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# Bathymetric patterns of body size: implications for deep-sea biodiversity

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## Abstract

The evolution of body size is a problem of fundamental interest, and one that has an important bearing on community structure and conservation of biodiversity. The most obvious and pervasive characteristic of the deep-sea benthos is the small size of most species. The numerous attempts to document and explain geographic patterns of body size in the deep-sea benthos have focused on variation among species or whole faunal components, and have led to conflicting and contradictory results. It is important to recognize that studying size as an adaptation to the deep-sea environment should include analyses within species using measures of size that are standardized to common growth stages. An analysis within eight species of deep-sea benthic gastropods presented here reveals a clear trend for size to increase with depth in both larval and adult shells. An ANCOVA with multiple comparison tests showed that, in general, size–depth relationships for both adult and larval shells are more pronounced in the bathyal region than in the abyss. This result reinforces the notion that steepness of the bathymetric selective gradient decreases with depth, and that the bathyal region is an evolutionary hotspot that promotes diversification. Bathymetric size clines in gastropods support neither the predictions of optimality models nor earlier arguments based on tradeoffs among scaling factors. As in other environments, body size is inversely related to both abundance and species density. We suggest that the decrease in nutrient input with depth may select for larger size because of its metabolic or competitive advantages, and that larger size plays a role in limiting diversity. Adaptation is an important evolutionary driving force of biological diversity, and geographic patterns of body size could help unify ecological and historical theories of deep-sea biodiversity. © 1998 Elsevier Science Ltd. All rights reserved.

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## 1. Introduction

This paper is dedicated to our colleague Robert R. Hessler, whose research and friendship have inspired and encouraged us, and so many others, to study deep-sea biodiversity. It is hard to think of any aspect of this article that is not based in some way on his extraordinarily original research, or on the insight gleaned from wonderful and memorable hours of conversation. Beginning with the discovery of unexpectedly high biodiversity in the deep sea (Hessler and Sanders, 1967), his remarkably varied research has fundamentally changed the way ecologists look at global diversity. The present paper is an effort to examine whether geographic variation in body size represents a connection between the evolutionary and ecological causes of deep-sea species diversity — areas to which Robert Hessler has made major and pivotal contributions.

Recently, there has been a strong resurgence of interest in factors controlling body size, one of the most basic problems in biology (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984; Reiss, 1989; Harvey and Pagel, 1991; Brown, 1995; Rosenzweig, 1995). Of particular relevance to this volume on biodiversity is the growing evidence that species diversity (May, 1986, 1989; Blackburn and Gaston, 1994; Sieman et al., 1996) and population abundance (Cotgreave, 1993; Currie, 1993; Blackburn and Lawton, 1994) scale to body size. Hence, body size relationships may have the potential to unify ecological and evolutionary theories of biodiversity. However, the causal connections among size, abundance and diversity remain obscure (Nee and Lawton, 1996). Size covaries with a large number of physiological, life history and ecological factors (Peters, 1983; Brown, 1995), and the shapes of these relationships can be affected by sampling error and by the spatial and temporal scales of observation (Blackburn and Gaston, 1994; Warwick and Clarke, 1996). A further complication is that while size is usually assumed to be an adaptive response to a history of natural selection, the possibility exists that some geographic variation in size represents environmentally induced changes in development that do not reflect genetic differences (Van Voorhies, 1996), though the range of growth responses may be an evolved form of phenotypic plasticity.

Much of the recent inquiry into body size and its possible relation to community structure draws on reanalyses of a few large existing databases for terrestrial birds and mammals (Blackburn and Gaston, 1994). Fewer data exist for marine systems. Given the complexity of the problem, it is important to examine as many databases as possible for different taxa on a variety of spatiotemporal scales in different environments. In this paper, we briefly review the literature on size in the deep-sea fauna, and discuss two theoretical approaches to understanding size variation: Thiel's (1975) influential and important synthesis, and Sebens' (1982) optimality theory. We present a new analysis of bathymetric patterns of size within eight deep-sea prosobranch species arrayed along a depth gradient in the western North Atlantic. The results are surprising and do not directly support predictions from earlier qualitative arguments that rely on tradeoffs among scaling factors, or the predictions of optimality models. We discuss the possible causes of the observed size–depth trends and their potential implications for biodiversity in the deep sea.

## **2. Body size variation in the deep-sea benthos**

The most conspicuous feature of the deep-sea benthos is the small size of most species. While this phenomenon has been well known since the great deep-sea expeditions of the 19<sup>th</sup> century, Thiel (1975) was the first to review bathymetric trends in body size and to explain them in plausible adaptive terms. Thiel (1975), (p. 575) phrased his size–structure hypothesis as “associations governed by constantly limited food availability are composed of small individuals on the average.” His principal evidence came from a comparison of bathymetric patterns of density in meiofaunal and macrofaunal assemblages. In both groups, density decreases exponentially with depth. However, he found the density of the meiofauna to be higher and to decrease at a significantly less rapid rate than did macrofaunal density (see also Thiel, 1979). The divergence of the two density–depth curves with increasing depth requires that, on average, organisms at greater depths are smaller; that is the meiofauna makes up a larger proportion of overall density.

Thiel’s explanation for the apparent decrease in average size with depth placed heavy emphasis on rates of nutrient input, which were assumed to decrease with depth – “one factor seems to be of overall prime importance: energy in the sense of food availability” (Thiel, 1979), (p. 25). Larger organisms respire at higher rates and place higher demands on the environment for resources. Standard metabolic rate increases with body mass for poikilotherms including invertebrates (Peters, 1983). However, metabolic rate per unit mass decreases with increasing body weight (Peters, 1983). The same kinds of metabolic rate–size relationships are obtained for deep-sea species (e.g. Childress et al., 1990; Shirayama, 1992; Mahaut et al., 1995). Larger organisms expend less energy per unit mass. Or, looked at another way, the cost of maintaining a given biomass for small organisms is greater than required to maintain the same biomass of larger organisms. Thiel (1975, 1979) recognized that larger organisms have an advantage over smaller organisms in terms of metabolic rate per unit weight. Selection for increased metabolic efficiency as a response to the reduced rate of nutrient input with increased depth should favor an increase in organism size; total standing stock also would be maximized with larger organisms.

Given the fact that the overwhelming majority of deep-sea species are smaller, and his demonstration that characteristically smaller forms become relatively more well represented at greater depth, Thiel (1975, 1979) proposed that selection favoring large size for reasons of metabolic efficiency must be counteracted by other selective forces. Of primary importance to Thiel’s theory was the concept that very low levels of food in deep-sea sediments would not permit large size to evolve despite its metabolic advantages. Large organisms place a large food demand on the environment, and would simply not be able to support themselves. Another factor might be the critical population density required to be reproductively viable in sexually reproducing and gonochoristic species. Thiel (1975, 1979) pointed out that most deep-sea species live at low density. Species comprised of a few sparsely distributed large individuals would be less reproductively viable in terms of the ability to acquire mates than species made up of a higher density of smaller individuals. So, small average size might represent a balance between food limitation, metabolic rates, and the effects of population size

on reproductive success. Thiel (1975), (p. 597) called this combination of physiological and ecological factors the “selective determinant” of average organism size.

