics and compared (island vs. mainland populations) using principal component analysis and Mann-Whitney tests. The results revealed that Azorean *C. adansoni* possess significantly thicker and wider shells with a narrower aperture than mainland *C. rustica*, which present a lighter shell and a higher spire. Comparisons of island and mainland *S. haemastoma* indicate that the Azorean population is lighter, with a wider aperture, thicker lip, and lower spire. The comparison of Azorean *S. haemastoma* fossils and extant specimens showed significantly narrower apertures and thicker lips in Pleistocene shells. Despite some evidence supporting the arguments used by Vermeij, our analysis failed to conclusively support this hypothesis as a whole.

KEY WORDS: Evolution on islands · Predatory impact · Island biogeography · *Columbella adansoni* · *Columbella rustica* · *Stramonita haemastoma*

INTRODUCTION

Since Darwin's masterpiece was published (Darwin 1859), islands — and particularly oceanic islands (those not connected to the mainland by continental slopes) — have been considered natural laboratories (Whittaker & Fernández-Palacios 2007) and are often used as models to test and develop evolutionary theory (e.g. MacArthur & Wilson 1967, Grant & Grant 2002, Emerson & Kolm 2005, Hubbell 2006, Whittaker et al. 2008). Evolutionary biologists have looked to islands as models for adaptive radiation, but have often focused on terrestrial organisms (e.g. Jordan et al. 2003, Grant & Grant 2006, Losos & Ricklefs 2009). As pointed out by Vermeij (2004, p. 239), islands are

> tidy places for seashore life as well. The water barriers that isolate islands from other lands may work differently for marine species than they do for terrestrial ones but they nonetheless prevent dispersal of shallow-water marine bottom-dwellers to islands, and render marine island ecosystems partially isolated from their counterparts around larger land masses.

In this context, Vermeij believes that the major difference between terrestrial and marine biota lies in the abundance of high-level predators, which in the sea are little constrained by dispersal. Vermeij formulates a hypothesis, which we will call 'Vermeij's hypothesis', wherein marine shallow-water organisms possess fewer defenses against predators around oceanic islands than along mainland coasts, probably due to lower predatory pressure.

This hypothesis was based on the comparison of structural shell characteristics such as length and projection of the shell spire, thickness of the shell, and size and degree of occlusion of the shell aperture. Vermeij noted that, in general, shallow-water molluscs from oceanic islands had: (1) a higher and more protruding spire, (2) a thinner shell, and (3) a larger and less occluded shell aperture compared to their counterparts on the mainland. These results were interpreted as a reduced defense capacity of island inhabitants, which he suggested to be caused by 'a reduced selection due to predators breaking or entering gastropod shells' (Vermeij 2004) of island species when compared with mainland species. Vermeij (2004) presented 2 factors which support this hypothesis: (1) the low frequencies of repaired injuries on island species, which suggest a lower selection pressure from shell-breaking predators; and (2) the low frequency of gastropod species with labral tooth (a feature which is thought to speed up predation on hard-shelled animals) on islands.

Nonetheless, as Vermeij himself wrote, those were preliminary results and 'systematic studies remain to be done'. In fact, the data was collected by different investigators, without the specific purpose of comparing the defenses of island and mainland species, and was mainly referring to South Atlantic and Pacific species.

In the present study, we compared the structural defenses of island and mainland forms of the species *Stramonita haemastoma* (Linnaeus, 1758), and 2 species of the genus *Columbella*, existing in the Azores and the Portuguese mainland (Northeast Atlantic).

Even though there is no clear consensus, *Stramonita haemastoma* can be considered a single taxon with an amphi-Atlantic distribution and a highly variable form (Vermeij 2001, Harding & Harasewych 2007, Claremont et al. 2011). This predatory whelk with planktonic larvae (Scheltema 1971) preferentially inhabits rocky shores (Rilov et al. 2001, Ramirez et al. 2009), where it preys on animals such as oysters, barnacles, gastropods, and bivalves (Rilov et al. 2004, Lopez et al. 2010).

