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C. Olabarria · M. H. Thurston

Latitudinal and bathymetric trends in body size of the deep-sea gastropod *Troschelia berniciensis* (King)

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Abstract Body size is a fundamental topic in ecology with important implications for community structure and biodiversity. Although there are numerous studies addressing patterns of geographic variation of body size in deep-sea benthos, results are conflicting. Thus geographic patterns of body size in deep-sea organisms remain poorly described. We analysed depth and latitudinal trends of body size in a species of gastropod, *Troschelia berniciensis* (King, 1846) from the eastern North Atlantic. We tested the hypotheses that (1) body size increases linearly with latitude and (2) body size increases with depth. Results partially supported the predictions. Firstly, there was a significant linear increase of body size with latitude, but this trend was weak. Secondly, body size decreased with depth. Environmental gradients that cause large-scale patterns of body-size variation in surface environments would have little effect on communities living at great depths. Latitudinal and depth clines may be produced by independent mechanisms that operate on different scales of time and space.

Introduction

Animal body size correlates strongly with many physiological, ecological, and life-history traits (e.g. McMahon and Bonner 1983; McKinney 1990; West et al. 1997). Body size can have an important influence on the organization of ecological communities and assemblages (e.g. Lawton 1990). For example, strong relationships between body size and abundance in diverse animal assemblages have been found (e.g. Peters and Raelson 1984; Blackburn and Lawton 1994; Marquet et al. 1990). Biodiversity has also been related to body-size patterns in diverse systems (Blackburn and Gaston 1994; Sieman et al. 1996; Rex and Etter 1998). Recently, many studies have been focused on the spatial distribution of body size, especially across large environmental gradients such as those associated with latitude (e.g. Cushman et al. 1993; Gaston and Blackburn 1996; Roy and Martien 2001) or depth (Rex 1979; Rex and Etter 1998; Rex et al. 1999; Clain and Rex 2000).

Several hypotheses have been proposed regarding a relationship between latitude and body size. One of the best known trends in body size is Bergmann's rule, which says that body size increases with increasing latitude (Bergmann 1947). Bergmann's rule has been tested for different organisms, but considerable debate exists about the generality of this trend and about the processes causing it (e.g. Gaston and Blackburn 1996; Partridge and Coyne 1997). Another hypothesis relating body size to latitude is based on latitudinal changes in energy availability (see Wright 1983). This hypothesis states that smaller body size occurs at high latitudes as energy availability is reduced in comparison to equatorial regions (Cushman et al. 1993). Nevertheless, most of these studies have been focused on terrestrial animals (e.g. Blackburn et al. 1990; Miller 1991; Silva and Downing 1995; Gaston and Blackburn 1996) or marine organisms inhabiting intertidal areas or shallow waters (e.g. Frank 1975; Lonsdale and Levinton 1985; Marquet et al. 1990; Roy and Martien 2001).

The mechanisms that have been proposed to explain latitudinal size trends focus largely on physiological and ecological aspects (e.g. McMahon and Bonner 1983; McKinney 1990). However, biogeographic dynamics may play an important role in shaping latitudinal size trends, especially the factors controlling the latitudinal distribution of species' geographical ranges (see for review Pyron 1999).

Size–depth relationships have been studied for various marine organisms (e.g. Smith and Hinga 1983;

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C. Olabarria (✉) · M. H. Thurston
DEEPSEAS Benthic Biology Group,
George Deacon Division for Ocean Processes,
Southampton Oceanography Centre,
Empress Dock, Southampton, SO14 3ZH, UK
E-mail: cola@soc.soton.ac.uk
Fax: +44-2380-596247

Lampitt et al. 1986; Sardá and Cartes 1993; Rex et al. 1999; Clain and Rex 2000). These studies have revealed no general patterns, showing that size–depth relationships vary considerably among taxa (see for review Rex and Etter 1998). Although different models have been proposed to explain depth–size patterns, for example, Thiel's (1975) size-structure hypothesis or Sebens' (1982) optimality theory, none seem to explain successfully the different patterns found in the deep sea (Rex and Etter 1998).

