

Faunal change and bathymetric diversity gradient in deep-sea prosobranchs from Northeastern Atlantic

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Abstract. Despite the plethora of studies, geographic patterns of diversity in deep sea remain subject of speculation. This study considers a large dataset to examine the faunal change and depth-diversity gradient of prosobranch molluscs in the Porcupine Seabight and adjacent Abyssal Plain (NE Atlantic). Rates of species succession (addition and loss) increased rapidly with increasing depth and indicated four possible areas of faunal turnover at about 700, 1600, 2800 and 4100 m. Depth was a significant predictor of diversity, explaining nearly a quarter the variance. There was a pattern of decreasing diversity downslope from ~250 m to ~1500–1600 m, followed by an increase to high values at about 4000 m and then again, a fall to ~4915 m. Processes causing diversity patterns of prosobranchs in the Porcupine Seabight and adjacent Abyssal Plain are likely to differ in magnitude or type, from those operating in other Atlantic areas.

Introduction

An increasing focus for biodiversity research in the deep sea has been to test for the existence of large-scale gradients in the diversity of marine soft-sediment fauna in deep sea (e.g. Rex 1981; Grassle 1989; Grassle and Macioleck 1992; Lamshead 1993; Rex et al. 1993; Dauvin et al. 1994; Patterson and Lamshead 1995; Lamshead et al. 2002). Molluscs form an ideal test assemblage for many hypotheses of diversity and its variation along environmental gradients because they are one of the more diverse and abundant groups of macrobenthos in the deep sea (Gage and Tyler 1991).

It is becoming increasingly recognised that adequate measures of diversity should include information on the 'relatedness' of the species rather than the number of species present and their relative abundances (Williams et al. 1991; Clarke and Warwick 1998). For example, assemblages with the same species richness may either comprise species which are closely related to one another taxonomically, or they may be more distantly related (Warwick and Clarke

1995). Phylogenetic information and, consequently, the evolutionary history of taxa should be used to assess priority areas and to protect biological diversity. Conservation measures would give priority to taxonomically distinct taxa, i.e. species not closely related to each other, and taxa that show restricted areas of distribution, i.e. endemism.

Standard diversity estimates depend on sampling effort (Hill 1973). Thus, any comparative study of biodiversity is sensitive to variations in sampling effort at different sites and/or times and methods are needed to reduce samples to a common size in order to compare species diversities. The rarefaction method (Sanders 1968), modified by (Hulbert 1971) has traditionally been the mainstay in assessing biodiversity in deep sea. Warwick and Clarke (1995) and Clarke and Warwick (1998) have defined a new diversity index to quantify the taxonomic diversity of a faunal assemblage capturing a component of the taxonomic relatedness of the species in each sample. This index measures the average path length along Linnean taxonomic classification of individuals of different species. It is a generalisation of the Simpson diversity index, incorporating information on taxonomic relationships within a sample into an index measuring species dominance (Rogers et al. 1999). One of the main characteristics of this index is that it is independent, on average, of the degree of sampling effort involved in the data collection. Thus, it can be compared across studies with differing levels of sampling intensity (Clarke and Warwick 1999).

This measure of taxonomic diversity has been applied to literature data on marine benthic assemblages (e.g. Warwick and Clarke 1995; Clarke and Warwick 1998) to illustrate the value of the index in assessment of environmental impacts. It has also been used in studies of diversity (e.g. Piepenburg et al. 1997; Hall and Greenstreet 1998; Rogers et al. 1999; Hooper et al. 2002; Woodd-Walker et al. 2002; Gambi et al. 2003; Tsurumi and Tunnicliffe 2003) providing additional insights of relevance to biodiversity assessment.

Meso and small-scale processes appear to be quite important in shaping patterns of deep-sea diversity because many species of macrofauna coexist in a mosaic of microhabitats (Grassle and Maciolek 1992). Nevertheless, patterns and processes of relatively small areas in deep sea are still poorly understood. Therefore, this study is focused on the Porcupine Seabight and adjacent Abyssal Plain region (NE Atlantic). This study considers a large dataset to examine the rate of turnover of prosobranch species with depth and the depth-diversity trend. In particular, the hypothesis tested was if there is a parabolic pattern of diversity as previously shown by other deep-sea molluscs and invertebrates elsewhere (e.g. Rex 1981; Etter and Rex 1990; Etter and Grassle 1992; Rex et al. 1997). To test this hypothesis the relatively new taxonomic diversity index (Warwick and Clarke 1995) together with the rarefaction method (Hurlbert 1971) and the Shannon–Wiener \log_2 -based index were used.

Material and methods

Sampling area

The area of study, the Porcupine Seabight and the Porcupine Abyssal Plain, is located more than 200 km southwest of Ireland. The Seabight opens onto the Porcupine Abyssal Plain through a relatively narrow entrance to the southwest (site described in Howell et al. 2002; Olabarria 2005).

Collection of samples

A total of 71 epibenthic sledge samples were collected at depths between 150 and 4915 m over a period of 23 years (Figure 1).