Attempts to test Thiel's hypothesis by measuring size–depth trends have produced conflicting and contradictory results. Thiel's main evidence, the difference in slopes of density–depth curves for the meio- and macrofauna, has not been observed in other studies (Shirayama, 1983; Sibuet et al., 1989), although analyses of sieve-fractionated components of the meio- and macrofauna combined have revealed a shift toward smaller average size with depth (Schwinghamer, 1985; Shirayama and Horikoshi, 1989). Important meiofaunal elements like the nematodes have been reported to increase in size (Shirayama, 1983; Tietjen, 1984, 1989), decrease (Pfannkuche, 1985; Soetaert and Heip, 1989) or show no relationship (Jensen, 1988) with depth. The surface-dwelling meiobenthos as a whole shows a decrease in size with depth, but subsurface elements show no pattern (Shirayama, 1983). Average size in the macrobenthic community is smaller in the deep sea than in coastal waters (Gage, 1977). However, within the deep sea, macrofaunal size can increase (Smith and Hinga, 1983), decrease (Carey, 1981; Smith and Hinga, 1983) or not vary with depth (Polloni et al., 1979). Individual taxa have been reported to have positive (Thurston, 1979) or negative (Sokolova, 1989) relationships of size to depth. Average size in the megabenthos as a whole shows no clear pattern with depth (Haedrich et al., 1980; Lampitt et al., 1986), but decreases significantly when the largest constituents are removed (Lampitt et al., 1986). Echinoderms show no clear size–depth relationship (Polloni et al., 1979). The average size of ophiuroid species can increase (Gage and Tyler, 1982), decrease (Fujita and Ohta, 1990) or show no pattern (Gage and Tyler, 1982). Decapods, another megabenthic taxon, can decrease in size with depth (Sardà and Cartes, 1993) or show no relationship (Polloni et al., 1979). It is interesting that benthopelagic fishes, which are not considered further in this paper, also show a broad range of effects both as a whole fauna and as individual species (Polloni et al., 1979; Percy et al., 1982; MacPherson and Duarte, 1991; Merrett et al., 1991a, 1991b; Haedrich and Merrett, 1992; Blackburn and Lawton, 1994).

Some of the wide variation in outcome among studies can be attributed to sampling and sorting methods (Shirayama, 1983) and the fact that depth, *per se*, is not a single consistent correlate of nutrient input (Gage and Tyler, 1982). However, a more fundamental problem is that body size simply has not been measured in a way that could convincingly demonstrate an adaptation to deep-sea conditions. There are three basic problems.

First, nearly all of the studies consider size as an average dimension or average biomass, among species or even whole faunal components separated by sieve size. Clearly, adaptation as an evolutionary adjustment to the environment also should include an analysis of geographic variation within species. Comparing different species or assemblages living at different depths involves a loss of both genetic and environmental control. Also, considering the tremendous diversity of body form and degree of calcification among deep-sea invertebrates, average measures cannot indicate any specific adaptive trend.

Second, measurements of size for purposes of studying adaptation and geographic variation should be standardized to some common growth stage such as a specific

instar in crustaceans (Wilson, 1983) or whorl number in gastropods (Gould, 1969; Rex et al., 1988; Rex and Etter, 1990). Frequency distributions of size, measured as total body dimensions, or weight, for a population merely reflect the recent history of recruitment and population growth, which can be very seasonal, highly localized or unpredictable in deep-sea species (Gage and Tyler, 1991). Of course, such information is directly relevant to studies of life history in deep-sea species. We stress that this paper is concerned with geographic comparisons of standardized size, and is not concerned directly with fitting growth parameters or equating size (i.e. common growth stage) with age. Studies that use whole faunal components are particularly confounded by the use of unstandardized size because different species can be out of phase in population growth, both in time and space.

There are only a few studies which meet criteria 1 and 2 by analyzing bathymetric trends in standardized size within species. Wilson (1983) showed that body length at common development stages of the isopod *Eurycope iphthima* increased with depth from 2500 to 4800 m. Rex et al. (1988), Rex and Etter (1990), and Etter and Rex (1990) presented biometrical analyses of standardized measures of shell form (size, shape, sculpture) in seven species of deep-sea gastropods. In this paper, we reanalyze the size data for these seven species and one additional unpublished species as a preliminary analysis of size–depth patterns within species. The predominant trend here is also an increase in size with depth.

A third problem with existing size–depth studies concerns the level of statistical analysis employed. Apart from Thiel (1979), no study has used an analysis of covariance to actually compare the slopes and elevations of size–depth relationships among groups, erected confidence limits about regression lines or explored and justified different regression models. Without criticizing individual studies here, it is very plain that more appropriate statistical methods would greatly strengthen the interpretation in some and completely alter the conclusions of others. ANCOVA with multiple comparison tests is a powerful analytical tool to compare bathymetric trends (Rex et al., 1990).

Given the conflicting results discussed above and these methodological problems, it remains unclear whether consistent geographic trends in size actually exist in the deep sea, except for the observation that deep-sea species seem on average smaller than their shallow-water counterparts.

### 3. A general approach using optimality theory

Body-size relations, such as the metabolic scaling in Thiel's hypothesis, can be useful for interpreting size patterns in nature. But they suffer from the same problems inherent in any inductive approach: a great many different physiological and life-history processes scale with size, and such relationships easily can be spurious. When one scaling factor does not provide a complete explanation, other counteracting or complementary factors must be postulated. Recently, optimality theory has provided a particularly successful way to analyze evolutionary adaptations from a more general and deductive perspective (Parker and Maynard Smith, 1990). Sebens (1982, 1987)

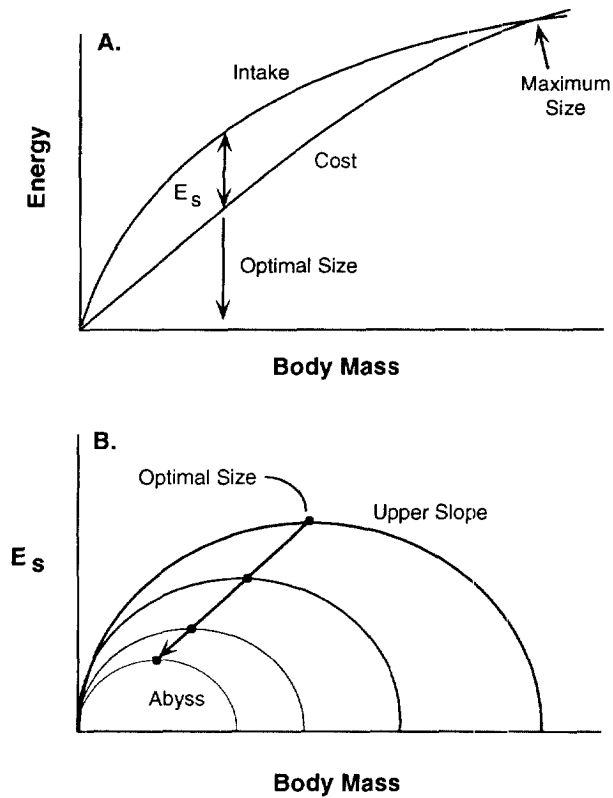


Fig. 1. A. Sebens' (1982, 1987) optimal size model applied to deep-sea organisms. Energy intake and energetic cost are shown as functions of body size. Energy surplus ( $E_s$ ) is the difference between intake and cost. Optimal size occurs where  $E_s$  is maximized; if growth ceases here, there is a maximum amount of energy to allocate to reproduction. B. Energy surplus ( $E_s$ ) curves, integrated over seasons of reproduction and growth from different levels of habitat suitability. Optimal size is expected to decrease from the upper continental slope to the abyssal plain as rates of nutrient input decrease causing intake to decrease and cost of foraging to increase. Modified from Sebens (1982) with permission from the Ecological Society of America.

proposed an optimality model for the size of marine invertebrates that includes some of the same basic ideas implicit in Thiel's size-structure hypothesis.

