



# The island rule and the evolution of body size in the deep sea

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## ABSTRACT

**Aim** Our goal is to test the generality of the island rule – a graded trend from gigantism in small-bodied species to dwarfism in large-bodied species – in the deep sea, a non-insular but potentially analogous system.

**Location** Shallow-water and deep-sea benthic habitats in the western Atlantic Ocean from the North to South Poles.

**Methods** We conducted regression analyses of body size of deep-sea gastropods species relative to their shallow-water congeners using measurements from the Malacolog ver. 3.3.3 database.

**Results** Our results indicate that, consistent with the island rule, gastropod genera with small-bodied, shallow-water species have significantly larger deep-sea representatives, while the opposite is true for genera that are large-bodied in shallow water. Bathymetric body size clines within the deep sea are also consistent with predictions based on the island rule.

**Main conclusions** Like islands, the deep sea is characterized by low absolute food availability, leading us to hypothesize that the island rule is a result of selection on body size in a resource-constrained environment. The body size of deep-sea species tends to converge on an optimal size for their particular ecological strategy and habitat.

## Keywords

**Bathymetric, depth, dwarfism, food availability, gastropods, gigantism, macroecology, Malacolog, miniaturization, resource limitation, size constraints.**

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## INTRODUCTION

Island environments produce distinctive selection pressures, including reduced predation, relaxed competition and diminished food supplies that can often yield complex evolutionary trajectories in body size (Van Valen, 1973; Angerbjorn, 1985; Clegg & Owens, 2002; Palkovacs, 2003). Typically small-bodied vertebrates exhibit gigantism on islands, while dwarfism is common in larger-bodied species (mammals, Lomolino, 2005; birds, Clegg & Owens, 2002; snakes, Boback & Guyer, 2003; turtles, Lomolino, 2005). In mammals, this pattern of body-size variation of insular populations seemed so general that Van Valen (1973) called it a 'rule' of ecology. The island rule is actually an intricate pattern encompassing not simply size extremes but rather a graded trend. This gradation implies that the relative importance of selective forces varies in a predictable manner from the smallest to the largest-sized species. Explana-

tions for these insular size shifts in vertebrates have focused on the main factors that may differ between mainland and island environments. Reduced interspecific competition on islands could lead to 'ecological release', allowing small-bodied species to gain the reproductive and starvation survival benefits of being larger, without the increased predation risk of the mainland (Lomolino, 2005). Similarly, in large-bodied species resource limitation coupled with reduced predation pressure on islands could confer higher fitness to smaller-bodied individuals because they require less energy to survive and reproduce. The resulting tendency toward insular dwarfism should be most prevalent in species requiring the most energy to maintain minimum populations sizes, i.e. the largest-bodied species (Anderson & Handley, 2002).

Here we test the island rule of body-size evolution in a non-island system, the deep sea. The current understanding of the deep sea is that much of its fauna died out in the

mid-Cenozoic Era and was replaced by shallow-water immigrants (Gage, 2004). During the period of 30–40 Ma, bottom temperatures throughout much of the deep sea decreased by up to 10 °C concurrent with an ocean-wide disoxygenation/anoxia event. The mass extinction was followed by a colonization of species from coastal sources. Hypothesized shallow-water origins include polar regions; the Mediterranean Ocean, other regions where the water column is isothermal; or multiple shallow-water areas (Wilson, 1999; Gage, 2004). The group we focus on here, Gastropoda, is proposed to have only recently (*c.* 30 Ma) immigrated to the deep sea from multiple coastal centres (Clarke, 1962). Although this recent colonization remains speculative, and some deep-sea taxa appear to be ancient with high levels of *in situ* speciation (Wilson, 1999), the predominant direction of migration for many organisms is into deeper water (Jacobs & Lindberg, 1998). We perceive this as analogous to the invasion of an island (the deep sea) from a mainland source (coastal shallow water).

