Patterns of bathymetric zonation of bivalves in the Porcupine Seabight and adjacent Abyssal plain, NE Atlantic

Celia Olabarria*

Southampton Oceanography Centre, DEEPSEAS Benthic Biology Group, Empress Dock, Southampton SO14 3ZH, UK

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Abstract

Although the organization patterns of fauna in the deep sea have been broadly documented, most studies have focused on the megafauna. Bivalves represent about 10% of the deep-sea macrobenthic fauna, being the third taxon in abundance after polychaetes and peracarid crustaceans. This study, based on a large data set, examined the bathymetric distribution, patterns of zonation and diversity–depth trends of bivalves from the Porcupine Seabight and adjacent Abyssal Plain (NE Atlantic). A total of 131,334 individuals belonging to 76 species were collected between 500 and 4866 m. Most of the species showed broad depth ranges with some ranges extending over more than 3000 m. Furthermore, many species overlapped in their depth distributions. Patterns of zonation were not very strong and faunal change was gradual. Nevertheless, four bathymetric discontinuities, more or less clearly delimited, occurred at about 750, 1900, 2900 and 4100 m. These boundaries indicated five faunistic zones: (1) a zone above ~750 m marking the change from shelf species to bathyal species; (2) a zone from ~750 to 1900 m that corresponds to the upper and mid-bathyal zones taken together; (3) a lower bathyal zone from ~1900 to 2900 m; (4) a transition zone from ~2900 to 4100 m where the bathyal fauna meets and overlaps with the abyssal fauna and (5) a truly abyssal zone from approximately 4100–4900 m (the lower depth limit of this study), characterized by the presence of abyssal species with restricted depth ranges and a few specimens of some bathyal species with very broad distributions. The ~4100 m boundary marked the lower limit of distribution of many bathyal species. There was a pattern of increasing diversity downslope from ~500 to 1600 m, followed by a decrease to minimum values at about 2700 m. This drop in diversity was followed by an increase up to maximum values at ~4100 m and then again, a fall to ~4900 m (the lower depth limit in this study).

*Departamento de Ecoloxía e Bioloxía Animal, Area Ecología, Universidad de Vigo, Campus Lagoas-Marcosende, 36200 Vigo (Pontevedra), Spain. Tel.: +34 986 812588; fax: +34 986 812556.
E-mail address: colabarria@uvigo.es (C. Olabarria).

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1. Introduction

Although zonation of fauna, i.e. change of species composition with depth, in the deep sea have been broadly documented (see Howell et al., 2002), most studies have dealt only with the megafauna (see Cartes et al., 2003; Cartes and Carrasson, 2004). Different faunal zones, i.e. regions of lesser faunal change bounded by regions of greater faunal change, have been proposed in the deep sea, but there is still some disagreement over the terminology of these zones (see for review Howell et al., 2002) and their bathymetric limits. Faunal boundaries reported in the literature vary depending on the taxonomic group considered (e.g. Vinogradova et al., 1959; Rowe and Menzies, 1969; Rex, 1973, 1981; Gage et al., 1985; Billett, 1991; Howell et al., 2002). Faunal zonation appears to be more apparent in higher trophic levels, e.g. fish and crustaceans, than in lower trophic levels, such as polychaetes or bivalves (see Cartes et al., 2003; Cartes and Carrasson, 2004).

Many of the previous studies focused on general faunal zonation patterns (e.g. Rowe and Menzies, 1969; Ohta, 1983), or on the zonation of specific taxonomic groups (e.g. Rex, 1977; Southward, 1979; Carney and Carey, 1982; Gage, 1986; Billett, 1991; Cartes and Sardà, 1993; Howell et al., 2002). Such studies have revealed that there is replacement of species with depth and that most of the species show restricted depth ranges (e.g. Murray, 1895; Rex, 1977; Carney et al., 1983; Etter and Rex, 1990; Howell et al., 2002). Causes of this zonation have been attributed to physical and/or biological factors such as temperature (Rowe and Menzies, 1969), pressure (Young et al., 1996), hydrographic conditions and topography (Lampitt et al., 1986; Rice et al., 1990), nutrient input (Rex, 1981; Rice et al., 1990), larval dispersal (Rowe and Menzies, 1969; Billett 1991), competition, predation and trophic level (Rex, 1977, 1981; Cartes and Sardà, 1993). Nevertheless, the causes for the change in species composition with depth are complex and several factors might act to produce the observed pattern. Therefore, detailed studies of bathymetric distribution of deep-sea organisms may help to elucidate the factors driving these patterns.