Sebens' basic model is shown in Fig. 1A. Energetic cost and intake curves are expressed as power functions of body size (mass):

$$I = k_1 M^{c_1}$$

$$C = k_2 M^{c_2}$$

where  $I$  and  $C$  are energetic intake rate and energetic cost respectively, and  $k_i$  and  $c_i$  are fitted constants. The exponents,  $c_i$  values, are species-specific scaling factors, and the  $k_i$  values are habitat dependent. Intake functions reflect food capture rates

(e.g. prey capture for predators, sediment intake for deposit feeders). Cost includes respiration, excretion and the cost of producing materials required for locomotion and feeding, such as mucus in snails. The energy surplus ( $E_s$ ) available for reproduction or growth (scope for growth) is the difference between intake and cost:

$$E_s = k_1 M^{C_1} - k_2 M^{C_2}$$

The  $E_s$  available to produce reproductive tissue is an indirect measure of fitness which is maximized where the difference between the cost and intake curves is greatest (see Fig. 1A). This corresponds to the optimal size; if growth ceases at this size there is a maximum amount of energy to devote to reproduction. Maximum size occurs where cost equals intake (where the curves cross, Fig. 1A). Here size is maximized, but no energy is available for reproduction.

Optimal size will vary with environmental influences on intake and cost. For example, in the deep-sea benthos (Rowe, 1983; Lampitt et al., 1986), including gastropods (Rex et al., 1990), standing stock decreases exponentially with depth as a result of decreased nutrient input (Pace et al., 1987; Watts et al., 1992). So, in general, the intake curve should be depressed with increasing depth. Costs may decline with depth in the upper continental slope region where the sharp decrease in temperature would cause lower metabolic rates; but, this would not seem to apply below the permanent thermocline at around 500 m. The cost function should rise with increasing depth throughout the depth range as animals expend more energy to forage on progressively rarer prey or organically poorer sediments. Organisms like snails would need to produce more mucus for locomotion to locate prey or process detrital food. The cost of pedal locomotion in snails is very high, mainly because of the high cost of pedal mucus production (Denny, 1980). Both of these depth-related effects, depressing the intake curve and elevating the cost curve, separately or together, act to decrease optimal size. This can be seen in Fig. 1B, which integrates  $E_s$  over a season of reproduction for different habitats. As habitat suitability decreases, in the sense of lower intake and/or higher cost, the optimal size decreases. In the deep sea, optimal size is expected to decrease from the upper slope to the abyss, assuming a rough relationship between depth and nutrient input. Patchiness and inter-regional variation in nutrient input could alter optimal size at appropriate scales.

Optimality models are not intended to imply that organisms are in some sense “optimal” as a perfect adaptation (Parker and Maynard Smith, 1990). Tradeoffs between growth and reproduction are complex, and many selective factors can shift populations away from optimal size (Sebens, 1982, 1987). For example, growth above the optimum, while it results in less energy allocated to reproduction (Fig. 1A), could be favored by selection if large size provided an escape from predation or a competitive advantage (Sebens, 1982). Such effects might be expected across the depth ranges of deep-sea species. Deep-sea snails show very rapid rates of species replacement with depth (Rex, 1977, 1981) and marked clinal effects (Rex et al., 1988; Etter and Rex, 1990) across the upper bathyal region where they experience a very steep decline in density (Rex et al., 1990). Over their depth ranges, species may experience a selective gradient for larger size to exploit more efficiently food resources (as Thiel suggested) and to exploit a wider variety of food items (Levinton, 1982, 1987) as food becomes more

scarce and limiting. At lower bathyal and abyssal depths the environment becomes more uniform, density changes less (Rex et al., 1990), species reveal much less geographic variation, and their bathymetric ranges become broad and overlapping (Rex and Etter, 1990; Etter and Rex, 1990). Changes in selective pressure may occur more gradually at these depths (Rex and Warén, 1982), and shifts away from optimal size consequently may be diminished.

Lampitt et al. (1986) and Jumars and Wheatcroft (1989) suggested that the apparent decrease in average size with depth reflects species replacement rather than changes within species. Indeed, this is all that Thiel's hypothesis required. As pointed out above, it is still uncertain what kinds of patterns actually exist in the deep-sea benthos. Sebens' optimality model predicts a general reduction in size with depth within and presumably between similar species, but also allows for a variety of selective pressures to cause departure from optimal size.

#### 4. Measurements and analytical methods

In what follows, we present an analysis of size–depth relationships within eight different species of deep-sea snails arrayed along a depth gradient from 500 to 5000 m in the western North Atlantic. Gastropods are especially well suited for this type of study because the growth history of individuals is preserved in shell form, and size can be compared at common growth stages (Etter and Rex, 1990). Data for seven species [*Frigidoalvania brychia* (Verrill), *Onoba pelagica* (Stimpson), *Pusillina harpa* (Verrill), *Pusillina pseudoareolata* (Warén), *Oenopota ovalis* (Friele), *Benthonella tenella* (Jeffreys) and *Benthomangelia antonia* (Dall)] are reanalyzed from a series of papers on geographic variation in shell form (Rex et al., 1988; Rex and Etter, 1990; Etter and Rex, 1990). These are biometrical, largely multivariate, studies of population differentiation that are not primarily concerned with size *per se*. Data for the eighth species [*Mitrella pura* (Verrill)] are unpublished. Details of sampling, measurement and regional maps can be found in the above references and in Rex et al. (1990). *Mitrella pura*, *B. antonia* and *O. ovalis* are neogastropod predators. The other five species are rissoid deposit feeders. *Benthomangelia antonia* and *B. tenella* have planktotrophic larval development with the potential for long-distance dispersal, and the remaining six species have non-planktotrophic development in an egg capsule with little or no dispersal ability (Rex and Warén, 1982; Killingley and Rex, 1985).

We present size–depth trends for standardized measurements of size at two life-history stages: (1) size of the larval shell (protoconch) at the larval–adult transition (end of larval life); and, (2) size of the adult shell at the end of the first whorl of growth. Both variables were measured somewhat differently in different species depending on the peculiarities of shell architecture, condition of the shells and the objectives of the original studies from which data were taken. In all species except *B. antonia*, protoconch shell size was measured as the exposed height plus width of the larval shell at the larval–adult transition (Rex and Etter, 1990). In *B. antonia*, we were able to measure only the protoconch width, because the apex of the larval shell was corroded in many specimens, making it impossible to accurately assess height. We show



variation in these variables for all species, and then compare bathymetric trends using protoconch width alone, the larval shell dimension that all populations share. Adult standardized size was measured as height plus width for the first post-larval whorl in *M. pura*, *O. ovalis*, *B. antonia* and *B. tenella* (Rex and Etter, 1990). In the four upper bathyal rissoids, adult size was measured as the height of the whorl located one revolution below the terminus of the larval shell (Rex et al., 1988). All of these larval and adult shell dimensions allow us to determine size–depth trends within species, which is our primary intention here. However, among-species comparisons are limited to subsets of species where shell size was measured in exactly the same way and there is some reasonable level of taxonomic affinity and ecological similarity.