Despite the importance of body size for the life history of an organism, the factors that influence body size over evolutionary and short-term time scales are still poorly known (Peters 1983). Molluscs form an ideal test assemblage for many hypotheses of body size and its variation along environmental gradients because (1) they are diverse and constitute the third most dominant group of animals of the macrofauna in the deep sea (Gage and Tyler 1999); (2) they occupy a three-dimensional habitat with both horizontal and vertical heterogeneity; and (3) their shells record the life history of each individual and are not subject to changes in shape due to preservation methods (Clain and Rex 2000).

In this study, we present an analysis of relationships between size and depth and size and latitude for a common species of deep-sea snail, *Troschelia berniciensis* (King, 1846). This relatively large morphologically variable species (length up to 177.8 mm; personal observation) belonging to the family Buccinidae is distributed in the north-eastern Atlantic from 56°01′N, 32°42′W to north-west Norway and southwards to 25°N at depths of 90–2,700 m (Bouchet and Warén 1985). Despite being a widespread species, its ecology and biology remain poorly known.

Here we test the hypotheses that (1) body size increases linearly with latitude as demonstrated for some marine snails (Frank 1975) and other invertebrates (e.g. James et al. 1995; Van Voorhies 1996) and (2) body size increases with depth, as has been described for other species of deep-sea gastropods (e.g. Rex and Etter 1998; Rex et al. 1999).

Materials and methods

Collection of samples

The present study is based on numerous samples housed mainly in the collections of the Southampton Oceanography Centre and the Muséum National d'Histoire Naturelle, Paris (MNHN). The samples were collected from different areas in the north-eastern Atlantic at latitudes from 25°39′N to 60°13′N and depths between 179 and 2,245 m. This species was chosen primarily because it was abundant enough in existing collections to allow reasonable statistical analyses across broad depth ranges. However, the sampling frequency is uneven across depth and latitude gradients (see Table 1 for summary).

Previous studies of latitudinal and depth distribution of body size have used diverse measures, ranging from linear morphological dimensions (e.g. Sardá and Cartes 1993; Roy and Martien 2001) to estimates of body mass (e.g. Marquet et al. 1990; Blackburn and Gaston 1994). In addition, some works on deep-sea gastropods have used standardized measurements of size at different life-history stages (for review see Rex and Etter 1998). Standardized measures are specially useful in studies that use the whole faunal components (Rex and Etter 1998).

In this study, measurements were made on 697 individuals collected from 106 stations (Table 1). Material from *Talisman* and Norway was obtained using dredges, and that from *Discovery* and *Challenger* using an epibenthic sledge (Rice et al. 1982), Granton trawl (Gordon and Duncan 1985), and otter trawl (OTSB14; Merrett and Marshall 1981). Scottish Marine Biological Association, Oban (SMBA) material was collected by Agassiz trawl (Gage and Tyler 1999). BIOGAS, INCAL, *Noratlante* and *Thalassa* samples were caught using two different types of beam trawl (Guennegan and Martin 1985), whereas PROCELT samples were taken from catches with a commercial trawl.

Important methodological problems arise in studies of body size using material from dredge samples (see McClain and Rex 2001). Deep-sea dredges collect both large and small individuals, so that the apparent variation in body size may simply reflect the

Table 1 Summary for samples measured in this study. *SMBA* Scottish Marine Biological Association, Oban