The genus *Columbella* has a wide distribution in the East Atlantic region, from the West African coast to the Portuguese coast, and is also found in the Macaronesian archipelagos (Azores, Madeira, Canary Islands, and Cape Verde) (Moolenbeek & Hoenselaar 1991, Oliverio 1995). The existence of 2 different species in the East Atlantic is recognized: *C. rustica* (Linnaeus, 1758) and *C. adansoni* Menke, 1853 (Moolenbeek & Hoenselaar 1991). The main characteristic that distinguishes both species is the protoconch, which is multispiral in *C. adansoni* (indicating a planktotrophic life stage) and paucispiral in *C. rustica* (indicating direct development) (Moolenbeek & Hoenselaar 1991). The *Columbella* populations between the Portuguese mainland coast and Senegal are thought to belong to the species *C. rustica*, whereas the Macaronesian populations (Moolenbeek & Hoenselaar 1991, Oliverio 1995, Segers et al. 2009), and the populations living south of Senegal (Oliverio 1995), are attributed to the species *C. adansoni*. These herbivorous species are commonly found in shallow waters, under rocks or in their crevices (Oliverio 1995).

Using both pairs of gastropod species as models, we tested Vermeij's hypothesis, by performing a systematic study comparing the structural defenses of island and mainland species.

MATERIALS AND METHODS

Study sites

Since a comparison between species from an oceanic island and from mainland waters was required, the Azores and the Portuguese mainland were selected. Both areas are located at similar latitudes and subject to similar environmental conditions.

Samples

Adult specimens were gathered by us or with the contribution of several shell-collectors. Island specimens (77 *Columbella adansoni* and 89 *Stramonita haemastoma* shells) were collected on São Miguel Island (Azores, Portugal), while their mainland counterparts (100 *C. rustica* and 79 *S. haemastoma* shells) were obtained in the Algarve (Portugal). The Pleistocene fossil record of *S. haemastoma* from Santa Maria Island (Azores, Portugal) was also studied (36 specimens, although some were too damaged to allow the measurement of all variables).

Measurements

Using a Vernier caliper, shells were measured to the nearest 0.05 mm for their total length, width, size of the spire (distance between the apex and the suture [in *Columbella* spp.] or the shoulder [in *Stramonita haemastoma*], 180 degrees from the aperture), size of the aperture, and shell thickness at the lip (Fig. 1), characteristics which are usually associated with defense. With the exception of the fossilized samples, shell weight was also measured using a scale with a precision of 0.001 g.
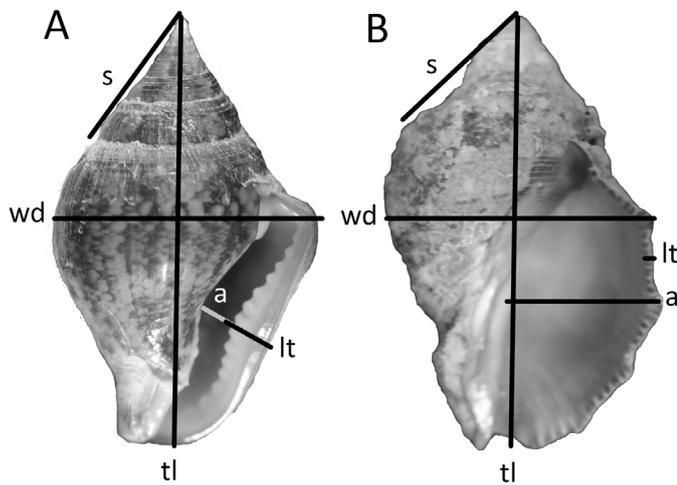

Fig. 1. (A) *Columbella* spp. and (B) *Stramonita haemastoma*. Measurement of total length (tl), width (wd), size of the spire (s), size of the aperture (a), and lip thickness (lt)
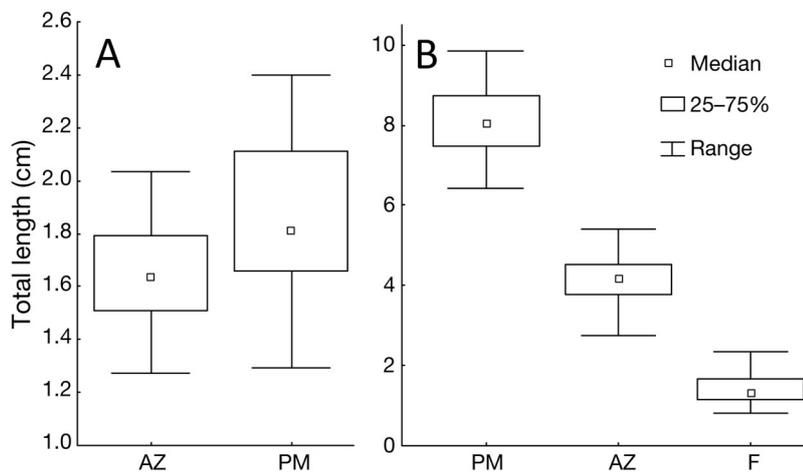