We first show the means and confidence limits for larval and adult sizes of populations at each sampling station. We then examine the relationship of size to depth by using regression analyses, and an ANCOVA with Tukey multiple comparisons to test for conformity of slopes among species. The regressions and ANCOVA's were first performed with a percent range transformation of size variables. This was done to help correct for differences in the way shells were measured, especially for adult size where there is no common dimension shared among all species. This transformation does not affect the significance of regressions. However, it should be borne in mind that the ANCOVA, in this case, reveals differences in proportional changes in size with depth (that is, the relative amount of change in size adjusted to the actual size of the shells). We also carried out the analyses using the raw data for protoconch size. Overall, the results are very similar.

One possible criticism of applying Sebens' (1982) optimality model is that it predicts the size at which animals stop growing rather than size standardized to a common growth stage. However, maximizing energy available for growth and reproduction should pertain to all life-history stages, and the model is only being used here to make very general predictions. Nevertheless, we also explore the relationship between standardized size and final size attained.

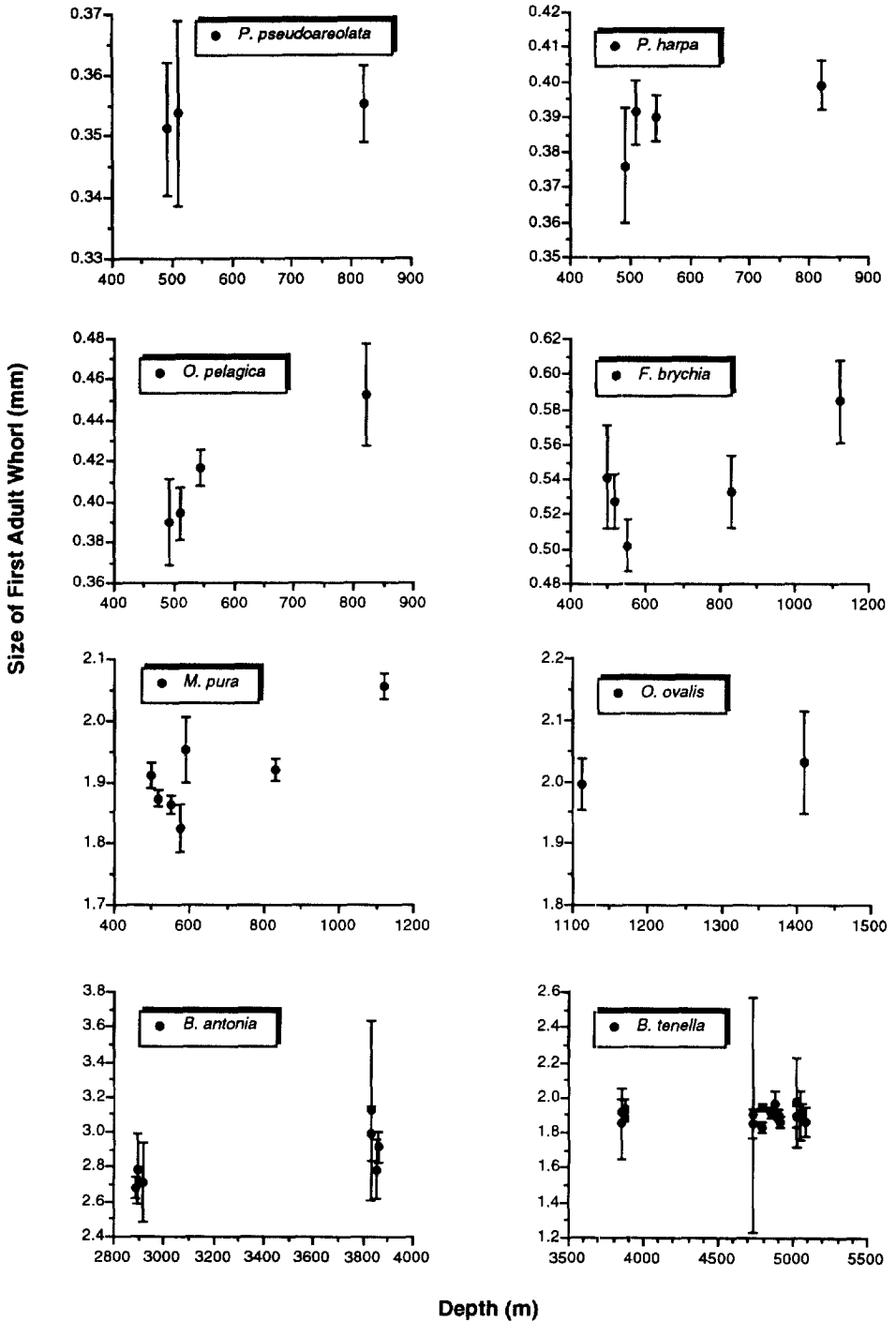
The null hypothesis of principal interest here is that size does not change with depth. The alternative hypothesis that follows from optimality theory and Thiel's size–structure hypothesis is that size decreases with depth. The signs and significance levels of size–depth regressions will be used as the main evidence to test these hypotheses. The ANCOVA should reveal any geographic shifts in the relative degree of clinal variation.

## 5. Results and discussion

### 5.1. Bathymetric patterns

#### 5.1.1. Adult shell size

Figure 2 shows the means and confidence limits for adult size in populations collected at different depths in the eight species. Upper bathyal species (~ 500–1500 m) show a tendency for size to increase over depth differences of 300–600 m. Two species, *O. pelagica* and *M. pura* have marked shifts in size, with



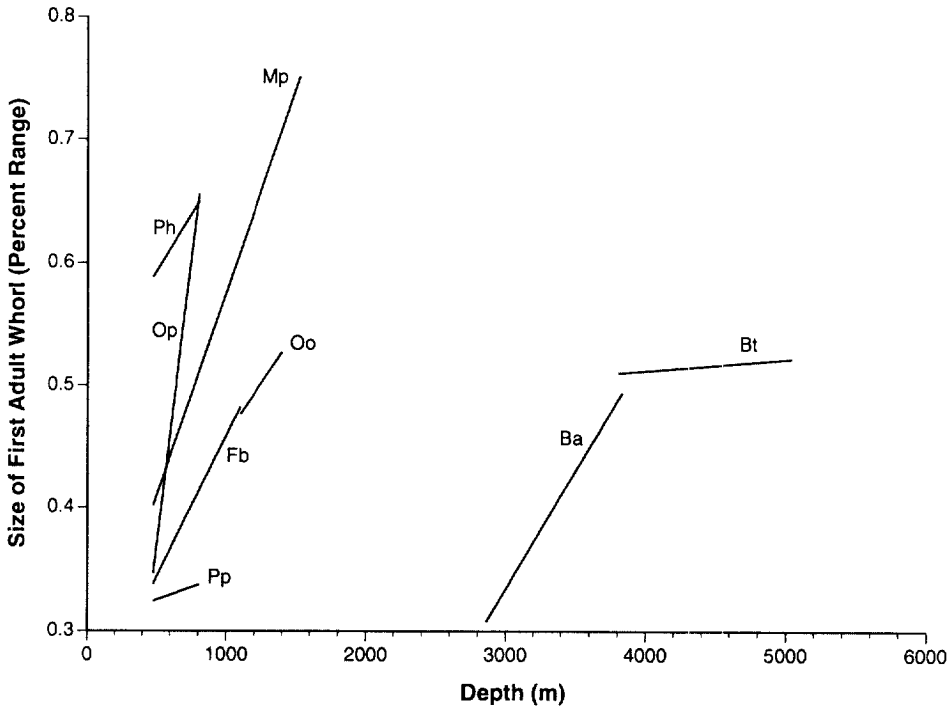


Fig. 3. Adult size (standardized size of the first whorl as in Fig. 2), converted to percent range, plotted as regression lines against depth. Data are from Fig. 2. Regression equations and their statistics are given in Table 1. Symbols refer to species in Fig. 2.