Cruise	No. stations ($n = 106$)	Depth (m) (Range 179–2,245)	Latitude (°N) (Range 25°39′–60°13′)	No. individuals ($n = 697$)
Talisman	3	865–1,216	25°39′–35°07′	7
Noratlante	2	1184–2,223	47°28′–55°08′	10
BIOGAS	4	994–2,245[a]	40°35′–47°42′	19
INCAL	1	2,054	57°58′	4
PROCELT I	9	565–700	48°03′–51°42′	38
PROCELT II	32	179–908	50°59′–53°26′	294
Thalassa I (north Gascony)	2	1,755–1,850	48°37′–48°45′	8
*Thalassa*II (south-east Gascony)	6	720–1,215	43°38′–46°32′	32
Norway	2	620–650	60°05′–60°13′	12
SMBA	5	1,075–2,240	56°00′–57°23′	24
Discovery 92	1	777	49°22′	5
Challenger 8/79	7	750–2,142	49°33′–51°51′	33
Challenger 9/79	10	400–1,150	49°11′–51°40′	54
Challenger 15/79	8	505–1,260	49°23′–52°00′	52
Challenger 11/80	6	506–1,263	49°26′–52°05′	48
Challenger 17/80	1	1027	51°21′	7
Challenger 8/81	3	515–940	51°26′–51°47′	28
Challenger 3/82	3	705–1,265	49°23′–51°51′	16
Challenger 9/84	1	952	51°55′	6

[a] Sample labelled as BIOGAS IV-CV34 appears to have come from 4,406 m, 1,700 m deeper than any other record for this species. It has been assumed that this material was mis-labelled and came from CV33, 1,913 m

recent history of recruitment (Rex and Etter 1998). Moreover, it is difficult to identify a particular habitat from which samples have been collected. Although several methods have been used in studies of body size of deep-sea species, most of them resulted in a loss of sample size and statistical power (see McClain and Rex 2001).

Two measurements, total height (H_t) and maximum breadth (B_m),were made to the nearest 0.1 mm for each shell using a vernier calliper. The geometric mean of these two dimensions (GM) was used as a measure of body size. This simple metric has been used previously and provides some degree of standardization for intra- and inter-specific shape differences (Stanley 1986; Jackson et al. 1996; Roy and Martien 2001). This metric is highly correlated with body mass as well as linear measurements of the gastropod shell (Roy 2002). Thus, these results should be directly comparable to other studies that used body mass or length of the shell as body-size estimators.

Statistical analysis

We tested the variation of body size with latitude and depth (see Introduction) in two different ways. Method 1 used a backwards stepwise regression analysis; method 2 used a quantile regression analysis.

Quantile regression is superior to least-square linear regression in several regards. This technique, based on least absolute models, is more robust to outlying values of the dependent variable and to sparseness within data sets (Scharf et al. 1998). This is a statistical method that provides a more objective assessment of trends in body size in age-structured assemblages without loss of sample size (McClain and Rex 2001). This method permits choosing a quantile ranging from 0.00 to 1.00 to test for relationships in a particular region of the bivariate distribution (McClain and Rex 2001). Hypothesis tests for this regression are performed by a rank-score test (based on a chi-squared distribution) that provides correct type I error rates for heterogeneous error distributions because the statistic is based on the sign of the residuals from the reduced parameter null model and not their size (Cade and Guo 2000). Quantile regression has a coefficient of determination R^1 obtained by subtracting from 1 the weighted absolute deviations from the original model divided by weighted absolute deviations from a null model (Cade and Richards 2001).

The statistical software packages STATISTICA version 5.1 (Statsoft, Inc.) and BLOSSOM (Midcontinent Ecological Science Centre, Colorado) were used for the backwards stepwise regression and quantile regression analyses, respectively. Body size was log transformed before analyses to reduce heteroscedasticity (Sokal and Rohlf 1981).

In the backwards stepwise regression, both independent variables, that is, depth and latitude, were entered together. *F*-to-enter was set at 4.0, and *F*-to-remove at 3.9. When one of the independent variables was found not to add significantly to the prediction it was removed from the equation.

A quantile regression analysis estimating the median (i.e. 50th quantile) was done to test for a significant relationship between body size and the independent variables, that is, latitude and depth. In addition, significance tests were conducted on the 10% (i.e. lower bound of body-size distribution) and 85% and 90% quantile regression lines (i.e. upper bounds of body-size distribution). The relationships of body size to depth and latitude were first examined separately and then in a full model. Subsequently, the full model (i.e. both parameters, depth and latitude included) was compared to a reduced null model (i.e. independent parameter of interest removed) to assess whether latitude or depth explains any additional variance when added to the model (see McClain and Rex 2001).