Fig. 2. (A) *Columbella* spp. and (B) *Stramonita haemastoma.* Boxplots for total length of samples from the Portuguese mainland (PM) and the Azores (AZ) and *S. haemastoma* Azorean fossil records (F). The box (25–75%) is the interquartile range

Statistical analysis

Parametric approaches were excluded, since neither the original data nor the data transformations met the required assumptions.

To analyze the possibility of allometric growth, measured variables were tested for correlation with total length, using Spearman's correlation test (p < 0.05). In order to compare individuals of different sizes, variables correlated with total length were divided by it.

Comparisons were made between mainland *Columbella rustica* and island *C. adansoni* and between mainland and island *Stramonita haemastoma*. The Azorean fossil record of *S. haemastoma* was also compared with extant Azorean specimens.

Comparison through multivariate analysis was performed using principal component analysis (PCA), which was based on the correlation matrix of the measurements of shell characteristics (corrected for total length), since the variable weight was measured on a different scale.

Variables were compared applying Mann-Whitney tests (p < 0.05) and all statistical analyses were performed using Statistica 7.0 (StatSoft 2004).

RESULTS

Measurements of both *Stramonita haemastoma* and *Columbella* spp. revealed considerable differences in total length between the compared populations (Fig. 2). For both pairs of species, samples from continental Portugal (*S. haemastoma*: 8.125 ± 0.783 cm [mean ± SD]; *C. rustica*: 1.891 ± 0.274 cm) were longer than their Azorean counterparts (*S. haemastoma*: 4.176 ± 0.571 cm; *C. adansoni*: 1.642 ± 0.183 cm). Spearman's correlation test (p < 0.05) revealed that, for both *C. adansoni* and *C. rustica*, all measured variables were significantly correlated with total length (Table 1). Defensive characteristics of Portuguese mainland *S. haemastoma* shells, along with the Azorean fossil record, also presented significant correlations with total length (Table 1). Extant Azorean *S. haemastoma* samples, however, did not display a significant correlation between total length and lip thickness (Table 1). In view of this and the large

Table 1. *Columbella* spp. and *Stramonita haemastoma*. Spearman's correlation test (p < 0.05) between total length and the other characteristics measured. Different sample sizes for Azorean fossils are related to damage of some shells, which did not allow measurement of all variables. ns: not significant; nd: not determined

| | *Columbella* spp. | | —— *S. haemastoma* —— | | |
| | Azores | Portuguese mainland | Azores | Portuguese mainland | Azorean fossils |
	(n = 77)	(n = 100)	(n = 89)	(n = 79)	
Width	0.925	0.911	0.948	0.891	0.976 (n = 30)
Lip thickness	0.557	0.454	0.163 (ns)	0.338	0.684 (n = 23)
Aperture	0.662	0.962	0.935	0.902	0.937 (n = 22)
Spire	0.798	0.879	0.934	0.848	0.885 (n = 36)
Weight	0.892	0.803	0.859	0.817	nd

difference in size between island and mainland specimens, we also corrected lip thickness for total length in order to make it comparable.

PCA

The results of the PCA indicate that, when corrected for total length, the shell of Azorean *Columbella adansoni* has a thicker lip and a narrower aperture than that of the Portuguese mainland counterpart *C. rustica* (Fig. 3). Although there is some overlap between samples, the PCA seems to also indicate a lower spire and a heavier shell in the Azorean specimens.

The analysis of extant *Stramonita haemastoma* showed clear differences between both populations (Fig. 4). The results reveal a thicker lip and a wider aperture in the Azorean *S. haemastoma*, whereas their mainland counterparts are heavier and possess a higher spire.

Comparison of characteristics

The comparison of characteristics using Mann-Whitney's test (Table 2) revealed that the Azorean *Columbella adansoni* shells are wider ($Z = 6.436$; $p < 0.05$) and present a thicker lip ($Z = 9.657$; $p < 0.05$) and a narrower shell aperture ($Z = 6.001$; $p < 0.05$) than mainland Portuguese *C. rustica* shells. No significant differences were found when comparing weight ($Z = 1.746$; $p > 0.05$) or size of the spire ($Z = -1.670$; $p > 0.05$).

