PATTERNS OF MORPHOLOGICAL VARIATION OF THE DEEP-SEA GASTROPOD *TROSCHELIA BERNICIENSIS* (KING, 1846) (BUCCINIDAE) FROM THE NORTHEASTERN ATLANTIC OCEAN

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ABSTRACT

Very little is known about population differentiation in bathyal species. The neogastropod *Troschelia berniciensis* occurs along the northeastern Atlantic continental shelf and upper slope. The species was relatively common at depths of 320–1265 m to the west and southwest of Ireland. Measurements of 435 specimens confirmed literature reports of variability in shell shape in this species. Shells varied significantly in relative spire height and in height-to-breadth ratios. Changes in shell shape were correlated strongly with depth, broad low-spired shells occurring at the shallow end of the bathymetric range, and slender high-spired shells in deeper water. A significant but weak trend for decrease in relative spire height with increasing latitude was identified. Possible causal factors for these patterns are discussed. These results support the theory that the upper slope is a site of potential importance for population differentiation for the deep-sea gastropod fauna.

INTRODUCTION

The deep sea supports a highly diverse benthic invertebrate fauna (e.g. Sanders & Hessler, 1969; Rex, 1981; Rex, Stuart & Coyne, 2000), and assemblage structure varies at scales from centimetres to kilometres (e.g. Grassle & Maciolek, 1992; Etter & Grassle, 1992; Rex *et al.*, 2000; Lambshead, Brown, Ferrero, Mitchell, Smith, Hawkins & Tietjen, 2002). An important first step to understanding patterns of speciation in the deep sea is to identify and quantify geographic variation within individual species (Gould & Johnston, 1972; Slatkin, 1987).

Studies of geographic variation have provided important information for understanding evolutionary processes of species inhabiting coastal marine environments (e.g. Gould & Johnston, 1972; Rex, Watts, Etter & O'Neill, 1988). In recent years, various studies have addressed key questions related to population differentiation and speciation in deep-sea organisms by quantifying either morphological (e.g. Wilson, 1983; Rex *et al.*, 1988; Rex & Etter, 1990; Rex, Bond, Etter, Rex & Stuart, 2002) or genetic (e.g. Siebenaller, 1978; Grassle, 1985; Bucklin, Wilson & Smith, 1987; Chase, Etter, Rex & Quattro, 1998; Quattro, Chase, Rex, Greig & Etter, 2001) patterns of geographic variation. Despite these significant advances, there is still an important gap in understanding basic evolutionary trends in the deep sea.

Variability in morphology among populations of a species may have a genetic basis (Janson, 1982; Johannesson, Johannesson & Rolán-Álvarez, 1993) as a response to selective pressures such as predation and physical disturbance (Vermeij, 1978), the need to conserve shell material (Graus, 1974) and factors favouring differences in life-history strategies (Rex, 1979). Alternatively, variability may result from phenotypic plasticity in response to different environmental factors (Janson, 1982; Boulding & Hay, 1993). Nevertheless, these mechanisms are not completely exclusive (for review, see Chapman, 1995).

Geographic variation in shell morphology has been documented for deep-sea molluscs (e.g. Rex *et al.*, 1988; Rex & Etter, 1990; Fuiman, Gage & Lamont, 1999; Rex *et al.*, 2002). Morphological differentiation appears to correlate more with depth than horizontal separation among populations (Rex *et al.*, 1988; Rex & Etter, 1990; Etter & Rex, 1990; Rex *et al.*, 2002) suggesting that environmental gradients such as hydrostratic pressure (Hochachka & Somero, 1984), sediment type (MacIlvaine & Ross, 1979), food availability (Rowe, Polloni & Haedrich, 1982), and biological interactions such as competition and/or predation (Vale & Rex, 1988; Rex *et al.*, 1988; Boulding & van Alstyne, 1993), play an important role in structuring these populations.

In this paper, we analyse bathymetric and geographic variation in shell form of a relatively common snail *Troschelia berniciensis* (King, 1846) (Fig. 1) of the neogastropod family Buccinidae. As with most deep-sea species, little is known of its natural history. Patterns of geographic variation in this species provide information of basic interest for population differentiation in bathyal species.