The epibenthic sledge (Rice et al. 1982) has some shortcomings depending, to a large extent, on the faunal group being studied (see review in Howell et al. 2002). For example, mobile benthopelagic forms, small animals and deeply

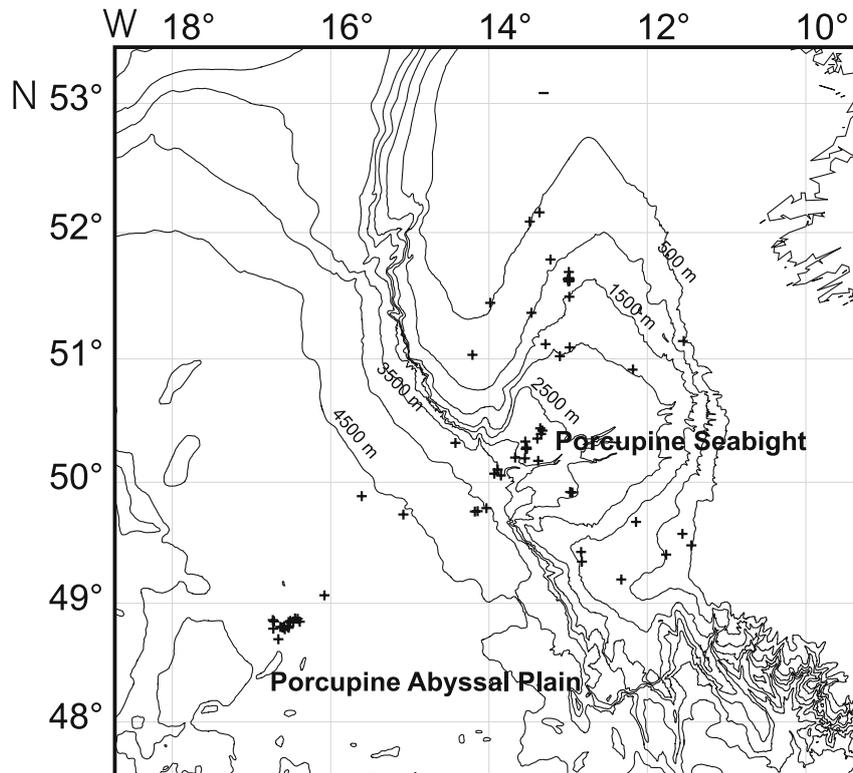


Figure 1. Location of the study area and sampling stations.

buried organisms are sampled less effectively than other groups. However, gastropods are generally slow moving, epibenthic macrofauna and such as are considered to be sampled quite effectively.

The area of the seabed sampled was calculated from the width of the sledge opening and distance of the sampling run over the seabed. Samples were sorted on deck, washed through a 1-mm mesh sieve, fixed in borax-buffered 4% formaldehyde in seawater and then preserved in 80% alcohol. Specimens were identified to species level when possible. Number of species were counted per sample and standardised to the number of individuals per 100 m².

Analysis of data

Bathymetric distribution

To analyse the bathymetric distributions of species, samples were grouped into 100 m depth bands. The range of species was assumed to be continuous between the depths of first and last occurrence. To investigate species change with depth, data were used to give depths of first and last occurrence of species. These values were then used to produce plots of species addition, loss and succession with increasing depth in order to identify possible boundaries where faunal turnover occurs (Howell et al. 2002); (Olabarria 2005). A non-metric multi-dimensional scaling using the Bray–Curtis similarity coefficient applied to the standardised and square root-transformed data was performed. Then the MDS x value output was plotted against depth to identify areas of faunal change (Howell et al. 2002). In addition, a Spearman rank correlation coefficient was calculated for the x value output of the MDS plot (change in species composition) and depth.

Analysis of diversity

Taxonomic diversity (Δ) was calculated following Warwick and Clarke (1995):

$$\Delta = [\sum_{i < j} \omega_{ij} x_i x_j] / [n(n-1)2],$$

where $x_i = (i = 1, \dots, s)$ is the abundance of the i th species of the total number of species, s , $n (= \sum_i x_i)$ is the total number of individuals in the sample and ω_{ij} is the weight given to the path length linking species i and j in the taxonomical classification. Therefore, taxonomic diversity is the average path length between any randomly chosen individuals from the sample. This index was applied to square root-transformed data.

Four taxonomic levels (species, genus, family and superfamily) were included in the analyses. The weights used were the simplest possible ones: $\omega = 1$ (different species), 2 (different genera), 3 (different families) and 4 (different superfamilies). Taxonomic weights were allocated according to the classification of deep-sea prosobranchs by Bouchet and Warén (1980, 1985, 1986, 1993) and Rosenberg (1998).

Furthermore, species diversity was estimated using the rarefaction method (Hurlbert 1971). This method has been used extensively as a measure of marine species diversity at small and large spatial scales (see Gray 2000 for review). Values for the expected number of species in a sample of 30 individuals (ES (30)) were extracted from the PRIMER programme. The ES (30) value was used in this study because of the patchy distribution and low abundance of many of the species observed. In addition, the Shannon–Wiener \log_2 -based index was used.

Diversity indices obtained were plotted against water depth and regression lines calculated to estimate bathymetric gradients.

Results

Faunistic composition and its variation with depth

A total of ~108,693 individuals belonging to 88 species and 24 families were collected (Table 1). Of these, the family Turridae was the most diverse with 20 species (Figure 2a). However, this diversity was not correlated with abundance as the families Rissoidae and Columbelloidea were more numerous than the Turridae (Figure 2b). This was due to the high number of *Benthonella tenella* (Jeffreys) and *Amphissa acutecostata* (Philippi) from the families Rissoidae and Columbelloidea, respectively. The abundances of these species accounted for more than 95% of the total number of individuals in both of these families.

