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## The relationship between dissolved oxygen concentration and maximum size in deep-sea turrid gastropods: an application of quantile regression

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**Abstract** Bathymetric gradients in body size are the most well-known patterns of geographic variation in deep-sea organisms. The causes of size–depth relationships remain uncertain, but most have been attributed to rates of nutrient input. Chappelle and Peck (1999, *Nature* 399:114–115) recently hypothesized that body size in marine invertebrates is a function of dissolved oxygen concentration. We tested this hypothesis by using quantile regression techniques to assess the relationship of dissolved oxygen levels to maximum size in deep-sea turrid gastropods collected from the North Atlantic. Relationships were examined for a group of nine turrid species and within the abundant lower bathyal species *Benthomangalia antonia* (Dall, 1881). We controlled the analysis for depth because size in deep-sea gastropods varies bathymetrically. When the effects of depth are accounted for statistically, maximum size in *B. antonia* increases with increasing levels of dissolved oxygen. In turrids as a group, both depth and oxygen appear to explain significant proportions of the variance in maximum size. These findings suggest that a suite of factors, including dissolved oxygen concentration, may influence maximum size in deep-sea organisms.

### Introduction

Body size is related to a broad range of ecological phenomena including species range size (e.g. Gaston and

Blackburn 1996), density (e.g. Warwick and Clarke 1996; Johnson 1999; Siemann et al. 1999), and taxonomic diversity (e.g. Siemann et al. 1996, 1999; Warwick and Clarke 1996). These associations are not surprising because body size is strongly correlated with many life history traits that can influence distribution (Blackburn and Gaston 1994). Most previous studies on body size concern terrestrial, aquatic, and coastal faunas. In the deep sea, size clines along depth gradients have been documented in several taxa. Most explanations for these relationships center on food availability, though a variety of biotic and abiotic factors may be involved (see Rex and Etter 1998 for a review).

Chappelle and Peck (1999) have recently proposed that oxygen availability controls maximum size in shallow-water marine invertebrates (referred to here as the OMS hypothesis). In this study we examine the OMS hypothesis both within and among species of deep-sea turrid gastropods. Specifically, we test whether there is a positive relationship between dissolved oxygen concentration and the maximum size attained.

The Turridae is the most diverse and broadly distributed family of gastropods in the deep North Atlantic (Bouchet and Warén 1980). This family consists of predators that specialize on polychaete worms (Shimek 1983). Geographic patterns of shell size have been documented in several species of turrids (Rex and Etter 1990, 1998; Rex et al. 1999; Clain and Rex 2000). These size studies all show that shell size increases with increasing depth.

Significant methodological difficulties arise when testing hypotheses related to maximum size using material from dredged samples in marine environments. Samples contain young and old individuals, and the size-frequency distributions reflect the recent history of recruitment. Also, most deep-sea species are sparsely distributed, causing considerable uncertainty about whether individuals representing the maximum size have been collected from a particular habitat. To estimate maximum size, Rex et al. (1999) used the two largest individuals of a species collected from 500 m depth

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intervals. This method results in a substantial loss of sample size, and thus statistical power. Arbitrary decisions must be made in selecting depth intervals and the number of individuals to use at each interval. Chapelle and Peck (1999), to address the same problem, chose a threshold size that separated the largest 5% from the smallest 95% of individuals. Again, this resulted in a loss of sample size and the use of ad hoc selection criteria.

Here, we examine the relationship between maximum size and oxygen concentration using quantile regression, a statistical method that provides a more objective assessment of trends in maximum body size without the loss of sample size (Scharf et al. 1998; Cade et al. 1999). Quantile regression is a form of regression that is based on least absolute deviations being minimized. It permits choosing a quantile (a family of statistics that allows a distribution to be divided into sections) ranging from 0.00 to 1.00 to test for relationships in a particular region of the bivariate distribution. Hypothesis tests for quantile regressions are performed by an asymptotic rankscore test based on a Chi-squared distribution (Cade and Guo 2000). Quantile regression, like normal regression, has a coefficient of determination,  $R_1$ . This is obtained by subtracting from 1 the weighted absolute deviations from the original model divided by weighted absolute deviations from a null model (regression model without an independent variable).  $R_1$  is interpreted as the proportionate reduction in variation between the simple quantile estimate of the dependent variable and the estimate conditioned on the independent variable. The weighted sums of absolute deviations are the quantities minimized in estimating a specified quantile (B.S. Cade, personal communication). Just as with regular regression,  $R_1$  values reflect the amount of scatter of data around the quantile regression line.