Troschelia berniciensis is broadly distributed along the continental shelf and upper slope in the northeastern Atlantic Ocean from northwest Africa to Norway (Bouchet & Warén, 1985). Some species of Buccinidae have a non-planktotrophic mode of development (Bouchet & Warén, 1985) and the larval shell morphology indicates that the same is true for *T. berniciensis.* Early descriptive studies have documented variation in shell shape, showing northern specimens to be broader than southern specimens, and individuals from greater depths to be relatively small and slender (Bouchet & Warén, 1985). Olabarria & Thurston (2003) found a trend from low-spired to high-spired shells with increasing depth.

The aim of this paper is to analyse and quantify the morphological variation in *T. berniciensis* since no previous works have studied this problem in detail. Hypotheses tested were, firstly, that there is geographic variation in shell morphology across depth and latitude, and secondly, that morphological differentiation in this species correlates more with depth differences than with horizontal separation, thus conforming to patterns described for other species of deep-sea snails.

MATERIAL AND METHODS

Sample collection

Material used in this study was obtained from two sources. The Biology Group at the Institute of Oceanographic Sciences

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Figure 1. *Troschelia berniciensis.* Left: Station 50717, 21 October 1979, Granton trawl, 510–500 m; H_t = 94.5 mm, H_s = 47.2 mm, B_p = 32.2 mm, B_m = 39.0 mm. Right: Station 50809, 1 August 1980, Granton trawl, 1250–1260 m; H_t = 101.1 mm, H_s = 68.6 mm, B_p = 27.8 mm, B_m = 34.1 mm. See Figure 2 for abbreviations of measurements.

Deacon Laboratory (IOSDL) (now Southampton Oceanography Centre) undertook an extensive sampling programme at slope and continental rise depths in the Porcupine Seabight area to the southwest of Ireland between 1977 and 1986 (Rice, Billett, Thurston & Lampitt, 1991). Towed gears including epibenthic sledge (Rice, Aldred, Darlington & Wild, 1982), otter trawl (OTSB14) (Merrett & Marshall, 1981) and Granton trawl (Gordon & Duncan, 1985) were used at depths ranging from 250 to 4500 m (Jackson, Thurston & Rice, 1991). In 1984–85 fishery investigation cruises PROCELT I and PROCELT II, organized by various laboratories (Centre National de le Recherche Scientifique, CNRS; Institut Spécialisé de le Technologie des Pêches Maritimes, ISTPM; Muséum National d'Histoire Naturelle, Université de Paris VII; Laboratoire de Biologie Marine de Concarneau; Institut Océanographique de Monaco) took samples on the Porcupine Bank and in the Porcupine Seabight using a commercial otter trawl. Material from these cruises was deposited at the Muséum National d'Histoire Naturelle, Paris. Samples selected for analysis contained a minimum of three undamaged *Troschelia berniciensis* shells resulting in a total of 44 samples collected between 49°23.2′ N and 53°25.2′ N in the depth range 320–1265 m (Table 1). Among locations the average horizontal separation was 170 km (range 2–451 km), and the average depth separation was 273 m (range 0–945 m).

The IOSDL sampling programme was confined almost exclusively to depths greater than 400 m. *Troschelia berniciensis* was recorded from 400 m down to 2078 m, but was rare in the deeper part of this range. The deepest sample conforming to the selection criteria (see above) was collected at 1265 m (Table 1). The 44 selected samples provided 435 shells for analysis (mean 9.9, range 3–31).

Four measurements and three ratios were used to quantify shell size and shape. Each shell was measured in axial view where the axis of coiling was perpendicular to the line of sight. Measurements were made to the nearest 0.1 mm using a Vernier caliper. The measurements made were: total height (H_t), height of spire (H_s), maximum diameter of penultimate whorl (B_p) and maximum breadth (B_m) (see Fig. 2). Shell shape was described by three ratios: total height/height of spire (H_t/H_s), total height/maximum breadth (H_t/B_m) and total height/maximum diameter of penultimate whorl (H_t/B_p).