The idea that the deep sea and shallow water may represent an island/mainland analogue is further supported by evidence of miniaturization and gigantism in deep-sea taxa – a pattern reminiscent of insular faunas. Numerous authors have commented on the dwarfism seen in some deep-sea taxa (Mosely, 1880; Hessler & Jumars, 1974; Thiel, 1975). The mean weight per individual can be up to an order of magnitude lower in deep-sea faunas compared with their shallow-water counterparts (Gage, 1977; Shirayama, 1984; Pfannkuche, 1985; Tietjen, 1989). The smallest ascidiacean, *Minipera pedunculata*, with a width of only 0.5 mm, is a deep-sea endemic. In contrast, other deep-sea groups exhibit gigantism (Timofeev, 2001). Examples include elongation of appendages in the pycnogonid ‘spiders’; flattening that increases the effective surface area in some isopods such as *Serolis*; and general increases in bulk in the giant isopod, *Bathynomus giganteus* and giant ostracod, *Gigantocypris agassizii*. The miniaturization of taxa is thought to be related to the drastic decrease in food availability (Thiel, 1975, 1979), whereas deep-sea gigantism is attributed to decreased predation and temperature (Timofeev, 2001).

The deep sea provides an ideal system to explore the importance of resource availability on body-size evolution. The lack of primary production in the deep sea (excluding chemosynthetic systems) results in these communities being intimately coupled to processes occurring in the pelagic zone at ecological to geological time scales (Smith, 1987; Cronin & Raymo, 1997). The structure and dynamics of deep-sea benthic communities are thus largely controlled by the magnitude and variability of organic carbon flux from the euphotic zone. This idea is reinforced by studies linking surface production to geographic gradients in abyssal species diversity (Rex, 1973; Rex *et al.*, 1993, 2000); biomass (Rowe, 1983); abundance (Rex *et al.*, 1989); migration (Bett *et al.*, 2001); reproduction (Gage & Tyler, 1991); and community metabolism (Rowe, 1996). As on islands, the deep sea is characterized by low total resource availability, resulting in decreased standing biomass (Rowe, 1983) and abundance (Rex *et al.*, 1989) compared to shallow-water systems.

Here we test whether the island rule of body size is a general rule that can be extended to non-insular systems and the extent to which this pattern may be related to food limitation. Specifically we utilize a database of gastropod sizes from the Western Atlantic Ocean to explore the pattern of size shifts from shallow to deep marine systems.

## METHODS

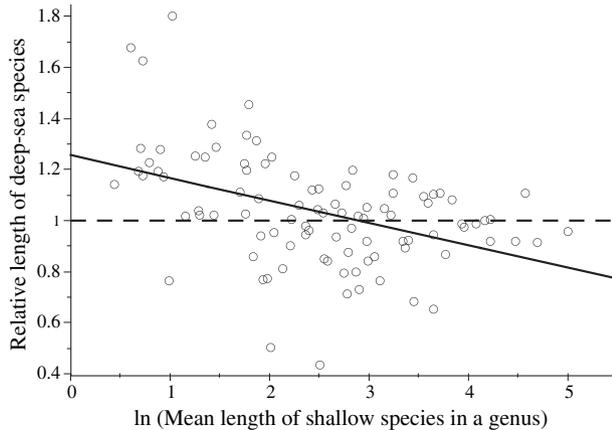
Data for these analyses are taken from Malacolog ver. 3.3.3, a database on the systematics, biogeography and diversity of western Atlantic gastropods. Complete details on the database can be found in Rosenberg (1993) or online at <http://data.acnatsci.org/wasp/>. The database includes all known marine gastropods from the North to South Poles, including their maximum reported lengths (mm) and geographic extent (latitude, longitude and depth). Here we utilize only those genera that have more than one representative species from both deep and shallow water. We define the division between shallow and deep water as 200 m, representing the average limit of the continental shelf in the Atlantic Ocean. This transition represents both a topographical and biogeographical transition that separates the two habitats (Gage & Tyler, 1991). The deep- vs. shallow-water separation of species was determined by three different methods based on mean, maximum or minimum depth of a species’ range. For minimum depth, deep-water species had to possess ranges completely within the deep sea, with shallowest depth > 200 m. For maximum depth, deep-water species had to possess some part of their range > 200 m. For mean depth, deep-water species had to have a majority of their range > 200 m. Despite the differences in defining the minimum depth of the deep sea, all three yielded nearly identical results (Table 1).