Results

Method 1

Although body size tended to increase with latitude, particularly between 40° and 51° where the highest values were reached (Fig. 1), this tendency was not significant. Backwards stepwise regression removed latitude from the equation (Table 2), indicating that this parameter did not account for variance of body size. In contrast, there was a significant tendency for size to decrease with increasing depth (Table 2). Body size was greatest between 179 and 950 m and decreased considerably below 950 m depth (Fig. 2). Nevertheless, the relationship between body size and depth was not very strong because depth accounted for only 22.5% of the variance of body size.

Method 2

Body size increased significantly with latitude for the 10% and 50% quantile lines, but not for the 85% and

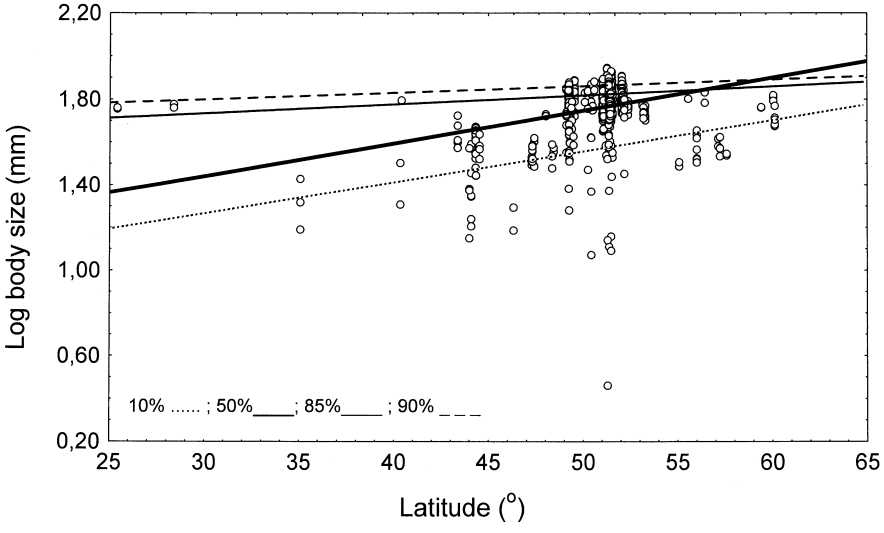


Fig. 1 The relationship between body size and latitude. Regression equations for the 10%, 50%, 85%, and 90% quantile lines are given: *10%* $y = 0.831 + 0.0145x$; *50%* $y = 0.981 + 0.0154x$; *85%* $y = 1.706 + 0.0031x$; *90%* $y = 1.608 + 0.0042x$. The *circle* at the lower part of the graph is a very small individual with only two whorls of growth

Table 2 Multiple regression analysis for predicting body size of *Troschelia berniciensis*. Latitude and depth are the independent variables. Results show that depth accounts for 22.5% of the variance in body size, but latitude does not explain any variance. Regression equation: body size = 1.871–0.452x_2 ($n = 697$, $F = 89.613$, $r^2 = 0.225$, $P < 0.001$)

Independent variable	t (694)	Contribution to r^2	P
Latitude (x_1) (removed)	0.782	0.0007	0.4344
Depth (x_2)	−13.361	0.2253	< 0.0001

90% quantile lines (Table 3, Fig. 1). In contrast, size decreased significantly with increasing depth for the 10%, 50%, 85%, and 90% quantile lines (Table 3, Fig. 2). The negative relationship between depth and body size was, however, marginal for the 85% and 90% quantiles lines (Table 3). Nevertheless, depth explained body size better than latitude (i.e. R^1 was higher in all cases when significant). The full model with latitude and depth included was significant in all cases (Table 3).