Data analysis

Principal component analysis (PCA) was used to test the hypothesis of geographical variation in shell morphology. This methodology has been used extensively to study geographic variation in molluscs (e.g. Janson & Sundberg, 1983; Boulding & Hay, 1993; Merkt & Ellison, 1998; Fuiman *et al.*, 1999). This analysis reduces the set of variables by linear transformations, so that a minimum of information is lost. The new variables given by the transformations are independent of each other, and account for, in declining order, as much of the variation as possible. The first principal component of a morphometrics data set has often been interpreted as a general size factor; the second and subsequent principal components are then interpreted as shape factors (Bookstein, Chernoff, Elder, Humphries, Smith & Strauss, 1985).

Principal component analysis was computed on $\log_{10}(x + 1)$ transformed data using correlation matrix after testing for normality with the Kolmogorov–Smirnov statistic. Varimax rotation of axes was used to maximize discrimination among the samples (see Gould, 1969).

The three ratios used to describe shell shape, H_t/H_s, H_t/B_m and H_t/B_p, were combined into a multivariate measure of phenotypic

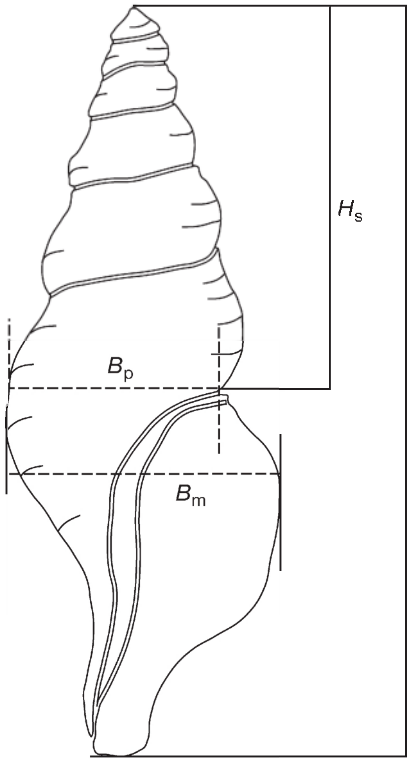

Figure 2. Measurements made on shells. Total height (H_t), height of spire (H_s), maximum diameter of penultimate whorl (B_p) and maximum breadth (B_m).

distance (Mahalanobis' generalized distance = D^2) to quantify the amount of interpopulation morphometric variation. D^2 is the morphological distance between population centroids within the multidimensional hyperspace (Atchley, Nordheim, Gunsett & Crump, 1982). Then, partial Mantel tests (Smouse, Long & Sokal, 1986) were used to test the second hypothesis that morphological variation, i.e. phenotypic distance, is more correlated with depth differences (in metres) than horizontal separation (in kilometres). A simple Mantel procedure (Mantel, 1967) assesses the significance of a regression between two distance matrices by calculating the sum of element-by-element products and then compares that statistic with a null distribution of values created from permutations of elements within one of the matrices. The partial Mantel test is an extended test for three matrices (Bonnet & Van de Peer, 2002) which estimates the correlation between matrices A and B while controlling the effect of a third matrix C, in order to remove spurious correlations (Bonnet & Van de Peer, 2002). The significance of the partial correlation coefficient was tested by permutation of the residuals (10,000 randomizations) of a null model (Anderson & Legendre, 1999), in which the independent variable of interest (i.e. depth differences or horizontal distances) was held constant. The statistical software package Zt, developed by Bonnet & Van de Peer (2002) was used for the analysis.

Table 1. Station data of samples.