Although several species showed very restricted depth ranges, i.e. occurrence at a particular depth or depth range less than 300 m (e.g. *Bathycyma* sp1, *Lissotesta* sp1, *Galeodea rugosa*, *Hemiaclis obtusa*; Table 1), most species (~60%) showed broad bathymetric ranges (e.g. *Calliotropis ottoii*, *Lamellitrochus* sp1, *Cerithiella metula*, *Amauropsis sphaeroides*, *Claviscala richardi*; Table 1). Few species' ranges extended over more than 3000 m (e.g. *C. ottoii*, *A. porcupinae*, *B. tenella*, *Oocorys sulcata*, *Troschelia berniciensis*). Two species, *A. porcupinae* and *Pleurotomella packardi* from the families Rissoidae and Turridae, respectively, had the widest bathymetric ranges. Families Muricidae, Buccinidae and Cassidae also showed broad bathymetric ranges (Table 1). Although there was a gradual replacement of species with depth many species overlapped in their depth ranges, i.e. approximately 67% of species coexisted in the 1100–2800 depth range. A low percentage of species (~19%) occurred deeper than 3000 m, whereas ~30% of species occurred shallower than 2000 m (Table 1). In general, most of species showed a patchy distribution through their depth range, often occurring, in any great abundance, only over a very narrow depth range. The depth range over which a species was present at maximum abundance did not always occur in the middle of its total depth range. About 40% of species had distributions skewed to the opposite ends of their depth ranges (see Table 1).

Table 1. Depth distribution of prosobranchs from the Porcupine Seabight and adjacent Abyssal Plain.

| Family | Species | Depth range | Depth of maximum abundance |
|----------------|--|-------------|----------------------------|
| Acmaeidae | <i>Bathyacmaea</i> sp nc | 1400–1500 | 1400–1500 |
| Scisurellidae | <i>Scisurella</i> sp nc | 1300–4900 | 1300–1400 |
| Trochidae | <i>Calliotropis ottoi</i> Philippi, 1844 | 1200–4900 | 2600–2700 |
| | <i>Calliostoma</i> sp1 c | 100–200 | 100–200 |
| | <i>Calliostoma</i> sp2 c | 4800–4900 | 4800–4900 |
| | <i>Lamellitrochus</i> sp | 1300–5000 | 1300–1400 |
| Skeneidae | <i>Granigyra</i> sp nc | 1200–1400 | 1200–1300 |
| | <i>Lissotesta</i> sp nc | 1200–1300 | 1200–1300 |
| | <i>Cyclostrema</i> sp1 nc | 1300–4000 | 1300–1400 |
| | <i>Cyclostrema</i> sp2 nc | 2000–3700 | 1900–2000 |
| Seguenziidae | <i>Seguenziella</i> sp nc | 1600–2900 | 1600–1700 |
| Cerithiopsidae | <i>Cerithiella amblytera</i> (Watson, 1880) c | 4000–4100 | 4000–4100 |
| | <i>C. metula</i> (Lovén, 1846) c | 900–2700 | 1300–1400 |
| | <i>Laiocochlis sinistrata</i> (Nyst, 1835) c | 1283–1400 | 1300–1400 |
| Turritellidae | <i>Turritella</i> sp nc | 100–200 | 100–200 |
| Rissoidae | <i>Alvania porcupinae</i> Gofas and Warén, 1982 nc | 100–4900 | 100–200 |
| | <i>Alvania cimicoides</i> (Forbes, 1844) nc | 100–200 | 100–200 |
| | <i>Alvania subsoluta</i> (Aradas, 1847) nc | 700–1200 | 700–800 |
| | <i>Benthonella tenella</i> (Jeffreys, 1869) nc | 400–4900 | 1100–140 |
| Aporrhaidae | <i>Aporrhais serresianus</i> (Michaud, 1828) nc | 400–2700 | 900–1200 |
| Capulidae | <i>Capulus simplex</i> Locard, 1898 nc | 2700–2800 | 2700–2800 |
| | <i>Torellia delicata</i> (Philippi, 1844) nc | 1100–2800 | 1100–1200 |
| Hipponicidae | <i>Leptonotis</i> sp? nc | 3600–3700 | 3600–3700 |
| Haloceratidae | <i>Haloceras tricarinata</i> (Jeffreys, 1885) c | 4000–4100 | 4000–4100 |
| Velutinidae | <i>Calyptoconcha pellucida</i> (Verrill, 1880) c | 1200–1300 | 1200–1300 |
| Naticidae | <i>Cryptonacia affinis</i> (Gmelin, 1791) c | 1400–2700 | 1900–2000 |
| | <i>Anauropsis sphaeroides</i> (Jeffreys, 1877) c | 2300–4900 | 2300–2400 |
| | <i>Polinices obtusa</i> (Jeffreys, 1885) c | 100–3600 | 1900–2000 |
| | <i>P. subplicata</i> (Jeffreys, 1885) c | 1200–3100 | 1300–1400 |
| Cassidae | <i>Oocorys sulcata</i> Fischer, 1883 c | 400–4100 | 2600–2700 |
| | <i>Galeodea rugosa</i> (Linnaeus, 1771) c | 400 | 400 |
| Epitoniidae | <i>Eccliseogyra</i> sp c | 3900–4000 | 3900–4000 |
| | <i>Epitonium dallianum</i> (Verrill and Smith, 1880) c | 100–1200 | 100–200 |
| | <i>Claviscala richardi</i> (Dautzenberg and de Boury, 1897) c | 700–4000 | 700–800 |
| Acliidae | <i>Aclis sarsi</i> (Dautzenberg and Fischer, 1912) | 700–1200 | 1100–1200 |
| Eulimidae | <i>Eulima bilineata</i> Alder, 1848 c | 1200–2800 | 1200–1300 |
| | <i>Haliella stenostoma</i> (Jeffreys, 1858) | 700–1300 | 700–800 |
| | <i>Rectilabrum lanceolatum</i> Bouchet and Warén, 1986 c | 4000–4100 | 4000–4100 |
| | <i>Melanella densicostata</i> Bouchet and Warén, 1986 c | 3600–3700 | 3600–3700 |
| | <i>M.cf charissa</i> (Jordan, 1895) c | 3600–4100 | 3600–3700 |
| | <i>M. jeffreysi</i> (Tyron, 1886) c | 1100–1400 | 1300–1400 |
| | <i>M. lucida</i> (Verrill, 1884) c | 1200–1400 | 1200–1300 |