## Materials and methods

The material used in this study was collected from the deep sea using box cores, epibenthic sleds, anchor dredges, Blake deep-sea trawls, and beam trawls. We combined two large existing databases on morphometrics of turrids from the western North Atlantic (Rex et al. 1999; Clain and Rex 2000), and added 67 new specimens from the following five areas: Norwegian Sea, West European Basin, Guiana Basin, Gambia Basin, and the equatorial Atlantic. Two separate groups of analyses were carried out. First, a within-species study was conducted on the most abundant and broadly distributed species, *Benthomangelia antonia*, collected from 9.48°N to 40.28°N, at 1934–3862 m depth in the western and eastern North Atlantic. The second is an among-species analysis using 353 individuals from nine species in the family Turridae [*B. antonia* (Dall, 1881); *B. decapitata* Bouchet and Warén, 1980; *B. macra* (Watson, 1881); *Gymnobela* sp. Verrill, 1884; *Pleurotomella packardii* Verrill, 1872; *P. sandersoni* Verrill, 1884; *P. anceyi* (Dautzenberg and Fisher, 1897); *P. lottae* Verrill, 1885; and *Theta lyronuclea* (Clarke, 1959)], with distributions spanning 0.77°S–76.93°N, at 478–4970 m depth in the western and eastern North Atlantic. Our selection criterion was to measure all known specimens, in sufficiently good condition, from the Woods Hole Benthic Sampling Program and American and European museums. We were also able to measure five specimens of *P. packardii* collected in the Norwegian Sea. Since the Norwegian Sea is a relatively small, semi-isolated basin, with

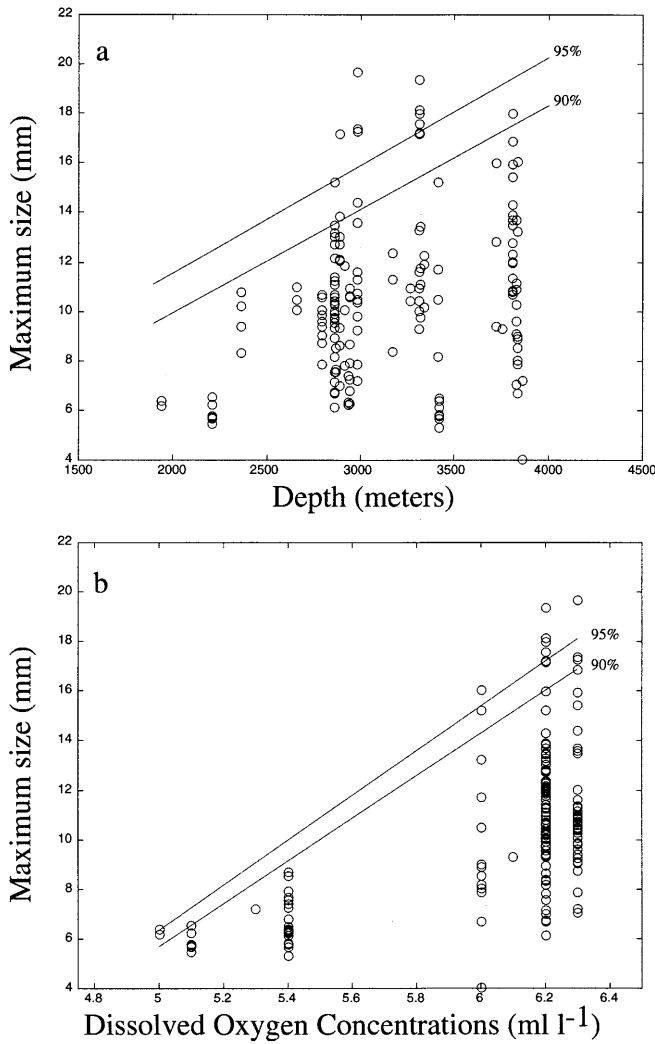
limited taxonomic representation in our data set, we carried out the among-species analysis with and without the Norwegian Sea data.