Station	Latitude (N)	Longitude (W)	Depth (m)	No. of individuals	Gear*
L245	53°25.2′	12°35.2′	320	5	FT
L246	53°19.8′	12°36.2′	333	5	FT
L203	51°45.3′	13°54.1′	414	9	FT
L190	51°18.3′	14°11.5′	502	10	FT
50717	52°00′	13°33.0′	505	6	GT
L204	51°39.2′	14°43.5′	506	13	FT
50608#2	51°19.3′	14°22.3′	510	4	ES
L209	51°43.0′	14°43.2′	511	14	FT
51112#1	51°26.5′	13°58.6′	523	4	ES
L205	51°41.3′	14°50.8′	585	8	FT
L189	51°05.2′	13°55.0′	589	13	FT
L201	51°38.3′	13°42.6′	591	6	FT
L191	51°08.2′	14°02.2′	600	18	FT
L228	52°39.0′	14°48′.0′	603	3	FT
K194	51°41.9′	11°47.8′	607	14	FT
L197	52°05.8′	13°17.3′	609	8	FT
K207	50°25.6′	11°04.3′	649	4	FT
L254	52°17.5′	12°30.1′	668	7	FT
L251	52°14.5′	12°55.2′	678	12	FT
L198	52°07.0′	13°05.2′	686	31	FT
50820	51°55.4′	13°18.7′	719	6	OT
51312	49°27.0′	11°37.0′	733	5	OT
50716	51°52.5′	13°26.0′	747	5	GT
50524	49°33.3′	11°36.1′	763	10	OT
50507	51°50.6′	13°18.2′	780	15	GT
50707	49°54.0′	11°16.0′	780	17	GT
L186	51°25.7′	13°35.0′	785	6	FT
50601	51°19.2′	11°41.1′	840	5	OT
50824#3	49°26.0′	11°36.3′	857	23	ES
L253	52°10.6′	12°34.8′	880	8	FT
L252	52°04.8′	12°40.9′	889	22	FT
L188	51°27.8′	11°57.0′	908	14	FT
51103#5	51°47.0′	13°13.1′	940	22	ES
50610#1	51°26.5′	13°24.1′	980	14	ES
K183	51°17.9′	11°35.1′	980	3	FT
51305	51°50.2′	13°05.1′	985	5	OT
51315	49°32.8′	11°52.1′	1015	5	GT
50503	51°37.1′	13°14.6′	1025	6	OT
50904	51°21.8′	13°27.4′	1027	8	OT
50708	49°23.2′	12°01.0′	1057	10	GT
50606#5	50°43.1′	13°56.1′	1130	7	ES
50520	49°33.6′	12°08.1′	1237	5	GT
50809	49°31.9′	12°09.7′	1255	16	GT
50801	49°35.0′	12°11.4′	1265	4	OT

*Sampling gear: ES, epibenthic sledge, OT, otter trawl (OTSB14), GT, Granton trawl and FT, French commercial otter trawl.

RESULTS

Patterns of morphological variation

The three principal components explained 97.8% of the variance: additional axes were excluded because each added very little variance. Axis 1 accounts for 47.6% of the total variance and size measures have highly positive loadings on PC1 ($\geq$0.739) (Table 2). Axis 1 is interpreted as a multivariate measure of shell size. The best individual expressions of size are maximum breadth, maximum diameter of the penultimate whorl and total height (PC1 loadings $\geq$ 0.989). Axes 2 and 3 account for 34.4% and 15.8% of the total variance, respectively, and shape measures have the largest absolute loadings on PC2 ($\geq$0.917) and on PC3 (–0.887). The best expressions of shape are the ratio total height/maximum diameter of penultimate whorl (PC2 loading = –0.925), ratio total height/maximum breadth (PC2 loading = 0.917), and total height/height of spire (PC3 loading = –0.887) (Table 2). These ratios show opposite patterns with regard to depth since H_t/B_p and H_t/B_m increase with increasing depth, i.e. slender forms predominated at greater depths (H_t/B_p, $r^2 = 0.164$, $F_{1,433} = 84.96$, $P < 0.0001$, Fig. 3A; H_t/B_m, $r^2 = 0.174$, $F_{1,433} = 79.74$, $P < 0.0001$, Fig. 3B), whereas H_t/H_s decreases with increasing depth, i.e. tall-spired shells predominated at greater depths ($r^2 = 0.344$, $F_{1,433} = 215.91$, $P < 0.0001$; Fig. 3C). The ratio H_t/H_s tends to increase with increasing latitude, i.e. relative spire height tended to decrease with increasing latitude ($r^2 = 0.101$, $F_{1,433} = 37.09$, $P < 0.001$; Fig. 3D), although this relationship is very weak. If the values at high latitudes (>53°) from the shallowest stations (<330 m; Table 1) are removed from the analysis, there is not a significant pattern ($F_{1,423} = 3.78$; $P > 0.05$).