Three different methods were used to test for the island rule in deep-sea gastropods. The first two compare the mean shell lengths of congeneric deep-sea species and shallow-water species. Method 1 is regression of the ratio of mean natural log-transformed ( $\ln$ ) body length of deep species/shallow species (denoted  $S_i$  by Lomolino, 2005) as a function of  $\ln$  mean length for shallow species (Fig. 1). If the island rule holds, the slope is predicted to be negative, reflecting graded trends of gigantism in small-bodied taxa and dwarfism in large-bodied ones. Method 2 is regression of  $\ln$  mean length for deep species as a function of  $\ln$  mean length for congeneric shallow-water species (Fig. 2). The slope is predicted to be significantly < 1. Method 3 is to randomly pair deep-sea and shallow-water species without replacement from within each genus, and then compare their log-transformed lengths. This method is analogous to method 2, but utilizes species pairs instead of generic means. This analysis is similar to that of Lomolino (1985, 2005) in which island and mainland populations of the same species are compared. By randomly pairing deep and shallow congeners, genera with many species are weighted more heavily in the final regression than in our method 2, where each genus has equal weight.

**Table 1** Regression statistics for analyses comparing mean lengths for congeneric shallow-water and deep-sea gastropods

	N	Method 1: $\ln S_i = m + b(\ln \text{shallow})$				Method 2: $\ln \text{deep} = m + b(\ln \text{shallow})$			
		$R^2$	Intercept	Slope	P	$R^2$	Intercept	Slope $\pm$ SE	P
Minimum depth	82	0.14	1.13	-0.07	0.0005	0.83	0.27	$0.82 \pm 0.08$	< 0.0001
Mean depth	101	0.14	1.20	-0.07	< 0.0001	0.81	0.21	$0.89 \pm 0.08$	< 0.0001
Maximum depth	96	0.19	1.26	-0.09	< 0.0001	0.84	0.28	$0.89 \pm 0.08$	< 0.0001

All three methods used to classify species as either shallow-water or deep-sea species (see Methods) yielded similar results. In method 1, slopes less than 0.0 are consistent with the island rule: a graded trend in deep-sea species from gigantism in the smaller species to dwarfism in the larger species. In method 2, slopes < 1.0 support the island rule. P values indicate whether slopes were significantly less than their predicted values.

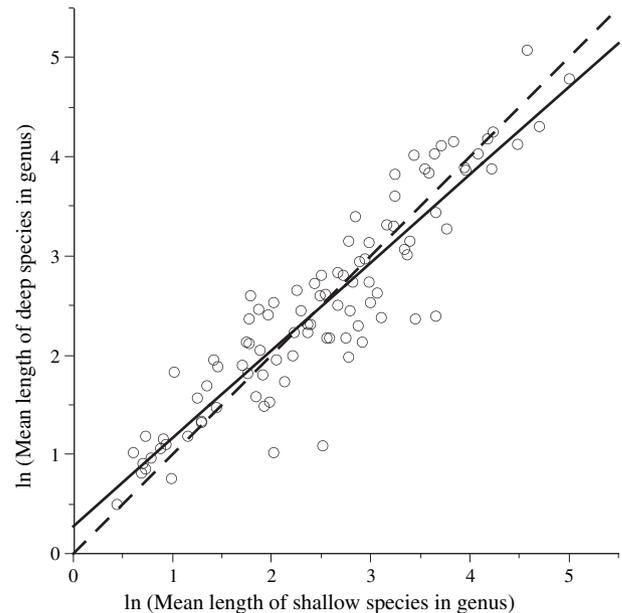


**Figure 1** Relative length ( $S_i$  = mean length of deep-sea species divided by that of congeneric shallow-water species) as a function of mean length of the shallow-water species. Regression equations are given in Table 1. Results are shown for method 1, in which species were classified as deep-sea or shallow-water species based on minimum depth. The slope of the regression was significantly less than zero, therefore the pattern was consistent with the island rule, a graded trend in the deep sea from gigantism in the smaller species to dwarfism in the larger species. All units in mm.