For *Stramonita haemastoma*, Azorean shells are lighter ($Z = -11.712$; $p < 0.05$), have a lower spire ($Z = -10.870$; $p < 0.05$), a wider aperture ($Z = 5.356$; $p < 0.05$), and a thicker lip ($Z = 8.305$; $p < 0.05$) than their counterparts from the Portuguese mainland. No significant difference in width was detected ($Z = 1.502$; $p > 0.05$).

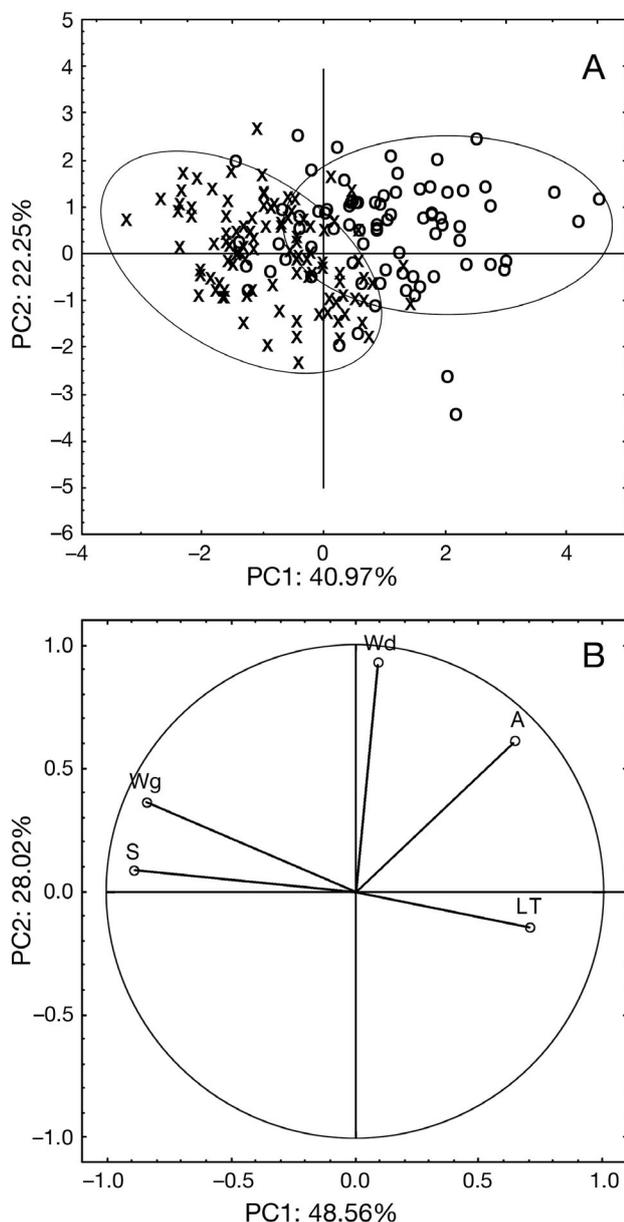The comparison of the *Stramonita haemastoma* fossil record from Santa Maria Island with extant