confidence limits showing no overlap between shallow and deep sites. *B. antonia* from the lower bathyal region and *B. tenella* from the abyssal plain display broadly overlapping confidence limits for sites separated by 1000 m.

In Fig. 3, adult sizes (here standardized to percent range) are plotted against depth as regression lines for all eight species. Regression equations and an ANCOVA are presented in Table 1. All of the size–depth relationships are positive, and five of the eight are significant. The ANCOVA shows the slopes to be heterogeneous (Table 1). Multiple comparison tests reveal that slopes of *O. pelagica*, *F. brychia*, *M. pura* and *B. antonia* exceed that of the deepest dwelling species *B. tenella*; and that the slope of *O. pelagica* (an upper bathyal species) exceeds that of all other species (Fig. 3, Table 1).

Fig. 2. Means and 95% confidence limits for samples of adult shell size measured as height at the end of the first adult whorl in *Pusillina pseudoareolata*, *Pusillina harpa*, *Onoba pelagica* and *Frigidoalvania brychia*, and as height plus width at the end of the first whorl in *Mitrella pura*, *Oenopota ovalis*, *Benthomangelia antonia* and *Benthonella tenella*. Means are plotted against depth (m) of sampling in the Western North Atlantic south of New England.

Table 1  
Regression equations and statistics for size–depth relationships of larval and adult snails shown in Figs. 3 and 5, and an analysis of covariance for the slopes. The inequality signs for the Tukey multiple comparison tests indicate significant differences ( $P < 0.05$ ) and the direction of the differences

Species	Regression		ANCOVA				
	Equation	df	$r^2$	F	df	F	Multiple comparison
<i>Size of first adult whorl</i>							
<i>P. harpa</i>	$y = 0.500 + 0.00019x$	1,158	0.030	4.95*	7,1175	12.807***	Op, Fb, Mp, Ba > Bt Op > all species
<i>P. pseudoareolata</i>	$y = 0.305 + 0.00004x$	1,78	0.001	0.112			
<i>O. pelagica</i>	$y = -0.101 + 0.00094x$	1,85	0.228	25.136***			
<i>F. brychia</i>	$y = 0.227 + 0.00023x$	1,214	0.121	29.522***			
<i>M. pura</i>	$y = 0.243 + 0.00033x$	1,295	0.373	175.405***			
<i>O. ovalis</i>	$y = 0.289 + 0.00017x$	1,44	0.018	0.799			
<i>B. antonia</i>	$y = -0.240 + 0.00019x$	1,86	0.228	25.447***			
<i>B. tenella</i>	$y = 0.474 + 0.00001x$	1,215	0.001	0.126			
<i>Protoconch Size</i>							
<i>P. harpa</i>	$y = -0.136 + 0.00114x$	1,158	0.365	90.920***	7,1108	33.708***	Ph, Op, Fb, Mp > Bt Ph, Fb, Mp > Ba Ph > Pp, Fb, Oo, Mp
<i>P. pseudoareolata</i>	$y = 0.190 + 0.00024x$	1,78	0.054	4.443*			
<i>O. pelagica</i>	$y = 0.193 + 0.00075x$	1,85	0.181	18.816***			
<i>F. brychia</i>	$y = 0.045 + 0.00047x$	1,214	0.345	112.685***			
<i>M. pura</i>	$y = -0.005 + 0.00056x$	1,266	0.512	279.297***			
<i>O. ovalis</i>	$y = 0.173 + 0.00026x$	1,44	0.038	1.735			
<i>B. antonia</i>	$y = 0.065 + 0.00014x$	1,48	0.119	6.467*			
<i>B. tenella</i>	$y = 0.248 + 0.00007x$	1,215	0.031	6.778*			

\* $P < 0.05$ .  
\*\*\* $P < 0.001$ .

In general then, size–depth clines tend to be steeper in the bathyal region (see also Etter and Rex, 1990).

Taken together these results do not support the null hypothesis of no change in size with depth, nor the basic prediction stemming from optimality theory and tradeoffs among scaling factors that organisms should get smaller with increasing depth. Most species show positive and significant increases in size with depth. There are no cases where size decreases significantly with depth. The only trends that are not significant are for upper bathyal species with the fewest data and sampling sites, where only narrow depth ranges have been sampled, and for the abyssal species that lives in an environment where geographic variation is diminished in prosobranchs (Etter and Rex, 1990).

One interpretation of the increase in size with depth is that the decrease in nutrient input across species' bathymetric ranges selects for above optimal size because of the advantages of large size for metabolic efficiency and competition. Obviously, for this to occur, selection for increased size must exceed the predicted decrease in optimal size that results from habitat deterioration in terms of lower food intake and the increased cost of foraging (Fig. 1B). This may be why size–depth relations are most pronounced on the upper slope where the selective gradient appears to be strongest. Extensive box-core sampling in this region demonstrated that the density of the rissoid complex analyzed in Figs. 2 and 3 decreases a full order of magnitude over 1000 m (Rex et al., 1988, 1990).

The proportional changes in size, while consistent in direction and frequently significant, are relatively small (Figs. 2 and 3). There must be severe limits on how much size can be increased above the optimum, especially when the optimum should continue to decrease. Over the entire bathymetric range sampled for snails in the western North Atlantic (200–5000 m), biomass (Rowe, 1983), density of benthos including snails (Rex, 1981; Rex et al., 1990) and community respiration (Smith and Hinga, 1983) all decrease several orders of magnitude. It seems inevitable that the reduction in optimal size predicted by Sebens' model would be enforced over the entire depth range. Since gastropod species tend to increase in size across their depth ranges, and show high rates of species replacement with depth (Rex, 1977, 1981), this reduction should be apparent among species as they replace one another along a depth gradient as Lampitt et al. (1986) and Jumars and Wheatcroft (1989) suggested. Clearly, an among-species size gradient should be evaluated by studying a large number of closely related and ecologically similar species. The eight species considered here do not suggest an among-species decline in size in the limited way that this can be examined. For example, the four upper bathyal rissoids, which share nonplanktotrophic development and are deposit feeders, show a significant increase in size of the adult first whorl ( $F = 71.343$ ,  $P < 0.0001$ ) from 500 to 1100 m when data from all species are combined. Similarly, *M. pura* and *O. ovalis*, which are carnivores with nonplanktotrophic development, show a significant increase in size from 500 to 1400 m ( $F = 191.671$ ,  $P < 0.0001$ ). When the third neogastropod *B. antonia* is added to the analysis, the relationship is highly significant ( $F = 3166.094$ ,  $P < 0.0001$ ) over a depth range from 500 to 3800 m, though this comparison has less control because *B. antonia* has planktotrophic development. Also, the lower bathyal and abyssal

species attain maximum size nearly twice that of upper bathyal species (cf. Rex et al., 1979, 1988; Rex and Etter, 1990).