Dissolved oxygen levels ( $\text{ml l}^{-1}$ ) were obtained from the World Ocean Atlas (NODC 1998, figures). This CD-ROM contains annual, seasonal, and monthly measurements of oxygen concentrations. Data consist of readings for  $1^\circ$  squares at vertically interpolated standard depth intervals. These 31 depth intervals extend from 0 to 5500 m, with 10 m increments at the shallowest depths increasing to 500 m in the deepest intervals. Annual means were chosen for this study because we expected shell size to respond mainly to longer term oxygen differences. At depths <1500 m, annual mean oxygen data represent an average of 12 monthly means. At depths >1500 m, the annual averages were taken on the four seasonal estimates. At the longitude and latitude of sampling stations we interpolated oxygen concentrations from the two closest depth intervals. Although patterns of dissolved oxygen concentrations in the North Atlantic are complex, there is a general increase in oxygen levels with increases in depth and latitude. The oxygen concentrations reported here ( $4.2\text{--}7.0 \text{ ml l}^{-1}$ ) do not approach the levels found in oxygen minimum zones, which exert a strong localized influence on community makeup and adaptation (Gage et al. 2000).

Maximum shell size was measured as height plus width (Gould 1969; Rex et al. 1999). The statistical software package, BLOSSOM, developed by the Midcontinent Ecological Science Center, was used for the analysis. Significance tests were conducted on the 95%, 90%, and 85% quantile regression lines for the nine turrid species and 95% and 90% lines for *B. antonia*. The additional 85% quantile regression for turrids was performed because of the expected increased variance in the data set that accompanies a loss of phylogenetic and geographic control. First, we examined separately the relationships of maximum size to depth and dissolved oxygen concentrations. The trend between maximum size and dissolved oxygen concentrations may be a spurious result of the relationship between depth and oxygen concentrations ( $r=0.103$ ,  $P=0.0537$ ). To account for this, we conducted analyses in which we assessed whether oxygen or depth explains any additional variance when added to the model. This was done by comparing a full model, containing both oxygen and depth, to a reduced null model, in which the independent variable of interest was removed. Even though depth and oxygen are weakly correlated it is still important to statistically account for depth in order to understand the independent association between size and oxygen, particularly since the bathymetric range studied is so large. We also statistically controlled for latitude and temperature, but observed no differences in the results. Matlab was used to plot both the scattergrams and quantile regression lines. Details of collection locations, shell measurements, and oxygen concentrations on the nine turrid species are presented in Appendix I of an electronic supplement available at <http://dx.doi.org/10.1007/s002270100617>.

## Results and discussion

In *Benthomangelia antonia*, maximum size increased significantly with depth for the 90% quantile line, but not for the 95% quantile line (Fig. 1a; Table 1). However, oxygen was a better predictor of size for the 90% quantile, and also predicted size significantly for the 95% quantile (Fig. 1b; Table 1). The full model, oxygen and depth included, was significant for both quantile lines (Table 1). For the 90% and 95% quantiles, a comparison of the full model to a null model with depth removed showed no significant difference, suggesting that depth does not explain any significant new variance when added to the model (Table 2). However, when the full model was compared to the null model with oxygen removed, the two models were significantly different



**Fig. 1a, b** *Benthomangelia antonia*. **a** The relationship between maximum size and depth. Lines represent 95% ( $y = 2.78 + 0.0044x$ ,  $P = 0.1904$ ,  $R_1 = 0.0159$ ,  $n = 169$ ) and 90% ( $y = 1.59 + 0.0041x$ ,  $P = 0.0078$ ,  $R_1 = 0.0882$ ,  $n = 169$ ) quantile regressions. **b** The relationship between maximum size and dissolved oxygen concentrations. Lines represent 95% ( $y = -38.83 + 9.04x$ ,  $P = 0.0002$ ,  $R_1 = 0.1756$ ,  $n = 169$ ) and 90% ( $y = -37.31 + 8.60x$ ,  $P = 0.0004$ ,  $R_1 = 0.1676$ ,  $n = 169$ ) quantile regressions

(Table 2). In other words, oxygen explains variance in maximum size that depth does not.