In the Porcupine Seabight and adjacent areas diverse zones of faunal change have been consistently reported. In general, though with important local variations, a first boundary related to the water mass structure and permanent thermocline occurs at ~700 m depth (e.g. Gage, 1986; Howell et al., 2002). A second faunal turnover associated with changes in currents occurs at ~1100 m (Howell et al., 2002). In addition, there is a third boundary at about 1700 m marked by a rapid faunal change and related to changes in temperature and water masses (Gage, 1986; Billett, 1991; Howell et al., 2002). Finally, there is a boundary at ~3000 m that separates bathyal and abyssal fauna (Lampitt et al., 1986; Billett, 1991; Howell et al., 2002). This zonation scheme is based on studies of megafaunal groups, whereas smaller macrofauna has been generally neglected. Studies focusing on macrofaunal assemblages belonging to lower trophic levels, e.g. polychaetes, gastropods or bivalves, could contribute to a better understanding of the structure of deep-sea communities in this area.

Bivalves represent about 10% of the deep-sea macrobenthic fauna, being the third taxon in abundance after polychaetes and peracarid crustaceans (Allen and Sanders 1996). Deep-sea bivalves have been studied largely from a faunistic and taxonomic point of view (e.g. Knudsen, 1970; Sanders and Allen, 1973; Allen and Turner, 1974; Allen and Morgan, 1981; Allen and Hannah, 1989; Allen 1998). Studies on the diversity patterns of deep-sea bivalves have been also reported from a number of areas (e.g. Rex, 1981; Grassle and Maciolek, 1992; Rex et al., 1993, 1997, 2000; Allen and Sanders, 1996). Nevertheless, few studies have investigated patterns of bathymetric distribution and zonation of bivalves in detail (but see Allen and Sanders, 1996).

This study, based on a large data set, examines the bathymetric distribution of bivalves from the Porcupine Seabight and adjacent Abyssal Plain (NE Atlantic), patterns of zonation and diversity–depth trends. Possible causes of these patterns are also discussed.
2. Material and methods

2.1. Study area

The Porcupine Seabight and Porcupine Abyssal Plain are located more than 200 km to the southwest of Ireland (Fig. 1). The Porcupine Seabight is an amphitheatre-shaped embayment in the continental margin to the southwest of Ireland, and its sides slope steadily from the edge of the Irish Shelf at ~200 m down to a depth of about 4000 m (site described in Rice et al., 1991). The Seabight opens onto the Porcupine Abyssal Plain through a relatively narrow entrance to the southwest (Rice et al., 1991). The Porcupine Abyssal Plain lies south of the Rockall Trough and north of the Iberian Abyssal Plain, at a depth between ~4000 and 5000 m. The Seabight is bound on its west and northwest side by the Porcupine Bank and on its south and southeast side by the Goban Spur, leaving a narrow entrance. The western slopes of the Porcupine Seabight are steeper than the eastern slopes. The eastern slope of the Seabight differs markedly from the western one because of the presence of many channels, which coalesce to form a single large channel or canyon running through the Seabight. The channels are still areas of active transport where large amounts of detrital material are accumulated. No sediment fan is evident where the channel opens onto the Abyssal Plain, indicating either little detrital material is transported or that such material is distributed once it reaches the Abyssal Plain (Rice et al., 1991).