A partial regression was used to better characterize the relationship between H_t/H_s and the two independent variables. If latitude is held constant, the depth–related pattern (i.e. decrease of H_t/H_s with increasing depth) is very strong ($r = -0.541$, $t_{(432)} = -13.833$; $P < 0.0001$), but when depth is held constant, the latitude-related pattern is only marginally significant ($r = -0.080$, $t_{(432)} = -2.053$; $P = 0.0436$).

PC2 and PC3 define a plane in which shell shape based on ratios H_t/B_p, H_t/B_m and H_t/H_s is the primary factor in separation of individuals (Fig. 4A). Although there is considerable

Table 2. Loadings for morphometric measurements on the first three principal components and proportion of total variance explained by each component.

Variable	PC1	PC2	PC3
Total height (H_t)	*0.881*	0.454	0.120
Height of spire (H_s)	0.739	0.544	0.388
Maximum breadth (B_m)	*0.991*	0.029	–0.041
Maximum diameter of penultimate whorl (B_p)	*0.989*	0.021	0.008
H_t/H_s	–0.021	–0.459	*–0.887*
H_t/B_m	0.069	*0.917*	0.312
H_t/B_p	0.190	*0.925*	0.238
Eigenvalue	4.381	2.064	0.401
Total variance explained	47.6%	34.4%	15.8%

Loadings are correlations between a component axis and a variable. Highest contributions of each variable in italics.