Maximum size and depth were significantly and positively related for the 85%, 90%, and 95% quantiles in the nine turrid species, excluding data from the five specimens of *Pleurotomella packardi* from the Norwegian Sea (Fig. 2a; Table 1). This confirms the findings of Rex et al. (1999) that size in deep-sea turrid gastropods tends to increase with depth. Maximum size also increased with increased oxygen levels for all three quantiles (Fig. 2b; Table 1). The full model, in all cases, was significantly different from the reduced null models, implying that both depth and oxygen have a role in predicting maximum size among the turrid species.

The analyses of the nine turrid species (Fig. 2a,b) indicate a group of outliers from the Norwegian Sea that was composed of conspicuously larger individuals of *P. packardi*. Four of these were larger in their absolute dimensions and had more whorls of growth. The single small individual was younger (solid circle, lower right of Fig. 2a,b), again emphasizing the need for a method like quantile regression to estimate maximum size in an assemblage of mixed age. Including Norwegian Sea data in the analysis does not significantly change the outcome of the quantile regressions. However, neither depth nor oxygen appear to account for this group. There are two characteristics of the Norwegian Sea that may be responsible for larger maximum size. First, while bottom temperature does not vary greatly within the region studied (3.7–4.2°C), the Norwegian deep sea does have a lower (~1°C) temperature (NODC 1998, figures), and body size is often correlated negatively with temperature (Van Voorhies 1996). Second, there is high surface production at higher latitudes, so nutrient input from sinking phytodetritus may be higher permitting larger size (Sebens 1982). It is difficult to know how typical these few data are. If the substantial difference in size between the Norwegian Sea and North Atlantic turrids is real, it may be comparable to shifts in size between coastal and deep-sea habitats (Rex et al. 1999).

According to the OMS hypothesis, maximum size is a positive function of oxygen concentration. Chapelle and Peck (1999) suggest that this relationship is caused by higher absolute concentrations of oxygen in the

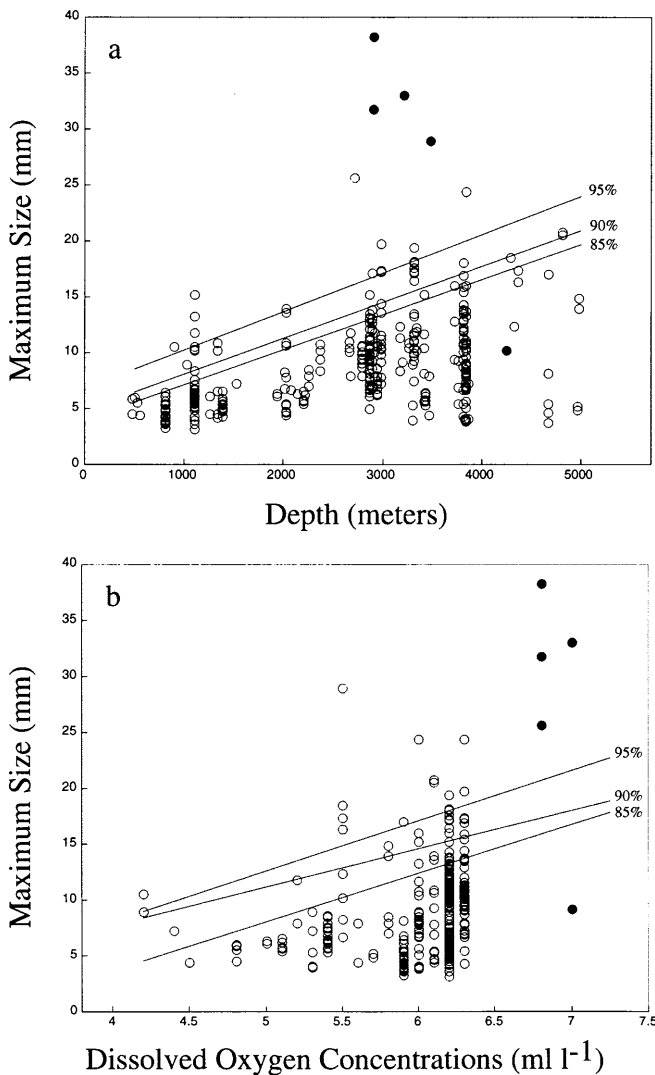
**Table 1** *Benthomangelia antonia* and family Turridae (nine species). Quantile regression summary for relationships between size and depth, dissolved oxygen concentrations, and a full model containing both depth and oxygen concentrations. *P*-values are

reported for each quantile regression line.  $R_1$  is the proportionate reduction in variation between the simple quantile estimate of the dependent variable and the estimate conditioned on the independent variable