Fig. 3. *Columbella* spp. Principal component analysis for samples from the Azores and Portuguese mainland. PC1 and PC2 explain 40.97 and 22.25% of the total variance, respectively. (A) Score plot (○: Azores; ×: Portuguese mainland). (B) Loading plot. Variables considered are: width (Wd), lip thickness (LT), spire (S), aperture (A) and weight (Wg)
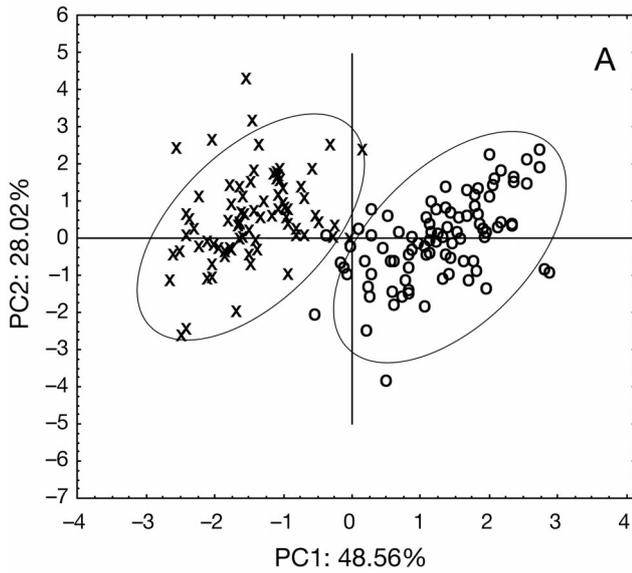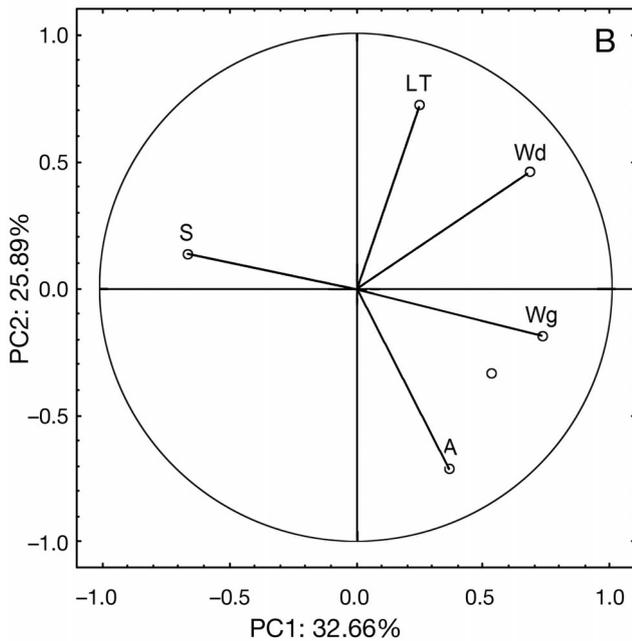
Fig. 4. *Stramonita haemastoma*. Principal component analysis for samples from the Azores and Portuguese mainland. PC1 and PC2 explain 48.56 and 28.02% of the total variance, respectively. (A) Score plot (O: Azores; ×: Portuguese mainland). (B) Loading plot. Variables considered are: width (Wd), lip thickness (LT), spire (S), aperture (A) and weight (Wg)

Azorean shells indicates that Pleistocene specimens had a thicker lip ($Z = 3.785$; $p < 0.05$) and a narrower aperture ($Z = -6.754$; $p < 0.05$). The comparisons of shell width ($Z = 0.532$; $p > 0.05$) and size of the spire ($Z = 0.453$; $p > 0.05$) did not reveal significant differences.

DISCUSSION

The hypothesis that marine shallow-water shelled molluscs possess better defenses against predators on mainland coasts than oceanic islands (Vermeij 2004) is not wholly supported by our data, as our results did not reveal better protected shells in mainland specimens.

Assuming that the variables considered in the present study reflect shell protection, the results obtained through the comparison of island and continental populations of *Columbella* spp. showed a better protection of the Azorean specimens. The shells were wider, with a thicker lip, indicating more robustness and resistance, putatively useful to prevent damage from shell-breaking predators (e.g. ballan wrasse; Figueiredo et al. 2005) or drilling predators (e.g. the muricid gastropods from the genus *Ocenebra*) (Vermeij 1978). In addition, the narrower aperture found on *C. adansoni* when compared to that of *C. rustica* suggests that putative predators such as octopus (Mather & Odor 1991) would have more difficulty in entering the shell of the island specimens (Vermeij 1978). To our knowledge, *C. rustica* and *C. adansoni* share the same ecological niche, living under boulders (Oliverio 1995), where they are less exposed to wave action. Thus, differences in shell robustness of Azorean and mainland Portuguese *Columbella* spp. should not derive from abiotic factors. Nevertheless, we cannot discard the fact that we are comparing 2 different species and that, despite their phylogenetic proximity, the differences

Table 2. *Columbela* spp. and *Stramonita haemastoma*. Comparison of defense-related shell characteristics using the Mann-Whitney test ($p < 0.05$). nd: not determined, ns: no significant differences

	Columbella spp.		*S. haemastoma*			
	Azores	Portuguese mainland	Azores	Portuguese mainland	Azores fossils	Azores extants
Wider	✓			ns		ns
Lower spire		ns	✓			ns
Narrower aperture	✓			✓	✓	
Thicker lip	✓		✓		✓	
Heavier		ns			✓	nd

might be due to species-specific characteristics rather than to selective pressure.