2.2. Collection and treatment of samples

A total of 76 epibenthic sledge and 50 otter trawl samples was collected between 500 and 4866 m over a period of 22 years. These samples were taken during the Institute of Oceanographic Sciences (IOS) biology programme in the Porcupine Seabight and adjacent Abyssal Plain between November 1977 and December 1986 (Rice et al., 1991) and during the BENGAL programme on the Porcupine Abyssal Plain between September 1995 and October 1998 (Billett and Rice, 2001). Despite this extensive sampling programme, there were several gaps in the data set (Fig. 2) that might affect the outcome of this study. Nevertheless, many depth bands were represented by more than 3 sampling runs (sledge and OTSB), so data were reliable and produced a quite comprehensive representation of species distribution.

The IOS epibenthic sledge (Rice et al., 1982) carries an acoustic monitor, which transmits information on the behaviour of the sledge on the seabed. The semi-balloon otter trawl (OTSB) (Merrett and Marshall, 1981) has an acoustic beacon mounted on one of the trawl doors to provide better estimates of the length of the tow. Mercury tilt switches in this monitor indicate the arrival and departure of the net at the seabed. Therefore, the area of seabed sampled was calculated from the width of the sledge/trawl opening and distance of the sampling run over the seabed. Nevertheless, the epibenthic sledge and the semi-balloon otter trawl, OTSB, have some shortcomings depending, to a large extent, on the faunal group under study (see for review Howell et al., 2002). For example, the otter trawl shows a fishing efficiency of 68% for larger megabenthos (Bett et al., 2001), but it does not provide reliable quantitative samples for epibenthic fauna or infauna. Despite the shortcomings, samples collected...
in this area over this long period of time provided an
important data set in order to get better understand-
ing of patterns of distribution of species and
processes driving these patterns in the northeast
Atlantic Ocean.

Samples were sorted on deck and fixed in borax-
buffered 4% formaldehyde in seawater and then
preserved in 80% alcohol. Specimens were identi-
fied to species level when possible. A total of
131,334 individuals belonging to 76 species were
collected. The number of species in each sample
was determined per sample and numerical density
was standardized to 100 m$^2$.

2.3. Data treatment

To analyse the bathymetric distributions of
species, sledge and trawl samples were grouped
into 100 m depth bands. Mean abundances per
100 m depth band were calculated for each species
and then converted to percentage of relative
abundance (Bett, 2001). Epibenthic sledge data
were used where possible and supplemented by
OTSB data where sledge data were lacking. As a
relative measure of abundance was used, as
opposed to absolute abundances, this was not a
problem in the data analysis. The range of a
species was assumed to be continuous between the
depths of first and last occurrence.

To investigate species change with depth, both
OTSB and sledge data were used together 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, i.e. zonation patterns.

To identify the main assemblages, both sledge
and trawl data were transformed into presence/
absence data (Clarke and Warwick, 1994) in order
to combine data from the two sampling gears. This
qualitative approach was adopted in an attempt to
avoid the bias introduced by the use of different
samplers. Samples were then grouped into 500 m
depth bands and labelled D1–D9. This grouping
allowed the data to be investigated in terms of
depth rather than species change (see Howell et al.,
2002). The Sorenson similarity coefficient (Clarke
and Warwick, 1994) was applied to the trans-
formed grouped data to obtain a similarity matrix.
Subsequently, hierarchical clustering with group-
averaged linking and non-metric multi-dimen-
sional scaling using the similarity matrix were
performed. To test the relationship between depth
and change in species composition a Spearman’s
rank correlation coefficient was calculated for the
$x$-ordinate of the MDS plot and depth.

Diversity was analysed with the rarefaction
method (Hurlbert, 1971). Values for the expected
number of species in a sample of 50 individuals
were extracted from the programme PRIMER
(Plymouth Routines in Multivariate Ecological
Research, ver. 5), and a graph of expected number
of species against depth was plotted. The ES (50) value was used in this study because of the patchy distributions of species and low abundances of many of them. Sledge and OTSB data were combined after separate analyses indicated similar results from both gears individually.