Table 1. (Continued).

| Family | Species | Depth range | Depth of maximum abundance |
|----------------|---|-------------|----------------------------|
| | <i>M. martynjordani</i> (Jordan, 1895) c | 2700–2800 | 2700–2800 |
| | <i>Melanella</i> sp1 c | 4800–5000 | 4800–4900 |
| | <i>Melanella</i> sp2 c | 900–1200 | 1100–1200 |
| | <i>Pisolamia brychia</i> (Watson, 1883) c | 4600–4900 | 4600–4700 |
| | <i>Eulitoma</i> sp c | 1100–1200 | 1100–1200 |
| | <i>Hemiaclis obtusa</i> Bouchet and Warén, 1986 c | 2700–2800 | 2700–2800 |
| Muricidae | <i>Trophon barviciensis</i> (Johnston, 1825) c | 100–200 | 100–200 |
| | <i>T. dabneyi</i> Dautzenberg, 1889 c | 1200–1300 | 1200–1300 |
| | <i>Trophon</i> sp c | 100–400 | 100–200 |
| Buccinidae | <i>Liomesus ovum</i> (Turton, 1825) c | 700–800 | 700–800 |
| | <i>Buccinum abyssorum</i> Verrill and Smith, 1884 c | 700–3600 | 700–800 |
| | <i>Troschelia berniciensis</i> (King, 1846) c | 100–4000 | 900–1100 |
| | <i>Neptunea antiqua</i> (Linnaeus, 1758) c | 3500–3600 | 3500–3600 |
| | <i>N. contraria</i> (Linnaeus, 1771) c | 700–2800 | 700–800 |
| | <i>Mohnia abyssorum</i> (Fischer, 1883) c | 1900–4700 | 3500–3600 |
| | <i>Mohnia</i> sp c | 700–4900 | 700–800 |
| | <i>Turrisipho</i> sp c | 100–2800 | 900–1000 |
| | <i>Belomitra quadruplex</i> (Watson, 1882) c | 1600–4100 | 3900–4000 |
| | <i>Colus islandicus</i> (Mohr, 1786) c | 700–5000 | 3000–3100 |
| | <i>C. jeffreysianus</i> (Fischer, 1868) c | 700–2400 | 2000–2100 |
| | <i>C.cf latericius</i> (Möller, 1842) c | 700–900 | 700–800 |
| Columbellidae | <i>Amphissa acutecostata</i> (Philippi, 1844) c | 700–2800 | 1100–1300 |
| | <i>Mitrella nitidulina</i> (Locard, 1897) c | 2700–2800 | 2700–2800 |
| Volutomitridae | <i>Volutomitra</i> sp | 700–800 | 700–800 |
| Cancellariidae | <i>Admete viridula</i> (Fabricius, 1780) c | 1900–2000 | 1900–2000 |
| | <i>Iphinopsis alba</i> Bouchet and Warén, 1985 c | 1300–3600 | 2600–2700 |
| Turridae | <i>Spirotropis monterosato</i> (Locard, 1897) c | 700–2700 | 700–800 |
| | <i>Micropleurotoma melvilli</i> (Sykes, 1906) c | 1300–1400 | 1300–1400 |
| | <i>Irenosyrinx hypomela</i> (Dall, 1889) c | 1300–4000 | 2700–2800 |
| | <i>Leucosyrinx verrilli</i> (Dall, 1881) c | 2600–2800 | 2600–2700 |
| | <i>Typhlomangelia nivalis</i> (Lovén, 1846) c | 200–2800 | 1300–1400 |
| | <i>Drilliola pruina</i> (Watson, 1881) c | 1900–3600 | 1900–2000 |
| | <i>Pleurotomella packardi</i> Verrill, 1872 c | 100–5000 | 1300–1400 |
| | <i>Benthomangelia antonina</i> (Dall, 1881) c | 2600–4000 | 3900–4000 |
| | <i>B. decapitata</i> Bouchet and Warén, 1980 c | 2000–4900 | 3900–4000 |
| | <i>B. macra</i> (Watson, 1881) c | 2800–3700 | 2800–2900 |
| | <i>Gymnobela frielei</i> (Verrill, 1885) c | 700–4900 | 3900–4000 |
| | <i>G. subaraneosa</i> (Dautzenberg and Fischer, 1896) c | 1100–4900 | 2700–2800 |
| | <i>Theta cf vayssieri</i> (Dautzenberg, 1925) c | 4800–4900 | 4800–4900 |
| | <i>T. lyronuclea</i> (Clarke, 1959) c | 3900–5000 | 3900–4000 |
| | <i>Bathybela nudator</i> (Locard, 1897) c | 4600–5000 | 4600–4700 |
| | <i>Oenopota ovalis</i> (Friele, 1877) c | 1600–2000 | 1600–1700 |

Table 1. (Continued).

| Family | Species | Depth range | Depth of maximum abundance |
|--------|---|-------------|----------------------------|
| | <i>O. tenuicostata</i> (Sars, 1878) c | 1300–3100 | 1300–1400 |
| | <i>Teretia teres</i> (Forbes, 1844) c | 100–1200 | 700–800 |
| | <i>Lusitanops</i> cf <i>lusitanica</i> (Sykes, 1906) c | 1600–2000 | 1600–1700 |
| | <i>Lusitanops</i> cf <i>sigmoidea</i> Bouchet and Warén, 1980 c | 4000–5000 | 4800–4900 |

Feeding types (carnivores/ non-carnivores) were also indicated following Valentine et al. (2002). The category of carnivores includes active predators and scavengers on animal tissue, consumers of sessile animals, and ectoparasites. c, carnivores; nc, non-carnivores.