## RESULTS

All the analyses indicate that the island rule holds in deep-sea gastropods. Relative shell length of deep-sea compared with shallow-water congeners gives a significant negative relationship, regardless of the method used for the division of shallow- and deep-water species (Table 1; Fig. 1), and regression of deep-sea and shallow-water congeners yields a slope significantly < 1 in all cases (Table 1; Fig. 2). The results of our randomizations, method 3, again indicate that the slopes of  $\ln$  length deep vs. shallow congeneric species are significantly < 1 ( $P < 0.0001$ ). These analyses document a strongly graded trend for deep-sea gastropods from gigantism in smaller-bodied taxa to dwarfism in larger-bodied ones.

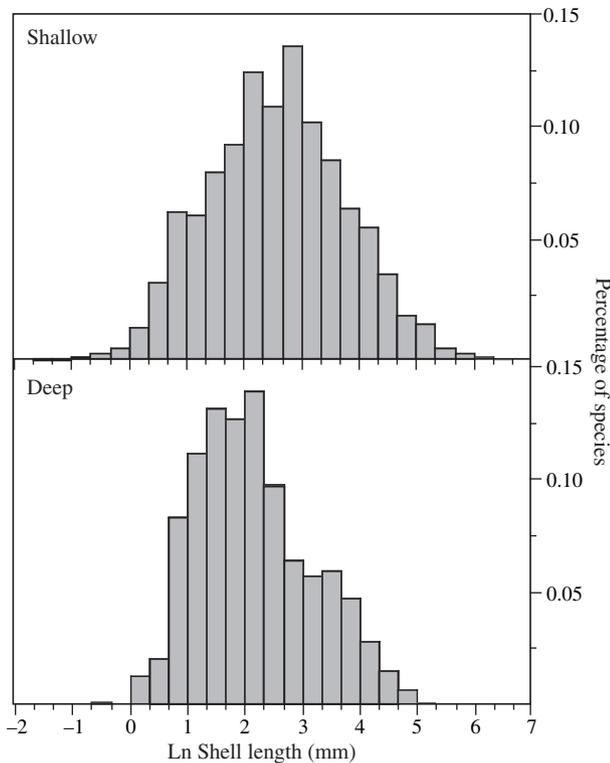
It is important to note that the size shifts reported here are in logarithmic space. Larger-bodied genera exhibit greater percentage size shifts than do smaller-bodied genera for the same  $S_i$ . For example, increases from 2 to 2.5 mm (25%) and 20 to 52 mm (160%) both yield 32% change in  $S_i$ . The overall



**Figure 2** Natural log mean length (mm) of the deep-sea species in a genus as a function of  $\ln$  mean length (mm) for the shallow-water species in a genus. Regression equations are given in Table 1. Dashed line represents a slope of 1; the solid line is the empirically fitted ordinary least squares regression. Species were classified as deep-sea or shallow-water species based on minimum depth. The slope of the regression was significantly < 1, therefore the pattern was consistent with the island rule.

effect of these size shifts, coupled with the absence of some of the largest-bodied genera of gastropods (e.g. *Busycon*, *Cassis*, *Charonia*, *Pleuroploca*, *Turbinella*), is an absolute shift of the size distribution towards smaller sizes in the deep sea (Fig. 3).