3. Results

3.1. Species distribution

In general, most of species showed a broad depth range with some species’ ranges extended over more than 3000 m (e.g. *Pristigloma nitens*, *Thyasira equalis*, *Kelliella atlantica*, *Abra profunda* and *Cuspidaria obesa*; Table 1, Fig. 3). Although there was a very gradual replacement of species with depth (Fig. 3) many species overlapped in their depth ranges, i.e. approximately 62% of species coexisted in the 2600–3000 m depth range. A high percentage (~67%) of species occurred deeper than 3000 m, whereas ~21% of species occurred shallower than 2000 m (Table 1). Only sixteen species showed comparatively narrow depth ranges (<300 m) (Table 1) and most of them occurred shallower than ~1700 m (but see *Nuculana* sp1, *Ledella aberrata*, *C. circinata*, *Halonympha* sp1, *Edentaria similis*; Table 1). Despite most species having broad bathymetric ranges, some zones of enhanced species turnover were identified (Fig. 4).

Most of species showed a patchy distribution through their depth range, often occurring, in any great abundance, only over a very narrow depth range of 100–300 m (Fig. 3). The narrow depth of greater abundance did not generally occur in the middle of their total depth ranges (Table 1; Fig. 3). For example, species such as *Bathypecten eucymatus*, *Similpecten similis*, *Parvamussium permirum*, *A. profundorum*, *L. ultima* and *Cardiomya knudseni* reached their respective relative high levels of abundance at the start or end of their depth ranges. In contrast, few species (e.g. *Malletia cf abyssorum*, *Verticordia cf triangularis*, *Yoldiella* sp1, *K. atlantica*) presented their maximum abundances in the middle of their total depth ranges.

Furthermore, various species co-occurred at their maximum abundances at a particular depth (see 2700–2800 m depth band; Table 1). Although some species’ vertical ranges were broad, their relative abundance patterns changed markedly below ~2500 m. For example, *Ledella pustulosa marshalli*, *Malletia obtusa* and *K. atlantica* were more abundant below this depth (Fig. 2), whereas *P. lucidum* and *Limatula* sp1. decreased in abundance.

Faunal discontinuities occurred at ~2000–2500 m and ~3100–3500 m. Very few species were present, and none occurred in large numbers (but see *Idas cf argenteus* and *Xylophaga* sp1). These depths correspond to gaps in the data set (Rice et al., 1991; Howell et al., 2001) and a rocky area (~3000–3500 m) at the base of the continental slope.

3.2. Assemblages and patterns of zonation

Both Hierarchical Cluster Analysis and MDS evidenced an arrangement of stations in 5 different groups (Figs. 5 and 6). These groups (A, B, C, D and E; Fig. 5) were very dissimilar to each other (similarity close to zero). Although a Spearman’s rank correlation of depth with the MDS-ordinate gave a significant result (0.64; p < 0.0001), some samples from different depths were grouped together (for example, group A). Despite the arrangement of the stations according to a depth gradient there was also some indication of alongslope organization within area of study (see assemblages; Fig. 7). Most species with broad bathymetric ranges were widespread in the area (e.g. *Thyasira obsoleta*, *Polycordia gemma*, *Yoldiella* sp1; Fig. 8); however, a few species showed more restricted horizontal distributions (e.g. *Propanussium centobi*, *Yoldiella inconspicua*; Fig. 9).

Nevertheless, four more or less clearly delimited bathymetric boundaries could be found. An upper slope zone from ~500 to 750 m could be identified by both cluster and MDS analysis (cluster E, Figs. 5 and 6). The rate of species succession was gradual in this region with an addition of 8 species that extended throughout the area and beyond (but see *Chlamys* sp2) (Fig. 3). Two species typified this zone, *Chlamys* sp1 and *Chlamys* sp2.
Nevertheless, the existence of this boundary at ~750 m should be interpreted with caution given the incomplete sampling of shallow stations (see sampling effort; Fig. 2).