Mean abundance for prosobranchs as a whole showed a peak abundance between ~ 1100 and 1300 m (437.87 ± 95.47 ind. 100 m²), but mainly due to the high abundance of *B. tenella*. Seven species, *B. tenella*, *A. acutecostata*, *Aporrhais serresianus*, *Polinices obtusa*, *P. packardi*, *Gymnobela subaraneosa* and *C. otto*, presented high densities in the area of study. *P. packardi*, *B. tenella* and *P. obtusa* presented their maxima abundance at mid-bathyal zone, i.e. between ~ 1100 and 1700 m (Table 1). In contrast, *A. serresianus* presented maximum abundance between ~ 900 and 1200 m, whereas *A. acutecostata* and *C. otto* showed peaks of abundance at low continental slope, i.e. between ~ 2600 and 2800 m.

The rate of species succession (addition and loss) increased rapidly with increasing depth (Figure 3). Moreover, a Spearman rank correlation of depth and MDS x -axis co-ordinates (a one dimensional measure of species change) gave a coefficient of 0.74 ($p < 0.01$) (Figure 4), indicating that samples were grouped by depth. The overall rate of faunal change was greater at shallower than deeper waters (Figure 4). Four possible areas of faunal turnover at about 700 , 1600 , 2800 and 4100 m were identified (Figure 3). In particular, the zone ranging from the shelf break to ~ 700 m showed a rapid turnover with an abrupt step-like change in rate of species accumulation at about 700 m, i.e. 15 species added (Figure 3). Most of these species had restricted depth distributions apart from *Claviscala richardi*, *Buccinum abyssorum*, *Colus islandicus* and *Gymnobela frielei* (Table 1). From ~ 700 m to ~ 1600 m species succession was also very rapid with high rate of species addition, i.e. 28 species (Figure 3) and species loss, i.e. 15 species. In fact, about 23% of total species number was added between ~ 700 and 1600 m. Below ~ 1600 m the rate of species addition was more gradual, whereas the rate of species loss was rapid showing two peaks at ~ 2800 m and ~ 4100 m (Figure 3). The zone below ~ 4000 m was marked by the presence of typical abyssal species, i.e. *Pisolamia brychia*, *Theta vayssieri*, *Bathybela nudator* or *Lusitanops sigmoidea* (see Table 1).

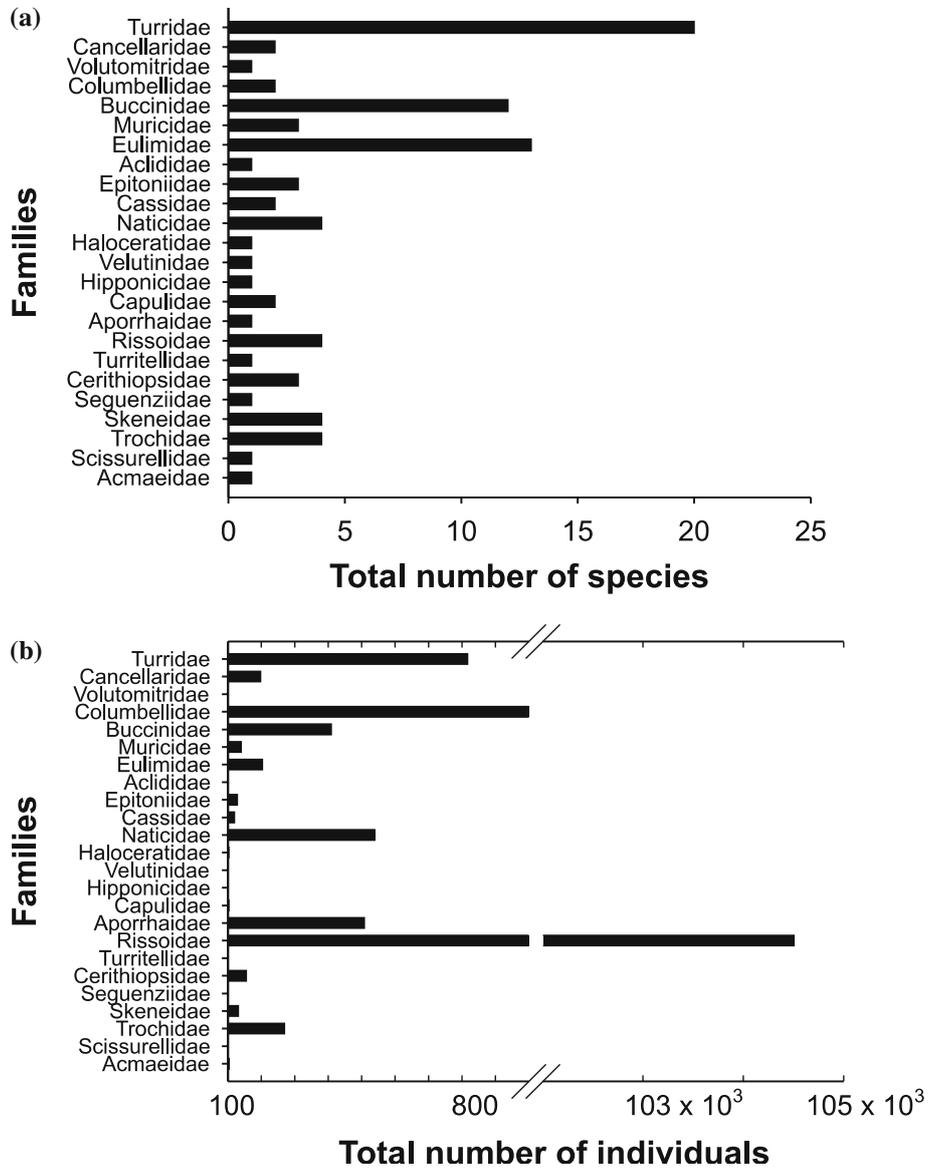


Figure 2. (a) Distribution of total number of species per family; (b) distribution of total number of individuals per family.