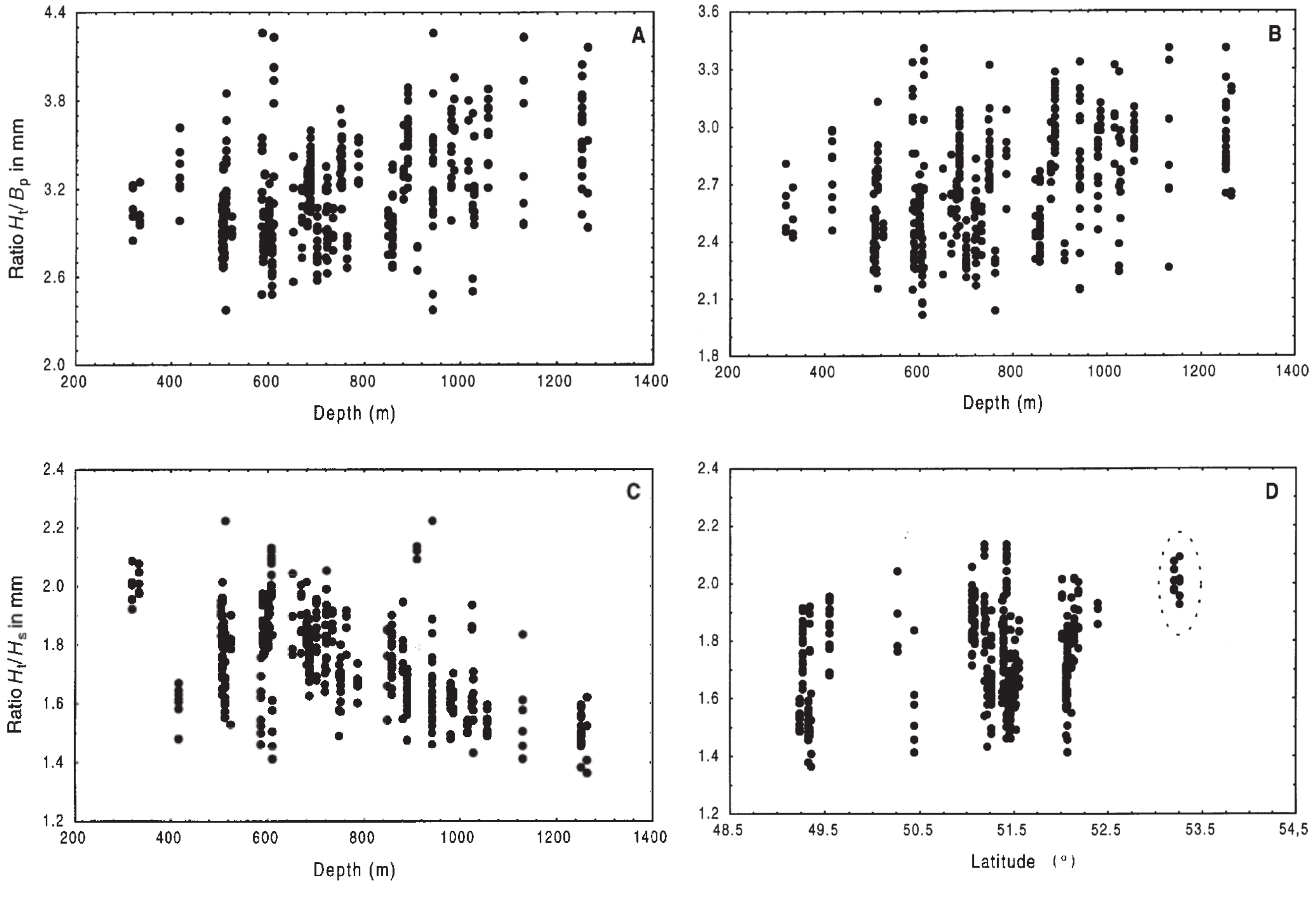

Figure 3. Variation of shell shape with depth and latitude. **A.** Variation of ratio H_t/B_p with depth. **B.** Variation of ratio H_t/B_m with depth. **C.** Variation of ratio H_t/H_s with depth. **D.** Variation of ratio H_t/H_s with latitude (points inside the dotted circle correspond to the shallowest stations).

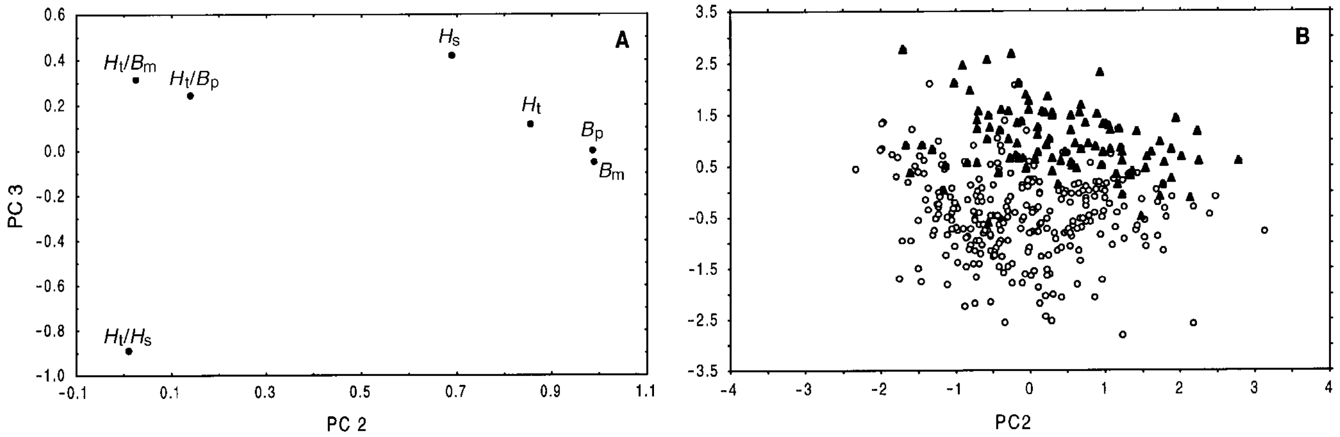

Figure 4. Patterns of shape variation with respect to PC2 and PC3. **A.** Loadings of each measurement on the two shape components. **B.** Factor loadings for individuals of *Troschelia berniciensis*. Loadings plotted againts PC2 and PC3 explained 91.53% of the variance. Triangles indicate individuals collected at >940 m.

overlap in phenotypes at and among different stations and depths (Fig. 4B), individuals from deeper (>940 m) and southern locations tend generally to occupy the mid-upper part of the graph determined by PC2 and PC3 components. These specimens have relatively high H_t/B_p and H_t/B_m ratios and low H_t/H_s ratio, i.e. these shells tend to be slender and high-spired.

Spearman's rank correlation between depth, latitude and factor loadings of individuals on axes PC2 and PC3 was used to show that the arrangement of individuals in the plane defined by the two axes relates to depth and latitude. Depth is correlated significantly with axis 2 (r_s = 0.325, N = 435, P = 0.0005) and axis 3 (r_s= 0.472, N= 435, P< 0.0001), and latitude is also correlated significantly with axis 3 (r_s = –0.30, N= 435, P= 0.0005) and marginally so with axis 2 (r_s = 0.196, N= 435, P= 0.02).