A bathyal zone extended from ~750 to 1900 m. Depth bands D1, D2 and D3 grouped together in clusters A1 and A2 (Figs. 5 and 6). Species succession in this zone was very rapid and the rate

<table>
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<th>Depth range (m)</th>
<th>Depth of maximum abundance (m)</th>
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*Taken from OTSB data. †Species considered as suspension feeder; ‡species considered as deposit feeder; ‡species considered as carnivore.
of species addition was high with a peak at ~1800 m. A high percentage of species (~20%) were restricted to this zone (e.g. *Deminucula atacellana*, *Nuculoma granulosa*, *Thyasira ultima* and *Lyoniella formosa*). The 1900 m boundary marked a change in the rate of species succession (Fig. 4). Approximately 70% of species were added at or above this depth and very few species were added at depths greater than 1900 m until abyssal depths were reached.

A lower bathyal zone was identified, spanning depths between ~1900 and 2900 m. Four species are added in this zone: *Ledella ultima* which has a depth range of ~1900–4900 m, *Limopsis tenella* with a range of ~2600–4900 m, *Hyalopecten undatus* with a depth range of ~2700–4100 m and *Xylophaga sp1* which was restricted to a depth range of ~2000–2500 m. Ten species were lost in this zone and the rate of species succession was gradual. However, this area, particularly between ~2100 and 2600 m, was poorly sampled (Fig. 2), which could account for the lack of addition of species.
An abyssal zone was suggested below ~2900 m in the Seabight and extending out to the Abyssal Plain (Figs. 5 and 6). This region was also identified by a change in the rate of succession (addition and loss), which was very rapid (Fig. 4). Six species were added in this area and 26 were
lost. There was, however, a transition zone between ~2900 and 4100 m (see clusters A1, C, and some samples of B2; Figs. 5 and 6) where only three species, Neilonella saliciensis Verticordia cf triangularis and Cuspidaria circinata, were added. In this region there was a gap in the data set (~3000–3500 m), which corresponded with very rough terrain (Rice et al., 1991; Fig. 2). This could account for the lack of species addition in the transition zone.

Samples from the “truly” abyssal zone, represented mainly by clusters B (most of samples) and few samples of A1 and D (Figs. 5 and 6), were marked by the presence of abyssal species, i.e. Nuculana sp1, Ledella aberrata, Silicula fragilis, Cuspidaria circinata and Halonympha sp1, with very restricted depth ranges (but see S. fragilis). The upper limit of this zone (~4000–4200 m) was characterized by the loss of 15 species, most of which had very broad depth ranges (> 3000 m).
The characterization of this zone was, however, quite difficult since it was poorly sampled. This is the area between the mouth of the Porcupine Seabight and the BENGAL sampling site on the Porcupine Abyssal Plain (Howell et al., 2002).

3.3. Diversity trends

There was a pattern of increasing diversity downslope from ~500 to 1600 m, followed by a decrease to minimum values at about 2600 m. This drop in diversity was followed by an increase up to maximum values at ~4100 m and then again, a fall to ~4900 m (the lower depth limit in this study). Although there was a significant trend with depth ($r^2 = 0.177; p < 0.05$) (Fig. 10), it was rather weak and not well represented by a linear correlation.

4. Discussion

The faunal composition of bivalves in the Porcupine Seabight and Porcupine Abyssal Plain area varied with depth, but this change was very gradual (Fig. 3). Most species occurred over broad depth ranges and overlapped in their distributions. Diversity showed a unimodal trend with a diversity maximum at ~4100 m.

4.1. Bathymetric distribution

Though boundaries of faunal renewal with depth were found changes were less obvious than those found for other deep-sea invertebrates (e.g. Rowe and Menzies, 1969; Billett, 1991; Rice et al., 1990; Cartes and Sardà, 1993; Howell et al., 2002). Most species exhibited broad depth ranges, i.e. some ranges extending over more than 3000 m (see Table 1; Fig. 3), in agreement with previous studies on bivalves (e.g. Sanders and Grassle, 1971; Grassle and Maciolek, 1992; Allen and Sanders, 1996). Nevertheless, nearly all species examined in this study reached their highest levels of abundance over more restricted depth ranges of 200–300 m (see Fig. 3). In general, the depth range over which a species was present at maximum abundance did not correspond with the centre of its total depth range (see Table 1).