Bathymetric gradient of diversity

Taxonomic diversity index (Δ)

There was a pattern of decreasing diversity downslope from ~250 m to ~1400–1600 m, followed by an increase to high values at about 4000 m and then

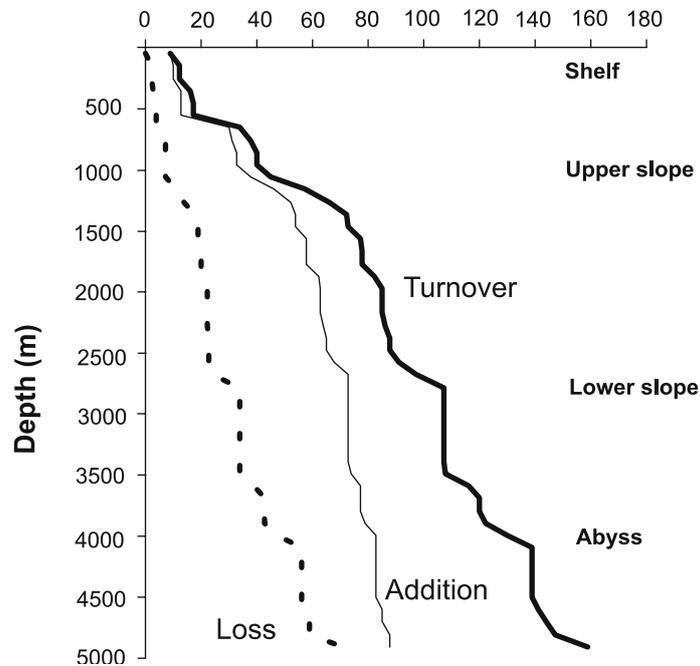


Figure 3. Cumulative addition and loss of species with depth from full dataset. Turnover (addition plus loss) of species is also plotted.

again, a fall to ~ 4915 m (the lower depth limit in this study) (Figure 5a). This trend of diversity with depth was significant and was represented by a three degree polynomial relationship ($r^2 = 0.321$; $F_{3,69} = 8.18$, $p < 0.001$).

Rarefaction method

Results were quite similar to those obtained by using the taxonomic diversity index. Depth did account for a significant portion of the variation in diversity ($r^2 = 0.262$; $F_{3,24} = 3.82$, $p < 0.05$). Diversity decreased up to minimum values at ~ 1500 m followed by an increase up to high values at ~ 4000 m (Figure 5b).

Shannon–Wiener index

This index showed the same trend than the other indices, but weaker (Figure 5c). Depth only accounted for $\sim 19\%$ of variance in diversity ($r^2 = 0.187$; $F_{3,69} = 5.30$, $p < 0.01$).

Discussion

Faunistic composition and depth

The family Turridae was the most diverse and it had the broadest bathymetric range, being observed over the whole sampling range, i.e. ~ 150 – 4915 m.

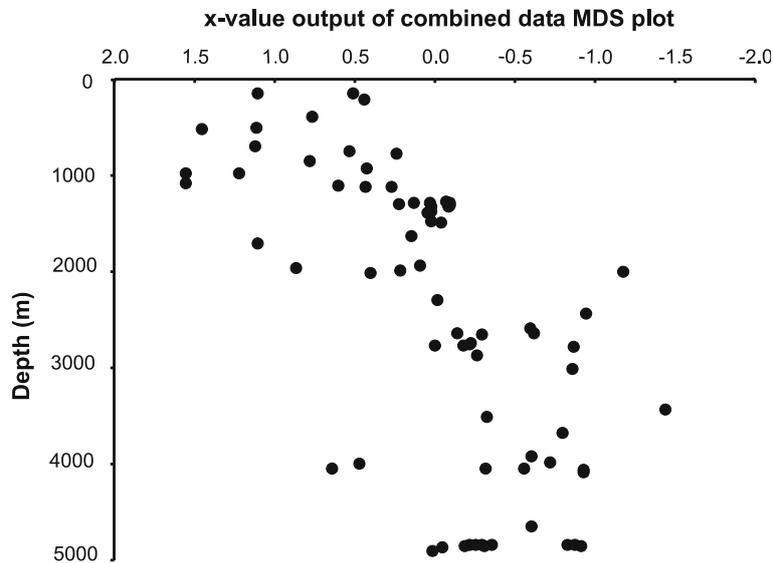


Figure 4. Plot of dataset MDS x value output against depth.

Bearing in mind that the highest abundances of the families Rissoidae and Columbelloidea were only due to two species, *B. tenella* and *A. acutecostata*, family Turridae occupied the third position in terms of abundance. The specific dominance of the family Turridae in this area agreed with findings in other deep-sea areas (Bouchet and Warén 1980) and also confirmed the observations by Rex et al. (1999) that turrids become increasingly abundant in the deep sea. Furthermore, the high abundances of *B. tenella* as found in the study area (i.e., in 45% of samples) have also been found in the Western Atlantic (Rex et al. 1979; Rex and Etter 1990). A planktotrophic development with ontogenetic migration gives this species high potential for large-scale dispersal (Rex and Etter 1990). This may, in part, explain the species' wide geographic range and abundance.