When the full model was compared to the reduced models, that is, depth or latitude removed, results were quite similar. For the 10%, 50%, 85%, and 90% quantiles, the full model differed significantly from the null model with depth removed. In contrast, there were not significant differences between the full model and the null model with latitude removed for the 85% and 90% quantiles (Table 4). Results suggest that depth explains variance in body size better than latitude, although both parameters account for a little of the variance in body size.

Discussion

The results obtained provide partial support for the proposed hypotheses. Firstly, body size did increase significantly with latitude, but the relationship was not strong. Secondly, body size decreased significantly with depth. Depth predicted variation in body size better than latitude. Nevertheless, the amount of variance explained by the two parameters was small.

Effect of latitude on body size

Although latitudinal trends in body size have long been of interest to biologists, few works have focused on intra- or interspecific latitudinal size trends in marine invertebrates over large spatial scales (but see Reaka 1980; Roy and Martien 2001). For ectotherms in general, data indicate that there may not be any consistent relationships between body size and latitude (e.g. Miller 1991; Hawkins and Lawton 1995; Roy and Martien 2001). Some studies on intertidal snails (see Frank 1975) and terrestrial invertebrates (James et al. 1995; Van Voorhies 1996) have, however, found an increase of body size with latitude. Results presented here show that latitude accounted for very little of the variance in body size (see method 2).

Although the quantification of latitudinal patterns in body size is important for many ecological reasons, the processes driving such patterns remain poorly understood (Lawton 1991; Hawkins and Lawton 1995). Some of the mechanisms to explain intraspecific gradients for ectotherms focus on the effects of temperature on cell size and/or number or on patterns of whole organism mortality (see Van Voorhies 1996; Spicer and Gaston 1999) or on dispersal abilities (Frank 1975). In addition, some of the proposed causal factors for interspecific latitudinal trends in body size are the availability of energy, availability of prey, heat conservation, competition (see McNab 1971), and also dispersal abilities (Gaston and Blackburn 1996). For bivalves, history and environmental barriers seem to be important components of the latitudinal distribution of body size (Roy and Martien 2001). However, body size in stomatopods seems to be closely related to life-history patterns rather than latitude (Reaka 1980). No evidence is available to show whether environmental barriers (i.e. basins,

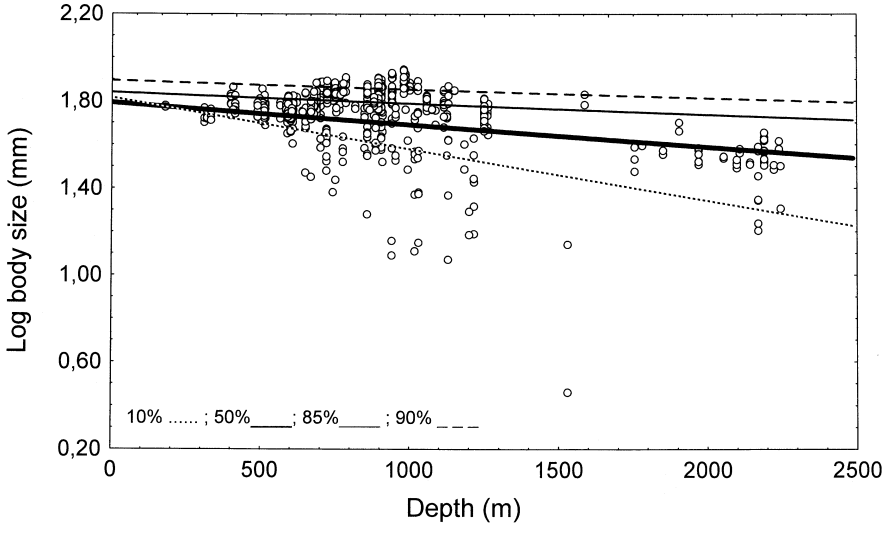


Fig. 2 The relationship between body size and depth. Regression equations for the 10%, 50%, 85%, and 90% quantile lines are given: *10%* $y = 1.815–0.00024x$; *50%* $y = 1.792–0.00010x$; *85%* $y = 1.840–0.00005x$; *90%* $y = 1.894–0.00004x$. The *circle* at the lower part of the graph is a very small individual with only two whorls of growth