Taxon	Test	<i>P</i> -value for quantile regression lines		
		85%	90%	95%
<i>B. antonia</i>	Depth		0.0078 ( $R_1 = 0.0882$ )	0.1904 ( $R_1 = 0.0159$ )
	O <sub>2</sub> ml l <sup>-1</sup>		0.0004 ( $R_1 = 0.1676$ )	0.0002 ( $R_1 = 0.1756$ )
	Full model		0.0002 ( $R_1 = 0.1730$ )	0.0004 ( $R_1 = 0.1833$ )
Turridae	Depth	0.0010 ( $R_1 = 0.0502$ )	0.0014 ( $R_1 = 0.0551$ )	0.0154 ( $R_1 = 0.0482$ )
	O <sub>2</sub> ml l <sup>-1</sup>	0.0040 ( $R_1 = 0.0368$ )	0.0034 ( $R_1 = 0.0509$ )	0.0100 ( $R_1 = 0.0619$ )
	Full model	0.0002 ( $R_1 = 0.0772$ )	0.0006 ( $R_1 = 0.0862$ )	0.0006 ( $R_1 = 0.0927$ )

**Table 2** *Benthomangelia antonia* and family Turridae (nine species). Summary of hypothesis tests of full model compared to reduced null model. *P*-values are the probability that the two models are the same or explain the same amount of variance

Taxon	Null model	<i>P</i> -value for quantile regression lines		
		85%	90%	95%
<i>B. antonia</i>	Size = constant + oxygen		0.6813	0.4852
	Size = constant + depth		0.0277	0.0158
Turridae	Size = constant + oxygen	0.0034	0.0299	0.0279
	Size = constant + depth	0.0022	0.0299	0.0204



**Fig. 2a, b** Turridae (nine species). **a** The relationship between maximum size and depth in the North Atlantic. *Solid circles* represent the five specimens of *Pleurotomella packardii* from the Norwegian Sea. Lines represent 95% ( $y = 6.85 + 0.0034x$ ,  $P = 0.0154$ ,  $R_1 = 0.0482$ ,  $n = 353$ ), 90% ( $y = 4.83 + 0.0032x$ ,  $P = 0.0014$ ,  $R_1 = 0.0551$ ,  $n = 353$ ), and 85% ( $y = 3.98 + 0.0031x$ ,  $P = 0.0010$ ,  $R_1 = 0.0502$ ,  $n = 353$ ) quantile regressions. **b** The relationship between maximum size and dissolved oxygen concentrations. Lines represent 95% ( $y = -9.901 + 4.51x$ ,  $P = 0.0100$ ,  $R_1 = 0.0619$ ,  $n = 353$ ) 90% ( $y = -5.93 + 3.42x$ ,  $P = 0.0034$ ,  $R_1 = 0.0509$ ,  $n = 353$ ), and 85% ( $y = -13.83 + 4.38x$ ,  $P = 0.0040$ ,  $R_1 = 0.0368$ ,  $n = 353$ ) quantile regressions

haemolymph of benthic amphipods, which allow greater path lengths in the circulatory system. Thus, it follows that an organism's length can increase at higher oxygen levels. Whether the relationship is stronger between oxygen and length, or oxygen and mass depends on branching patterns in the circulatory system. This hypothesis centers on a direct physiological effect of oxygen concentration; however, it is possible that oxygen concentration is only one factor involved, or that the mechanism is indirect, since size is related to so many aspects of life history and ecology (Peters 1983). Size trends may also reflect ecological interactions modified by oxygen concentrations.