Many invertebrates are known to form aggregations in deep sea (e.g. Billett 1991; Gage and Tyler 1991; Howell et al. 2002). These aggregations may be for feeding and/or reproduction (Howell et al. 2002). The patchy distribution of prosobranchs in this area suggests that this pattern might be related to factors operating at local scale (e.g. food availability, reproduction and biological interactions) rather than global factors operating a larger scale, i.e. temperature, pressure, currents. Nevertheless, water mass structure and depth of the permanent thermocline have been proposed as possible factors controlling megafaunal zonation in Porcupine Seabight (i.e. Billett 1991; Howell et al. 2002). Furthermore, flow velocities and organic matter supply have been found to play an important role in structuring the benthic community on a very close area, Goban Spur (Flach et al. 1998). Topographical features of Porcupine Seabight, i.e. canyon-like topography, might also exert a strong effect in

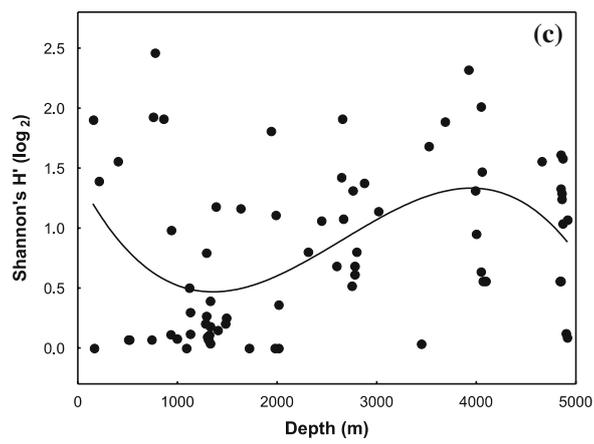
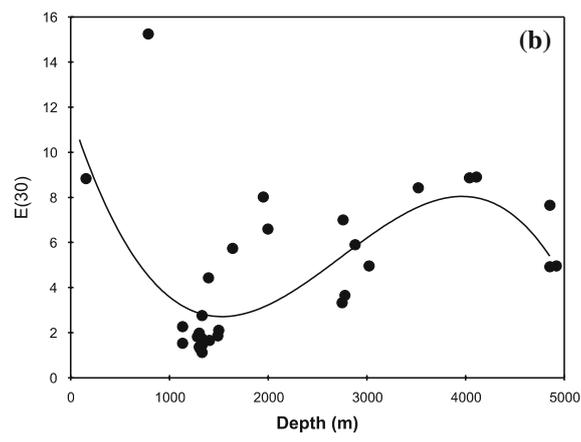
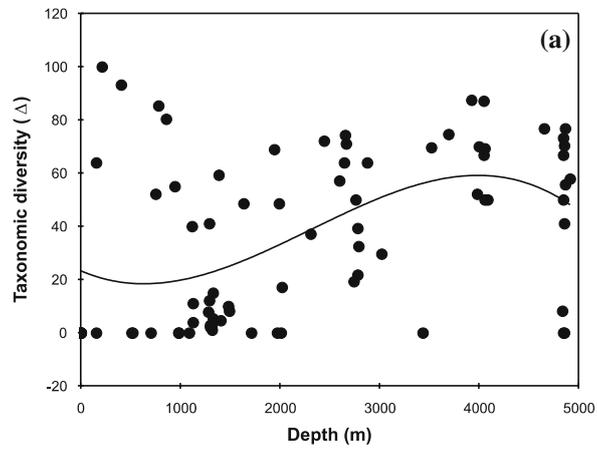




Figure 5. Bathymetric variation of diversity in deep-sea prosobranchs from Porcupine Seabight and adjacent Abyssal Plain. The solid line is the regression line. (a) Graph shows variation of taxonomic diversity (Δ) with depth; $y = 69.581 - 0.083x + 4.091E - 05x^2 - 5.11E - 09x^3$ ($r^2 = 0.321$; $F_{3,69} = 8.18$, $p < 0.001$). (b) Graph shows variation of E (S_{30}) with depth; $y = 12.764 - 0.0143x + 6.241x^2 - 7.404x^3$ ($r^2 = 0.262$; $F_{3,24} = 3.82$, $p < 0.05$). (c) Graph shows variation of H' with depth; $y = 1.424 - 0.0015x + 7.89E - 07x^2 - 9.921E - 11x^3$.

patterns of distribution of prosobranchs (see Olabarria 2005). In fact, the fauna of canyons can show different patterns of distribution than the fauna of adjacent non-canyon areas at the same depth (Gage et al. 1995). In addition, we have to bear in mind that temporal variability, i.e. seasonal and/or inter-annual, in abundance of species might have affected the patterns observed in this study. For example, species such as *B. tenella*, *A. acutecostata*, *P. packardi* and *A. serresianus* had peaks of abundances at certain depths between 1979 and 1982 as those shown by bivalves in the same area (Olabarria 2005). These changes in abundances might be related to temporal variations in quality and/or quantity of food (e.g. Danovaro et al. 1999; Billet et al. 2001).