Table 3 Quantile regression summary for relationships between body size and latitude and depth, and a full model with both parameters. *P* values and coefficient of determination (R^1) are reported for each quantile regression line ($n = 697$)

Test	*P* value for quantile regressions			
	10%	50%	85%	90%
Latitude	1.190E−13 ($R^1 = 0.0626$)	1.365E−04 ($R^1 = 0.0337$)	0.1280 ($R^1 = 0.0032$)	0.3530 ($R^1 = 0.0012$)
Depth	7.208E−39 ($R^1 = 0.1987$)	4.064E−09 ($R^1 = 0.0649$)	0.0490 ($R^1 = 0.0097$)	0.0313 ($R^1 = 0.0044$)
Full model	2.679E−44 ($R^1 = 0.2511$)	3.778E−10 ($R^1 = 0.0835$)	0.0044 ($R^1 = 0.0124$)	0.0086 ($R^1 = 0.0106$)

Table 4 Tests of full model, that is, body size = constant + latitude + depth, compared to reduced null model. *P* values are the probability that the two models explain the same amount of variance

Null model	*P* value for quantile regressions			
	10%	50%	85%	90%
Body size = constant + latitude	6.045E−48	2.435E−06	0.0492	0.0052
Body size = constant + depth	2.013E−11	2.408E−04	0.1071	0.5324

provinces) might be important in determining latitudinal body-size patterns in gastropods. *T. berniciensis* and other species lacking larval dispersal mechanisms might be more susceptible to size variations among different basins or provinces than species with a long pelagic larval stage.

Effect of depth on body size

Maximum shell height appears to vary little throughout the depth range of *T. berniciensis* (unpublished observations). The decrease of body size with depth, as measured by shell dimensions, results largely from a reduction of shell breadth relative to height (Olabarria and Thurston unpublished manuscript).

The decrease of body size with depth is a widely observed phenomenon (e.g. Carey 1981; Smith and Hinga 1983; Pfannkuche 1985; Lampitt et al. 1986; Sokolova 1989; Fujita and Ohta 1990; Sardá and Cartes 1993). The pattern observed in this study contrasts with earlier reports on geographic variation in deep-sea gastropods (Rex and Etter 1990, 1998; Rex et al. 1999; Clain and Rex 2000). The decrease of size, observed mainly below 950 m, has been reported for other faunal groups such as decapods (Sardá and Cartes 1993). In contrast, increasing size with depth has been reported for different meio- and macrofaunal groups (e.g. Thurston 1979; Shirayama 1983; Gage and Tyler 1982) and some species of fishes (e.g. MacPherson and Duarte 1991).

The important question is to know which factors are responsible for a decrease of size with depth. Temperature gradients have been cited frequently as one of the most important factors causing body-size clines (Rex et al. 1999 and references therein). At the cellular level, cell size increases at lower developmental temperatures (e.g. Van Voorhies 1996). However, in the ocean below the permanent thermocline conditions are nearly isothermal, and temperature is unlikely to have a major effect on deep-sea populations (Rex et al. 1999). Another commonly accepted factor is food availability, coupled with how species exploit available food resources and patterns of energy distribution with their life-history strategies (Hessler and Jumars 1974; Carey 1981). According to Thiel (1975), small size in the meio- and macrobenthos would be favoured at greater depths where food resources are less abundant.