Results for the most phylogenetically and ecologically coherent data set, the within-species comparison using *B. antonia*, indicate that higher oxygen concentrations are correlated with a larger maximum size. The among-species comparison also exhibits a positive trend in size with increasing oxygen, despite the loss of taxonomic and geographic control. The physiological mechanisms involved are uncertain, but the significant depth-controlled relationship between oxygen concentrations and body size in turrids extends comparative support for Chappelle and Peck's (1999) hypothesis to deep-sea invertebrates. A multiplicity of factors, including food availability and physiological constraints, may affect geographic patterns of size in the deep sea. The analysis also shows that quantile regression is a useful tool for exploring maximum size trends in age-structured populations such as those recovered by deep-sea sampling gear. As with all studies based on remote sampling in this very inaccessible environment, results should be interpreted with caution; but, the findings point encouragingly to potential physiological determinants of body size.

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## References

Blackburn TM, Gaston KJ (1994) Body size and density – the limits to biomass and energy use. *Oikos* 69:336–339

- Bouchet P, Warén A (1980) Revision of the North-East Atlantic bathyal and abyssal Turridae (Mollusca, Gastropoda). *J Molluscan Stud Suppl* 8:1–119
- Cade BS, Guo Q (2000) Estimating effects of constraints on plant performance with regression quantiles. *Oikos* 91:245–254
- Cade BS, Terrel JW, Schroeder RL (1999) Estimating effects of limiting factors with regression quantiles. *Ecology* 80:311–323
- Chapelle G, Peck LS (1999) Polar gigantism dictated by oxygen availability. *Nature* 399:114–115
- Clain AJ, Rex MA (2000) Size-depth patterns in two bathyal turrid gastropods: *Benthomangelia antonia* (Dall) and *Oenopota ovalis* (Friele). *Nautilus* 114:93–98
- Gage JD, Levin LA, Wolff GA (2000) Benthic processes in the deep Arabian Sea: introduction and overview. *Deep-Sea Res II* 47:1–8
- Gaston KJ, Blackburn TM (1996) Range size – body size relationships: evidence of scale dependence. *Oikos* 75:479–485
- Gould SJ (1969) An evolutionary microcosm: Pleistocene and Recent history of the land snail *P. (Poecilozonites)* in Bermuda. *Bull Mus Comp Zool* 138:407–532
- Johnson CN (1999) Relationships between body size and population density of animals: the problem with scaling of study area in relation to body size. *Oikos* 85:565–569
- NODC (National Oceanographic Data Center) (1998) World Ocean atlas. Available as CD-ROM from the Ocean Climate Laboratory, NODC, Washington, DC
- Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge
- Rex MA, Etter RJ (1990) Geographic variation in two deep-sea gastropods, *Benthonella tenella* (Jeffreys) and *Benthomangelia antonia* (Dall). *Deep-Sea Res* 37:1229–1249
- Rex MA, Etter RJ (1998) Bathymetric patterns of body size: implications for deep-sea biodiversity. *Deep-Sea Res II* 45:103–127
- Rex MA, Etter RJ, Clain AJ, Hill MS (1999) Bathymetric patterns of body size in deep-sea gastropods. *Evolution* 53:1298–1301
- Scharf FS, Juanes F, Michael S (1998) Inferring ecological relationships from the edges of scatter diagrams: comparisons of regression techniques. *Ecology* 79:448–460
- Sebens KP (1982) The limits to indeterminate growth: an optimal size model applied to passive suspension feeders. *Ecology* 63:209–222
- Shimek RL (1983) Biology of the northeastern Pacific Turridae. I. *Malacologia* 23:281–312
- Siemann E, Tilman D, Haarstad J (1996) Insect species diversity, abundance and body size relationships. *Nature* 380:704–706
- Siemann E, Tilman D, Haarstad J (1999) Abundance, diversity and body size: patterns from a grassland arthropod community. *J Anim Ecol* 68:824–835
- Van Voorhies WA (1996) Bergmann size clines: a simple explanation for their occurrence in ectotherms. *Evolution* 50:1259–1264
- Warwick RM, Clarke KR (1996) Relationships between body-size, species abundance and diversity in marine benthic assemblages: facts or artefacts? *J Exp Mar Biol Ecol* 202:63–71