Morphological divergence and relationships to depth and horizontal separation

The partial Mantel test between phenotypic divergence and depth differences, while controlling the effect for horizontal separation, shows a significant positive correlation (r = 0.447, P= 0.000010). In contrast, the correlation between phenotypic divergence and horizontal separation when the effect for depth differences controlled is not significant (r= 0.045, P= 0.2114). Phenotypic divergence increases with the increase of depth differences, but not with horizontal separation. Therefore, depth differences have an effect on the morphological variation of the shell.

DISCUSSION

Shell shape in *Troschelia berniciensis* varies with depth and latitude, although the latitude-related pattern is very weak. In general, shells from greater depths are more slender and have taller spires than those from shallow water. Individuals from lower latitudes tend to be more slender and high-spired, but this pattern may be spurious (see results of partial regression) as many samples from lower latitudes are from deep stations (see Table 1). Secondly, morphological variation is related to differences in depth, but not to horizontal distance.

Changes in shell form in marine molluscs have been related to different factors such as physical disturbance (Vermeij, 1978), habitat type (Merkt & Ellison, 1998), hydrodynamic regime (Fuiman *et al.*, 1999), conservation of shell material (Graus, 1974), competition (Rex *et al.*, 1988), predation (Boulding & van Alstyne, 1993; Rugh, 1997) and factors favouring differences in life-history strategies (Rex, 1979). Growth rate may have an influence on shape, although there are conflicting reports on the connection between growth rate and shape (see Spight, 1973; Kemp & Bertness, 1984).

In this study, there is a wide but continuous shape spectrum. Shell shape varies between extremes of broad shells with width nearly as great as spire height found at shallower stations, and slender shells with spire height greatly exceeding maximum width that occur only at deeper stations (Fig. 1). Broader shells have a relatively larger internal shell volume than the tall-spired shells (personal observation) and the body size, expressed as the geometric mean of total height and maximum breadth, is greater (Olabarria & Thurston, 2003).

Slender, high-spired gastropods are less efficient in their use of calcium carbonate in terms of volume enclosed than are short-spired and globose species. In shallow water, high-spired shells are more abundant in environments with high calcium carbonate availability, i.e. areas of higher temperatures (Graus, 1974). The temperature differential through the sampled range of *T. berniciensis* in the Porcupine Seabight is about 5°C (Rice *et al.*, 1991). This temperature drop, together with the increased solubility of calcium carbonate resulting from increased pressure, would suggest that high-spired slender shells should occur at shallow depths with broader short-spired shells in deeper water, contrary to the evidence from the samples. However, recent studies show that gastropods do not construct their shells with optimal efficiency on a basis of geometric considerations (Heath, 1985; Stone, 1999).

Troschelia berniciensis shells from shallower depths in the Porcupine Seabight tend to be thicker, particularly at the lip, than those from deeper water (personal observation). Although shell thickness may be affected by calcium carbonate availability, Olabarria & Thurston (2003) have postulated that predation pressure may influence shell morphology. Large males of the crab *Geryon trispinosus* (Herbst, 1803) together with other large crab species occur in the upper part of the depth range of *T. berniciensis* (Clark, 1986; Attrill, Hartnoll, Rice & Thurston, 1990). Broad shells from shallower depths are isometric whereas slender shells from greater depths show a degree of allometry as evidenced by the convex profile (Fig. 1). On the premise that predation pressure in the deeper part of the depth range is more intense on smaller individuals, rapid somatic growth early in the life cycle would be advantageous.