Trophic habits of *T. berniciensis* remain unknown, but characteristics of the radula (Bouchet and Warén 1985) indicate that this species may be predator or necrophage. Polychaetes, bivalves, and small gastropods seem to be the primary diet of other species of the family Buccinidae (Taylor 1987; Tan and Morton 1998). Decreases in densities of potential prey organisms with depth have been reported in many studies (e.g. Thistle et al. 1985; Lampitt et al. 1986; Rex et al. 1990) and could be a cause of decreasing body size with depth in *T. berniciensis*. In fact, Rex et al. (1990) reported a trend of decreasing density of neogastropods and opisthobranchs with increasing depth on the Atlantic continental slope and rise. Larger predators at high trophic levels may be particularly sensitive to decreased food availability in food-poor environments that characterize much of the deep-sea floor (Merrett 1987; Rex et al. 1990). This decrease in prey availability coupled with an increase in energetic costs (e.g. production of mucus for locomotion and localization of prey) can lead to a decrease of optimal size with depth (Rex and Etter 1998).

Predation pressure may influence depth-related size distribution. Many of the shells measured in this study show overgrowth of damaged lip margins. Areas of damage resemble those caused by decapod crustaceans to *Buccinum* (Thomas and Himmelmann 1988). Large individuals of the brachyuran crab *Geryon trispinosus* (Herbst, 1803) are common in the upper part of the *T. berniciensis* depth range (Attrill et al. 1990) and are likely causal agents for the observed shell damage. Thus smaller snails with less heavily calcified shells could benefit from lower predation pressure at greater depths.

Results presented here show that depth had a stronger effect than latitude on body-size distribution

of *T. berniciensis*. Environmental gradients that cause large-scale patterns of body-size variation in surface environments would have little effect on communities living at great depths. Phenotypic differences among populations of diverse invertebrates are more related to differences in depth than to horizontal separation (Bucklin et al. 1987; Rex et al. 1988; Rex and Etter 1990). Some latitudinal patterns of diversity of invertebrates in the deep sea are affected to a major degree by depth (e.g. Rex et al. 1993, 2001). Latitudinal and depth clines may be produced by different processes that operate on different spatio-temporal scales (Rex et al. 1993).

An important task in the future is to assess whether the trend of decreasing body size with depth observed in *T. berniciensis* reflects any incipient evolutionary divergence. Species with a non-planktotrophic mode of development have a restricted gene flow (Hansen 1983) and a greater tendency to show phenotypic and genetic differentiation across environmental gradients. Nowadays, there is an increasing controversy on the mechanisms causing body-size clines. Although evolutionary processes or genetic differences seem to be the main forces driving size clines, environmental factors may have a strong effect as well (Van Voorhies 1996).

Depth and latitude appeared to affect body-size patterns in *T. berniciensis*, although the latitude effect was weaker. Nevertheless, other factors apart from depth and latitude are likely to have a stronger effect on the body size of this species. Body size is a complex attribute and its variation is likely to result from a combination of factors such as resource use, food supply, competition, predation, age-dependent mortality, longevity, and reproductive success (Van Voorhies 1996 and references therein). Recent studies have suggested that oxygen availability may have a strong influence on body size in marine invertebrates from shallow waters (i.e. amphipods; Chapelle and Peck 1999) and deep sea (i.e. the snail *Benthomangelia antonia* (Dall, 1881); McClain and Rex 2001).

Our results do not support earlier studies on geographic variation in small deep-sea gastropods (i.e. increase of size with depth; Rex and Etter 1990, 1998; Rex et al. 1999). Do small species of gastropods in general present different pattern from larger species of gastropods? If so, what are the causes? It is possible that absolute size and size changes related to depth are a result of different mechanisms operating at different spatio-temporal scales (Rex et al. 1999). Therefore, it is important not to generalize from one taxon to another, and to achieve good sampling coverage to assess geographic patterns in the deep sea. Nevertheless, results presented here are of interest because currently there are few studies that cover such a wide bathymetric and latitudinal range for a single species.

On the other hand, different outcomes of this type of study can result from differences in statistical methods (see Results as an example). There is also an increasing necessity to unify methodological criteria to clarify geographic trends in the deep sea. Quantile regression analysis has been shown as a useful tool for exploring trends in body size in this and previous studies (e.g. Scharf et al. 1998; McClain and Rex 2001). This method is robust with respect to extreme outlying y values and sparseness contained within data sets relative to regression procedure based on least square models. (Scharf et al. 1998).

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