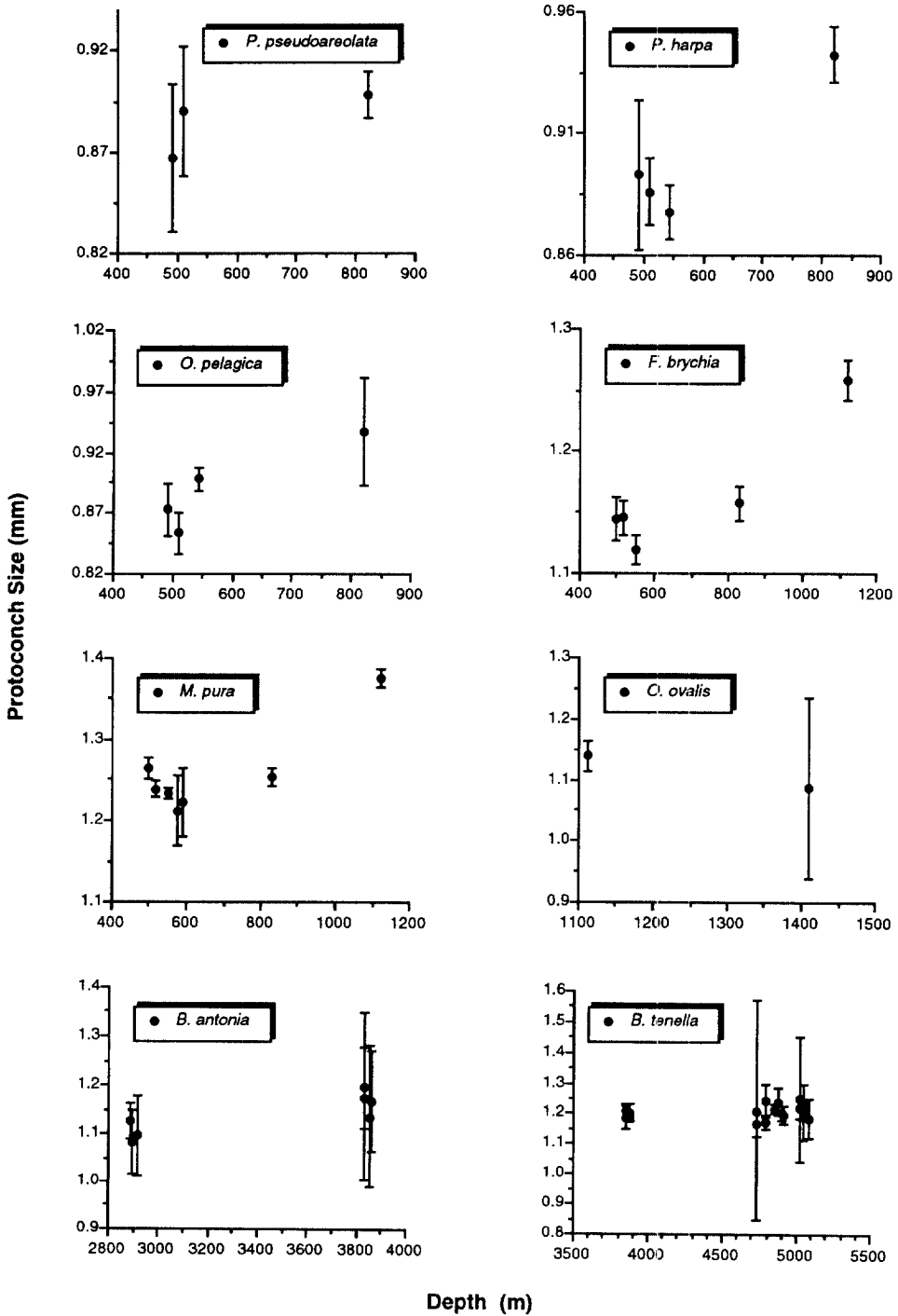
As mentioned earlier, Sebens (1982) optimality model predicts the size at which animals stop growing, though it also should apply to all stages of life history such as first whorl size. The final size to which members of a population grow is difficult to determine accurately in deep-sea organisms with indeterminate growth, particularly from relatively small samples of species that are sparsely distributed and for which some highly variable proportion of large individuals is collected. For a given first whorl size, there is typically a wide range of final sizes depending on the different phases of growth represented in a sample – many individuals simply have not reached their potential final size by adding additional whorls. Generally, plots of final size against first whorl size tend to be triangular in shape with an upward sloping upper boundary suggesting a positive relationship between first whorl size and final size. We compared first whorl size to final size by using the largest individuals from this upper boundary. First whorl size was positively and significantly correlated with final size in five of the eight species (*O. pelagica*,  $F_{1,7} = 9.047$ ,  $P < 0.020$ ; *F. brychia*,  $F_{1,11} = 14.516$ ,  $P < 0.003$ ; *O. ovalis*,  $F_{1,7} = 27.043$ ,  $P < 0.001$ ; *B. antonia*,  $F_{1,10} = 10.855$ ,  $P < 0.008$ ; *B. tenella*,  $F_{1,7} = 5.604$ ,  $P < 0.050$ ). Relationships in the two species of *Pusillina* were positive, but not significant. We could not perform the analysis for *M. pura* because we lacked data on final size. We also conducted an analysis in which we selected the largest five individuals from each sample and then included all individuals for each species that were as large as the smallest individual found by this procedure. Using this very conservative criterion for larger-sized individuals, we then normalized the data on first whorl size and final size within species in order to combine species. First whorl size is positively and significantly related to final size for the upper bathyal group (Fig. 2) of six species ( $F_{1,248} = 15.502$ ,  $P < 0.0001$ ) and for the two lower bathyal and abyssal species ( $F_{1,113} = 19.553$ ,  $P < 0.0001$ ). While highly subject to sampling error and other sources of uncertainty, the analyses suggest that standardized first whorl size in these species also may reflect the relative size of snails when growth ceases.

### 5.1.2. Larval shell size

It is interesting that larval shell size shows similar size–depth trends (Fig. 4), with *P. harpa*, *M. pura* and *F. brychia* exhibiting very marked shifts between shallow and deeper stations and the lower bathyal and abyssal species showing broad overlap of confidence limits. All species show positive size–depth trends, and seven of the eight regressions are significant (Fig. 5). Figure 5 suggests a decrease in the slope of size–depth relationships with increasing depth. The ANCOVA shows that the slopes are heterogeneous. The multiple comparison tests reveal some differences among

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Fig. 4. Means and 95% confidence limits for samples of larval shell size measured as height plus width of the exposed protoconch for all species except *B. antonia* which represents width only (the apex of many larval shells were corroded in this species). Means are plotted against depth (m) of sampling in the western North Atlantic south of New England.