Despite many species exhibiting quite broad bathymetric ranges, their depth distributions were more restricted than those found for other molluscs such as bivalves in the same area (Olabarria 2005). More restricted distributions for gastropods in comparison to other deep-sea invertebrates have been also reported elsewhere (e.g. Sanders and Grassle 1971; Rex 1981, 1983; Allen and Sanders 1996). There was also a rapid rate of species turnover with depth (Figures 3 and 4) as previously shown by gastropods (Rex 1977). Trophic factors exert an influence on species zonation through competitive interactions (Rex 1977). Rates of zonation increase with trophic level (or size) (Rex 1977; Cartes and Carrason 2004) so faunal replacement with depth is more rapid among predators than infaunal deposit-feeders such as polychaetes and bivalves (Rex 1977). This model was also supported in this study by the fact that there was an increase in the carnivores/non-carnivores ratio with increasing depth ($r^2 = 0.20$; $F_{1,53} = 5.46$, $p < 0.01$). A rapid rate of turnover with depth would be related to an increase in the C/NC ratio with increasing depth. A traditional view has been that in a fluctuating environment the ability of an organism to exist in as wide as a range of habitats as possible and to have a wide trophic scope, is adaptative, whereas greater environmental stability leads to more specialisation. Thus niche width might be expected to be greater at shallower depths, with a corresponding increase in number of generalist species, i.e. non-carnivores (Valentine et al. 2002). The increase in number of carnivores with depth might respond to an increase of environmental stability with increasing depth. In addition, life history strategies, i.e. larval development, egg size, fecundity and mobility, have been reported as some of the causes affecting the rate of species turnover (Sanders and Grassle 1971; Allen and Sanders 1996; Cartes and Carrason 2004). In summary, the bathymetric distribution of prosobranchs

in the area of study may be explained by a combination of biological and physical factors.

Diversity pattern

In this study, depth was a significant predictor of diversity, explaining nearly a quarter the variance. There was a pattern of decreasing diversity down-slope from ~250 m to ~1500–1600 m, followed by an increase to high values at about 4000 m and then again, a fall to ~4915 m (Figure 5a, b). However, this pattern differed from those observed for seastars and bivalves in the same area (Howell et al. 2002; Olabarria 2005). For example, in the case of seastars there were two diversity maxima at both ~1800 and 4700 m and a minimum at about 2600 m. Bivalves presented a pattern of increasing diversity from ~500 to 1600 m, followed by a decrease to minimum values at about 2600 m. The depth-diversity pattern in this study did also differ from those found for other invertebrates elsewhere (e.g. Rex 1981, 1983; Patterson and Lamshead 1995; Rex et al. 1997; Flach and Bruin 1999; Gage et al. 2000). For example, across a bathymetric range from 0 to 5000 m for the NW Atlantic, Rex (1983) found a parabolic pattern in diversity with maxima at intermediate depths (~2000–3000 m) for polychaetes, gastropods, protobranchs and cumaceans. Paterson and Lamshead (1995) also found a parabolic trend in diversity, peaking at about 1800 m for polychaetes at the Hebridean slope. Flach and Bruin (1999) found a slight increase of molluscs diversity with increasing depth in the Northeastern Atlantic. Gage et al. (2000) found a parabolic pattern in diversity of macrobenthos on the Scottish continental slope, with low values for the stations at about 400 m, and higher values at around 1400 m. Clearly, there is no global consistency in such patterns suggesting that processes structuring bathymetric patterns of prosobranch diversity in the Porcupine Seabight and adjacent Abyssal Plain are likely different, either in magnitude or type, from those operating in other Atlantic sites. In addition, these processes are likely different from those affecting other taxa in the same area (e.g. seastars, bivalves).

The low values of diversity found at about 1400–1600 m may be in part a result of high abundances (~3000 ind./m²) of *B. tenella*. Both rarefaction method and Shannon diversity indices are largely dependent on sample size and patterns of species' distribution (Gray 2000). For example, the expected number of species occurring at this depth, based on a sample of 30 individuals (see Material and methods) is very low (Figure 5b). The use of such a low ES number might have overemphasised the decrease in diversity at this depth. Furthermore, the permanent thermocline from about 600 to 1400 m over which the temperature decreases from ~10 °C to ~4 °C (Rice et al. 1991) might cause the decrease of diversity with minimum values at ~1400–1600 m. The peak of diversity at ~4000 m was previously found for

bivalves in the West European Basin (Allen and Sanders 1996) and Porcupine Seabight region (Olabarria 2005). Flach and de Bruin (1999) also found high diversity values for molluscs at ~4000 m in the Porcupine Seabight and Howell et al. (2002) reported increasing values of diversity for seastars in Porcupine Abyssal Plain from ~4000 to 4700 m. Although the abyssal zone is thought to receive a low food input (e.g. Rex 1973; Flach and de Bruin 1999), several studies have reported strong fluxes of organic matter to the Porcupine Abyssal Plain (e.g. Thurston et al. 1998; Billett et al. 2001; Fabiano et al. 2001). Although seasonally variable, this supply of organic matter at abyssal depths might be in part responsible for the increase of diversity observed at ~4000 m (Gili et al. 2000; Cartes et al. 2002; Olabarria 2005). Moreover, Rex et al. (2005) in their source-sink hypothesis proposed that many abyssal molluscan populations of North Atlantic might be maintained by immigration from adjacent bathyal populations of species with high dispersal ability. Therefore, source-sink dynamics might increase local diversity in the abyss and it might be particularly important in explaining the downslope patterns of diversity observed in this study.

In summary, turrids were the most diverse family with the broadest bathymetric range in the Porcupine Seabight and adjacent Abyssal Plain. The rate of species succession (addition and loss) increased rapidly with increasing depth and indicated four possible areas of faunal turnover at about 700, 1600, 2800 and 4100 m. Depth was a significant predictor of diversity, explaining nearly a quarter the variance. There was a pattern of decreasing diversity downslope from ~250 m to ~1500–1600 m, followed by an increase to high values at about 4000 m and then again, a fall to ~4915 m. In this study, the depth-diversity trend in prosobranchs differed from those patterns previously shown by other invertebrate groups in the same area or elsewhere. Clearly, there is no global consistency in such patterns suggesting they are more a reflection of local conditions than expressing any fundamental response to depth.

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