The pattern we document is robust, but there is considerable noise in the data. For example, *Bulla* (Bullidae) exhibits a substantial decrease in average size from shallow water to the deep sea (26.88–9.43 mm). The three deep-sea species of *Bulla* have not been revised in the literature since they were described over 100 years ago, and it is possible that they are not congeneric with the shallow-water species. An example potentially consistent with the island rule is provided by the large-bodied *Siratus*, a carnivorous muricid, with 10 shallow-water (73.93 mm) and four smaller deep-water species



**Figure 3** Frequency distributions of body length in all shallow-water and deep-sea gastropod species from the western Atlantic Ocean currently in the Malacolog database. Species were classified as deep-sea or shallow-water species based on minimum depth. All units in mm.

(55.60 mm) that form a tight taxonomic cluster. Similarly, small-bodied marginellids exhibit an increase in size with depth, exemplified by *Dentimargo* (4.32–4.87 mm), *Granulina* (2.02–2.47 mm) and *Volvarina* (10.5–12.76 mm), meriting further investigation. Counter to the island rule, the eulimid *Melanella* is small-bodied in shallow water (9.27 mm) but even smaller in deep water (6.15 mm). Eulimids are parasitic on echinoderms, so the size decrease may reflect something about the biology of the hosts rather than evidence against a particular hypothesis. Our data show an overall trend in accordance with the island rule, but further study may be necessary to ascertain why certain individual genera follow the rule and others do not.

## DISCUSSION

Our findings suggest that the island rule describes a general pattern of body-size evolution under a specific set of selection pressures common to both islands and the deep sea. The most probable selection pressure to account for the 'island rule' phenomenon on islands and in the deep sea is decreased total food availability, a feature common to most insular faunas (Vermeij, 2004). On islands, this energetic limitation is due to restricted habitat area, while in the deep sea the rate of resource supply is limited per unit area. Given the enormous

spatial extent of the deep sea compared with coastal/shallow regions for the world's oceans, habitat size *per se* is unlikely to drive the patterns observed. While the factors limiting resource availability differ between islands and the deep sea, the selective pressures on organisms, specifically overall lowered food availability, are similar.

Authors have proposed several hypotheses to account for island body-size trends under food (or energy) limitation. By becoming larger in the absence of former competitors, insular populations of small-bodied species can use broader resource bases (competitive release: Lomolino, 2005), and large-bodied animals may experience selection towards smaller body size due to resource limitation on islands (resource limitation: Lomolino, 2005). The relative importance of interspecific competitive release should decrease with increasing body size, while the relative importance of resource limitation should increase (Lomolino, 2005). Marquet & Taper (1998) propose that resource limitation may cause both dwarfism in large-bodied mammals and gigantism in small-bodied ones, due to changes in intraspecific competition that are related to home-range size. According to their hypothesis, medium-sized species are able to sustain higher population densities, on average, than larger or smaller species. A change in body size that reduced energetic requirements would allow more individuals per unit area and larger total population sizes, and consequently would reduce extinction risk. The island rule may also relate to optimal body size, as predicted by trade-offs in life history and metabolic constraints (Brown *et al.*, 1993; Sebens, 2002), which yield the highest  $r_{max}$ . Thus, while the overall causes of body-size changes on islands remain an open area of research, most reviews to date infer that selection for size changes on islands is due to relaxed interspecific competition and increased food/energy limitation (Heaney, 1978; Lomolino, 1985; Roth, 1992).

The rate of food supply to the deep-sea floor is a function of both primary production in the euphotic zone and the subsequent remineralization of that material as it descends through the water column (Gage & Tyler, 1991). The fraction of surface production reaching the deep sea is thought to be quite small (Falkowski *et al.*, 1998), with input decreasing as a function of increasing distance from productive nearshore waters and increasing water-column depth. Thiel (1975) invoked this food limitation as an explanation for the miniaturization of deep-sea fauna, with larger body sizes not being able to support viable population sizes, similar to the proposed mechanisms of resource limitation of Lomolino (1985). Indeed, recent work on body size in deep-sea gastropods suggests a threshold in food availability where both large body sizes and self-sustaining populations cannot be maintained simultaneously (McClain *et al.*, 2005b). However, this accounts for only one aspect of the size gradient: large-bodied species becoming smaller. There is evidence that the highest population densities are found at intermediate body sizes for deep-sea gastropods (McClain, 2004), supporting the hypothesis of Marquet & Taper (1998). However, the role of competition, required by many of the resource hypotheses,