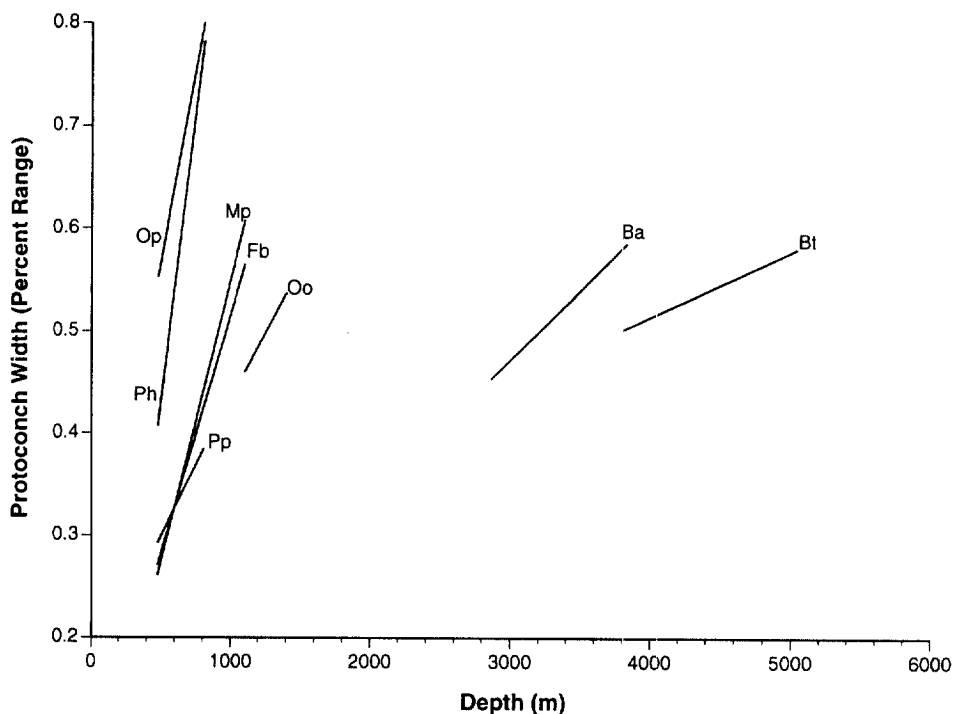


Fig. 5. Larval size (width of the larval shell), converted to percent range, plotted as regression lines against depth. Data are from Fig. 4. Regression equations and their statistics are given in Table 1. Symbols refer to species in Fig. 4.

upper bathyal species, and that slopes of several upper bathyal species exceed those of the deeper-dwelling *B. antonia* and *B. tenella*. When the analysis was repeated on raw size data, the within-species regressions retained the same  $F$  values (all regressions are positive, and 7 out of 8 are significant). The slopes remain heterogeneous ( $F = 19.728$ ,  $P < 0.001$ ), and the slopes of *P. harpa*, *F. brychia*, *M. pura* and *B. antonia* exceed that for the abyssal *B. tenella*. A conservative interpretation of these ANCOVA results is that bathyal species show stronger clinal effects than does the abyssal species, with some indication that the lower bathyal species is intermediate.

The connection between parameters of the optimality model or Thiel's size-structure hypothesis is much less obvious and consistent for various larval types than for adults which all live and forage on the bottom. *Benthomangelia antonia* and *B. tenella* have planktotrophic development, and the other six species have nonplanktotrophic development. Planktotrophic larvae hatch early and develop in the pelagic environment; nonplanktotrophic larvae develop in egg capsules in the benthic environment (Rex and Warén, 1982; Killingley and Rex, 1985; Potter and Rex, 1992; Stuart and Rex, 1994). Spight (1976) discussed the advantages of larger size at hatching for larvae of marine snails. These include greater locomotion to find food, a larger range of



available food items, greater ability to withstand starvation, and lower vulnerability to predators. Larger larval size may be a consequence of selection to exceed optimal size at greater depths in adults of nonplanktotropic species (i.e. a shift toward K-selected characters including larger adult size and fewer larger offspring). Conversely, larger larval size may, in itself, result in larger first whorl size through geometric constraints on subsequent adult whorl growth (Gould, 1969). However, the strong correlation between larval size and depth, and the weaker (but still significant) correlation between adult size and depth in *P. harpa*, suggest that simple growth constraints may be less important than selection acting independently on adults and larvae. Larval size is only weakly related to depth in *B. antonia* and *B. tenella*. This might be expected since larvae probably migrated from a number of different populations and are not as subject to local selection as in species with nonplanktotrophic development. These increases in planktotrophic larval size, if meaningful, might result from selection favoring larger settling larvae at greater depths for all the same reasons that Spight (1976) suggested for hatching larvae.

### 5.2. *Body size and biodiversity*

Explanations of deep-sea biodiversity have centered almost exclusively on ecological phenomena, primarily because of the short time scales available for observation at this early stage of exploration (Rex, 1997). Undoubtedly, ecological causes do contribute to shaping patterns of diversity on local (Hessler and Jumars, 1974; Grassle and Maciolek, 1992), regional (Hessler and Sanders, 1967; Rex, 1981; Etter and Grassle, 1992), and global (Hessler and Wilson, 1983; Rex et al., 1993) scales. However, it is the historical-evolutionary processes of adaptation and speciation that ultimately generate the rich and endemic deep-sea fauna (Etter and Rex, 1990; Stuart and Rex, 1994; Rex et al., 1997). Geographic patterns of body size may enable us to study the interface between ecological and macroevolutionary causes of species diversity.

There is now tremendous interest among macroecologists in the relationships among body size, species diversity and abundance. But the nature and direction of causality of these relationships remain controversial, and are beset with difficult methodological and analytical problems (see e.g. Nee and Lawton, 1996; Warwick and Clarke, 1996). In general, on larger scales, there appears to be a negative relationship between animal abundance (density) and body size across many taxa (Currie, 1993; Cotgreave, 1993; Brown, 1995). Less is known about the relationship of diversity to size, but it also appears to be negative in many cases (e.g. May, 1988; Blackburn and Gaston, 1994). In a very general way, this is also true in the deep-sea benthos. The large megafauna is much less diverse than the smaller macrofauna (Rex, 1983; Gage and Tyler, 1991). It remains less clear how the relationships among diversity, abundance and body size vary among communities, and at different spatial scales (Blackburn and Gaston, 1994).