Differential growth rates among environments have been reported as a cause of variation in shell morphology (Kemp & Bertness, 1984; Gould, 1984; Boulding & Hay, 1993, Merkt & Ellison, 1998). The depth-related variation of shape found in this study could be the result of differential growth rates of populations from shallow and deep areas in response to a trade-off between the energy available for growth in terms of food supply and costs associated with carbonate skeletons (see Palmer, 1992). Despite geographical variation in absolute values, benthic biomass, and hence potential food sources for *T. berniciensis*, decreases exponentially with increasing depth (Thiel, 1975; Rowe, 1983; Lampitt *et al.*, 1986). Costs associated with calcareous structures include an energetic depositional cost involving organic matrix production and mineralization, and post-depositional costs of maintenance and transport of the skeleton. These costs, and others such as production of mucus for locomotion probably increase with depth (Rex & Etter, 1998). At shallow stations where food resources are more abundant and costs associated with carbonate skeletons are less, rapid growth might be expected, resulting in broad shells, i.e. width increases faster relative to shell length, to accommodate a larger body mass within a given amount of shell. In contrast, in deeper areas, where food resources are less and the costs of carbonate skeletons are higher, slower growth would generate elongated shells and smaller internal volume.

Although there is a controversy on the mechanisms responsible for morphological variation in gastropods, both genetic and environmentally mediated plasticity have been documented (e.g. Newkirk & Doyle, 1975; Palmer, 1985; Janson, 1987; Boulding & Hay, 1993; Johannesson & Johannesson, 1996). Despite the geographic variation observed in *T. berniciensis*, our data do not provide a basis to decide on the mechanisms (genetic and/or phenotypic plasticity) causing the observed pattern of variation.

Mode of development plays an important role in phenotypic and genetic differentiation of deep-sea snails (Rex & Etter, 1990). Species with a non-planktotrophic mode of development such as *T. berniciensis*, have more restricted gene flow (Hansen, 1983) and show stronger tendencies to phenotypic and genetic differentiation. In contrast, planktotrophic species of gastropods such as *Benthomangelia antonina* (Dall, 1881) and *Benthonella tenella* (Jeffreys, 1869) found at continental rise and abyssal depths, show very little differentiation in shell shape on large bathymetric (1000 m) and horizontal (100s of kilometres) spatial scales (Rex & Etter, 1990). Limited phenotypic differentiation may be a result of higher gene flow and the environmental uniformity at great depths (Rex, 1981; Rex & Etter, 1990).

In the deep sea, high phenotypic and genetic variability have been reported (Rex & Etter, 1990; Chase *et al.*, 1998; Fuiman *et al.*, 1999; Quattro *et al.*, 2001; Rex *et al.*, 2002). Phenotypic differentiation shown by many taxa seems to be more associated with depth than with horizontal separation (e.g. Wilson, 1983; Rex *et al.*, 1988; Bucklin *et al.*, 1987; Rex & Etter, 1990, France & Kocher, 1996). The geographic differentiation in *T. berniciensis* and its association with depth rather than horizontal distance agree with this general trend and with the geographic variation observed in some other deep-sea snails (Rex *et al.*, 1988; Etter & Rex, 1990; Rex & Etter, 1990). *Troschelia berniciensis* shows a degree of change similar to that observed in some rissoid snails from the upper slope (Rex *et al.*, 1988), but more than that found for other benthic gastropods from the lower continental rise and abyssal plain (Rex & Etter, 1990; Rex *et al.*, 2002). Etter & Rex (1990) found that intraspecific variation in shell shape is highest on the upper continental slope and that it decreases with increasing depth to the abyssal plain. In addition, it has been found in snails that the rate of species replacement with depth decreases with increasing depth and is correlated with phenotypic differences (Rex, 1981; Etter & Rex, 1990). The clinal variation in shell shape of *T. berniciensis* within its depth-range agrees with the model proposed by Etter & Rex (1990) that suggests the upper bathyal zone, mainly upper slope, is conductive to evolutionary diversification.

The most important result is that *T. berniciensis* shows a clear geographic variation, particularly with depth. Differential growth rates in response to different environmental conditions with regard to availability of food and costs associated with calcareous skeletons may explain this morphological variation through the depth range. This interpretation is very tentative and speculative. Further information is required with regard to food resources, the real costs associated with shell deposition and maintenance, and growth rates under different environmental conditions. Nevertheless, we are confident that the present observations and interpretations are of interest and provide a useful framework to develop future experimental work to elucidate patterns and causes of morphological variation in deep-sea species. In addition, application of morphometric methods in combination with genetic techniques on large and small geographic scales are necessary for the assessment of the mechanisms that are responsible for the observed patterns.

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