may be questionable in soft-bottom benthic communities where many of these gastropods dwell. Experiments in shallow-water communities demonstrate that interspecific competition is weak and unlikely to be crucial in structuring these communities (Grant, 2000). However, it remains unclear whether these conclusions can be extended to intra- or interspecific competition in the deep sea. The predatory release hypothesis is unlikely to account for these patterns, because intense predation has been proposed as a mechanism to explain high species diversity in the deep sea (Dayton & Hessler, 1972), and there is direct evidence of substantial predation on deep-sea gastropods (Vale & Rex, 1988, 1989; Walker & Voight, 1994). It is likely that the increased size of the smallest-bodied species may result from selection for increases in fasting potential, foraging area, or per unit mass metabolic efficiency (McClain *et al.*, 2005b). In addition, unlike their mainland/island analogues, the size trends reported here may also be affected by the lowered temperature of the deep sea, which slows biological rates and may influence optimal body size (Sebens, 2002; Brown *et al.*, 2004).

In a resource-poor environment such as an island or the deep sea, we might also expect size clines as resource concentration decreases, and selection pressures increase, over either temporal or spatial gradients. Figures 1–3 suggest that the modal size determining if species shift to smaller or larger sizes occurs between 12.2 and 20 mm (2.5–3 natural log units). Species below this modal size would be expected to increase in size over a continuous gradient of lowered food availability, and larger-bodied species would become smaller. Depth within the deep serves as a proxy for food availability, mirroring the offshore gradient in surface production and increased remineralization. McClain *et al.* (2005b) report positive relationships between shell size and depth, or food availability, for the majority of non-abyssal deep-sea gastropods. Over 97% of the gastropods in this study have a maximum shell length below 12.2 mm (2.5 natural log units), placing them in the left part of the distribution in Fig. 3. Abyssal gastropods, exhibiting negative slopes, probably represent a unique case in which source–sink dynamics lead to sink populations dominated by smaller individuals (McClain *et al.*, 2005b; Rex *et al.*, 2005). The Eastern Atlantic gastropod, *Troschelia berniciensis*, with a length near 80 mm (4.3 natural log units) placing it on the right side of the distribution in Fig. 3, displays decreasing body size with depth and lowered food availability (Olabarria & Thurston, 2003). Given the striking congruence between the observed patterns and those expected under the island rule, these results may have the potential to resolve the preponderance of positive, negative and zero slopes (Rex & Etter, 1998; McClain *et al.*, 2005a) seen between depth and body size among deep-sea organisms. Thus the slope of the bathymetric size trend may be predictable for deep-sea taxa under energetic constraints.

The ecological and evolutionary lessons drawn from terrestrial islands are beginning to provide a framework in which to identify process in marine faunas as well (Vermeij, 2004). The extent to which the island rule of body size will clarify mechanisms of body-size evolution will be determined

only by examination of other taxa over other resource gradients and time spans. Here we demonstrate that the island rule could be more general than previously thought, potentially describing the general evolution of body size under specific constraints. Although mechanisms such as island size and predation have been hypothesized in previous studies, these are unlikely to explain the patterns seen here for deep-sea gastropods. The most parsimonious explanation for both islands and the deep sea, considering the results from previous studies and those presented here, is selection pressure for intermediate sizes under decreased food availability. Further support for this hypothesis is found in studies on bathymetric size patterns. Under decreasing energy resources, smaller-bodied species exhibit gigantism and larger-bodied species show dwarfism with depth. These findings also yield the potential to reconcile 30 years of bathymetric size studies that have reported often disparate patterns within the same taxon.

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