Assuming that size is an adaptive property, could the increase in size with depth affect biodiversity, and, if so, how and on what spatial scales? The abundance of

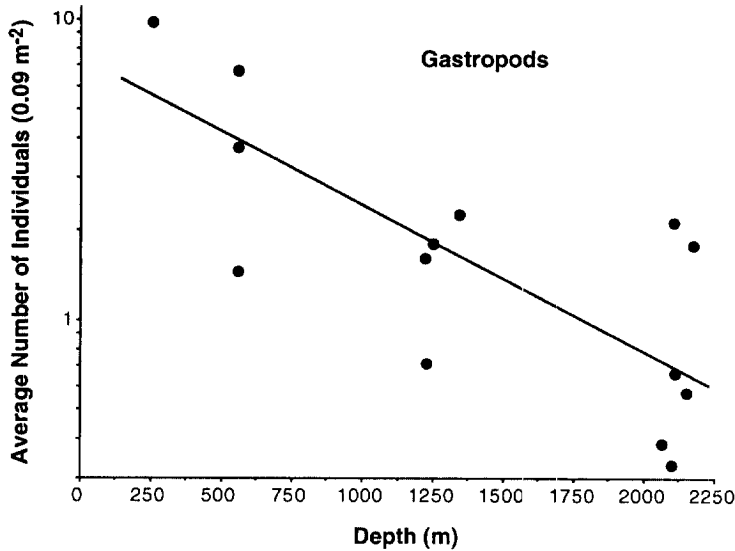


Fig. 6. Animal abundance measured as the average number of gastropod individuals  $0.09 \text{ m}^{-2}$  in replicates of boxcores taken at 14 stations south of New England sampled in the Atlantic Continental Slope and Rise Study (Maciolek et al., 1987, Rex et al., 1990). The regression of abundance against depth is  $A = 6.559 \times 10^{(-0.000456D)}$ ,  $r^2 = 0.557$ ,  $P < 0.01$ .

gastropods (density measured as the number of individuals per  $0.09 \text{ m}^2$ ) declines exponentially with depth in the western North Atlantic (Rex et al., 1990; Fig. 6). Diversity measured as species density of gastropods (number of species per  $0.09 \text{ m}^2$ ) shows a simple linear decline with depth (Fig. 7). This decline of diversity at very small scales, the probable scale of inter- and intra-species interactions, is enforced by the steep drop in density with depth. [At larger local scales, diversity shows a parabolic pattern with depth (Rex, 1981; Etter and Grassle, 1992)]. Consequently, both within and among species, a trend toward larger size is associated with a decline in density and diversity, just as it appears to be in other ecosystems. Thus, the possibility exists that the decrease in food availability with depth, as reflected in decreased abundance, selects for larger size, which in turn limits diversity since the finite amount of energy available at any particular depth can support fewer larger than smaller individuals.

Among the species considered here, there is also an expansion of geographic range with increased depth of occupancy (Etter and Rex, 1990). Interestingly, this also corresponds to a well known relationship in terrestrial systems; larger animals have broader ranges (Gaston and Blackburn, 1996). Species with larger geographic ranges are less vulnerable to extinction. It may not be necessary to invoke minimal population size for reproduction and persistence as a primary factor limiting body size, as did Thiel (1975, 1979) in his size–structure hypothesis. Rather, species may successfully occupy a certain vertical and horizontal distribution at viable population size within

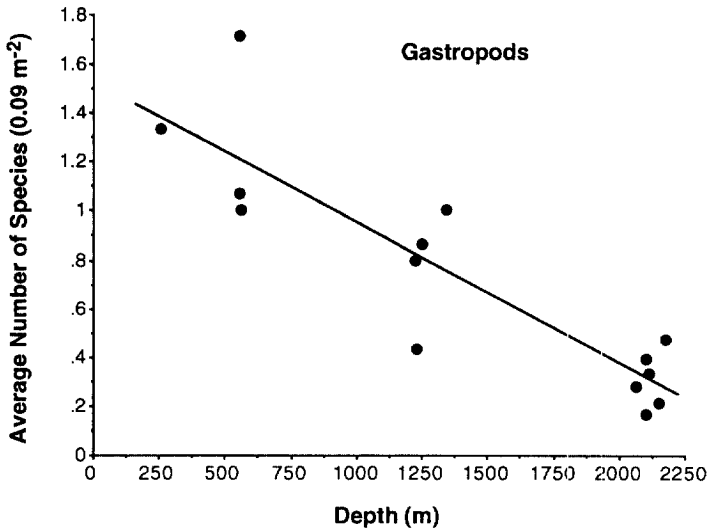


Fig. 7. Species density measured as the average number of species  $0.09 \text{ m}^{-2}$  in replicates of boxcores taken at 14 stations south of New England sampled in the Atlantic Continental Slope and Rise Study (Maciolek et al., 1987). The regression of species density against depth is  $S = 1.531 - 0.001D$ ,  $r^2 = 0.783$ ,  $P < 0.001$ .

which selection acts to cause geographic variation in body size and this, to some degree, mediates biodiversity within the taxon. As with many macroecological phenomena, the relationships among body size, density, diversity and range size obtain at larger, regional to global, scales. At smaller scales, patterns tend to disintegrate or to assume a variety of poorly understood shapes (Currie, 1993; Blackburn and Gaston, 1994). The analysis presented here, as well, suggests that if size affects biodiversity, then the interaction comes into play on fairly large scales, probably hundreds of meters of depth in the upper bathyal region to around 1000 m in the abyss (Figs. 2 and 4; Table 1).

The analysis of geographic variation in size data also reinforces the impression that the bathyal region is an evolutionary hotspot that has an integral role in deep-sea taxon cycles (Rex and Warén, 1981). Etter and Rex (1990) presented a multivariate analysis of the relative amount of divergence in shell architecture of populations of snail species arrayed along a depth gradient in the western North Atlantic (including seven of the species analyzed here). The degree of inter-population differentiation decreased with depth. We proposed that the potential for radiation in the deep sea varies geographically and is highest at bathyal depths, where the selective gradient is steeper and there is more opportunity for geographic isolation, and where food resources permit a higher level of coexistence than in the abyss. Results of the ANCOVAs (Table 1), which here are restricted to one dimension of our earlier analysis, support the notion that clinal variation is more pronounced at bathyal depths.

## 6. Summary and conclusions

Compared to coastal faunas, the single most prominent adaptive feature of the deep-sea benthos is the small size of most species. Studies of geographic variation in size *within* the deep-sea environment present a confusing picture, partly because of methodological problems and the lack of phylogenetic and ecological control. We emphasize here that interpreting size as an adaptation to the deep-sea environment should include analyses within species using standardized measures, as well as comparisons among species. Earlier theoretical considerations of size–depth patterns predict that size should decrease with increasing depth. Our analysis of intraspecific patterns of size in eight gastropods arrayed along a depth gradient revealed a recurrent tendency for size to increase with depth in both larval and adult shells. There was no indication that size decreased with depth. Size also appeared to increase with depth interspecifically in subsets of species that were most closely related and had similar ecologies. Of course, any study based on only eight species of one taxon in one ocean basin must be interpreted with caution. Nevertheless, the results of the present study are remarkably consistent and show that there appear to be very similar effects in divergent species of gastropods with different life styles. The important finding here is the positive size–depth pattern itself; the causes remain very uncertain. Numerous selective agents could favor larger body size with increased depth, and these agents may act in idiosyncratic ways on different species. We suggest a simple explanation – that decreased nutrient input with increasing depth selectively favors increased size because of its metabolic and competitive advantages to both larvae and adults. For this group of species, there is no need to invoke counterselection for small size to maintain viable population density, as in earlier explanations, because deeper-dwelling species have much broader geographic ranges making them less vulnerable to local extinction. The negative relationships of body size to abundance and species density suggest that body size may help mediate biodiversity, on large scales at least. Thus, there may be a connection between the evolved adaptive properties of species and contemporary levels of diversity. This is not a new idea in evolutionary ecology, but our present understanding of deep-sea biodiversity is based almost exclusively on potential ecological causes exerted on short time scales rather than evolutionary-historical causes. Results of the ANCOVA, showing that the degree of clinal variation decreases with depth, support the idea that the bathyal environment is an important site of diversification leading to high biodiversity in the deep sea.

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