The results of the comparison between Azorean *Stramonita haemastoma* and its mainland counterpart are ambivalent and require careful attention. According to our data, Azorean muricids tend to have a lower spire and a thicker lip, while mainland specimens are heavier with a narrower aperture. The higher spire and thinner lip of mainland *S. haemastoma* could make this specimen a preferential target for some shell-breaking predators (Zipser & Vermeij 1978), as the shell is more conspicuous and easier to peel or crush (Vermeij 1978), rendering it less defended than its island counterpart. Even so, the heavier shell of mainland specimens might contribute to a more resistant shell and could be a better measurement for shell robustness than lip thickness in this case, as the lip is the thinnest part of the shell. In addition, the size of the aperture might not be such a relevant feature to *S. haemastoma* defense, since it is usually very large. In fact, as this species inhabits rocky, wave-exposed habitats, differences in size of the aperture may be related to differences in wave action and consequent risk of dislodgment (Rilov et al. 2004). A wider aperture allows a broader foot area and, as a result, a stronger adhesion to the substrate (Trussell et al. 1993, Trussell 1997). Therefore, the broader aperture on islander *S. haemastoma* might be explained by an environmental factor — higher wave action — rather than by lower predatory pressure. These environmental factors might also influence the shorter spire of the island *S. haemastoma*, which reduces the risk of dislodgement by making the shell squatter and, consequently, reducing the exposed area (Rilov et al. 2004). In the well-known littorinid gastropods, the sheltered ecotype (more exposed to predation) has a taller spire than the wave-exposed ecotype (less exposed to predation) (see Johannesson 2003), which seems to support the importance of environmental factors on the size of the spire. Despite all these constraints, the results do not clearly reveal a more protected shell in mainland *S. haemastoma*.

Size matters

Our results were obtained using data corrected for total length. Notwithstanding this, there was an obvious size difference between samples, with mainland specimens of both species presenting larger sizes than their island counterparts. Differences in size between animals from oceanic islands and continents has been a highly discussed subject (e.g. Foster 1964,

Case 1978, Meiri et al. 2011). Some authors defend the existence of an island rule (sensu Van Valen 1973), wherein species that are smaller on the mainland will tend to reach larger sizes on islands, and vice versa (Lomolino 1985, 2005). Predation, among other agents, is thought to play an important role on these size shifts in insular populations (Palkovacs 2003). When dealing with terrestrial biotas, a lower predatory pressure is generally assumed on islands (e.g. Heaney 1978). Thus, phenotypes that are selected against by predation in mainland populations are more likely to occur on islands.

Several authors suggest that predators such as decapod crustaceans preferentially prey on small molluscs (Juanes 1992, Seed & Hughes 1995, Smallegange & Van der Meer 2003, Smallegange et al. 2008). Therefore, the smaller size of island populations might reflect a lower predatory pressure than what exists on the mainland, where smaller individuals are negatively selected. This fits Vermeij's hypothesis: the greater size of mainland specimens might be considered a defensive characteristic, in response to more intense predatory pressure. Notwithstanding this, the differences in size might also reflect a lower growth rate in the Azores, due to a lower productivity likely to occur in oceanic islands (Vermeij 2004).

Clues from the past

Our results showed a better protected shell in Pleistocene specimens than in extant Azorean *Stramonita haemastoma* specimens. Although this species has an amphi-Atlantic distribution, recent studies indicate that the most probable source of colonization of the Azores during the Pleistocene was from the Eastern Atlantic (Avila et al. 2009). It is possible that, arriving in an area with a lower predatory pressure (oceanic island) than the center of speciation (mainland), defense-related shell characteristics might have stopped being positively selected. Therefore, this analysis of the Azorean *S. haemastoma* Pleistocene fossils seems to support an evolutionary trend towards less-defended shells.

Insights on a hypothesis

The present work represents a systematic study supported by large samples from areas with similar macro-environmental conditions. However, our results do not allow either a generalization or refutation of Vermeij's hypothesis. Despite the obvious impact

that predator–prey relationships have on organisms' evolution, we cannot discard other variables when trying to understand its importance. Moreover, it is not possible to control all the factors that shape evolution. Besides working with large samples, comparing more populations occupying different ecological niches might be the wiser strategy to overcome such obstacles and unveil these macroevolutionary patterns.

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