Two species, Kelliella atlantica and Myonera atlantica, presented the broadest depth ranges (~500–4900 m). Despite their similar total depth ranges, the depths of maximum abundance of these two species were distinct (Table 1). The two species show different feeding characteristics: K. atlantica is a suspension feeder, whereas M. atlantica is a carnivorous species (Allen and Morgan, 1981; Allen, 2001). In contrast, some species with different total depth ranges occurred at their maximum abundances at around the same depth (e.g. Brevinucula verrilli, Yoldiella sp1, Hyalopecten undatus and Edentaria simplis; Table 1). Some of these species had similar feeding modes (Allen and Turner, 1974; Allen and Morgan, 1981; Allen and Sanders, 1996). Although physical factors have been suggested as important regulators of the bathymetric...
distribution of species (see Rowe and Menzies, 1969; Haedrich et al., 1980), biological interactions seem to have an important role in governing the ranges of distribution of many taxa (Rex, 1977, 1981; Cartes et al., 2003). The results of this study suggest that the distribution of species, i.e. with a total depth range over thousands of metres and occurrence of maximum abundances over narrow depth ranges (<300 m), might be related to factors operating at the local scale (e.g. food availability and biological interactions) rather than global factors such as temperature or pressure. It is possible, however, that temporal variability, i.e. seasonal and/or interannual fluctuations, in abundance of species might have affected the bathymetric patterns observed in this study. Several species such as Dacrydium ockelmanni, Delecpecten vitreus, K. atlantica, Limopsis minuta and Neilonella saliciensis showed peaks of abundances at certain depths between 1979 and 1982. Particularly, K. atlantica showed a dramatic increase in densities between ~1300 and 2700 m, attaining a maximum abundance of 840 ind 100 m$^{-2}$ at ~2700 m in September 1979. These spatially localized changes in populations have been reported in the same area (see Billett et al., 2001) and may be related to higher availability of food input (Billett et al., 2001; Cartes et al., 2002). In deep-sea domains, peaks in recruitment and gametogenesis in macrofauna have been related to availability of food (e.g. Witte, 1996; Cartes et al., 2002; Ramirez-Llodra et al., 2002). Short- and long-term changes in deep-sea populations have been attributed to seasonal and interannual variation in food supply (e.g. Billett et al., 1983; Rice et al., 1994; Danovaro et al., 1999; Billett et al., 2001). Thus, the increase in abundances of adults and juveniles of these species between 1979 and 1982 might be related to quality and/or quantity of food supply rather than to localized stochastic population variations.

4.2. Assemblages and patterns of zonation

Although there were changes in the vertical distribution of bivalve assemblages in the Porcupine Seabight and Porcupine Abyssal Plain, these changes were not as strong as those reported for other taxa in the same and adjacent areas (Gage, 1986; Rice et al., 1990; Billett, 1991; Howell et al., 2002). However, various studies have shown that patterns of faunal change vary considerably between taxa and geographic locations (Rex, 1981; Billett, 1991; Gage and Tyler, 1991; Grassle and Maciolek, 1992; Cartes et al., 2003). In general, the observed changes were very gradual given that most species present had very broad ranges of distribution. Species did undergo a repeating sequential change with depth (see Fig. 3). Previous studies have also reported comparatively low rates of zonation for bivalves (Sanders and Grassle, 1971; Rex, 1981; Allen and Sanders, 1996). The pattern of species turnover, i.e. appearance/disappearance, was very rapid down to ~1800 m and then more gradual at greater depths. A slow decline in the standing stock of bivalves with depth might lead to this decrease in the turnover rates with depth.

The distribution of samples following a “horizontal gradient” (see assemblages; Fig. 7) might be due to the fact that most of species with broad bathymetric ranges had distributions skewed to the opposite ends of their depth ranges (Fig. 3), i.e. depths of maximum abundance varied along a horizontal range. Nevertheless, four bathymetric discontinuities, more or less clearly delimited, occurred: at ~750, 1900, 2900 and 4100 m (see Figs. 3–5). These boundaries translate to five faunistic zones in this area. (1) A zone above ~750 m marked the change from shelf species to bathyal species. (2) A zone from ~750 to 1900 m corresponds to the upper and mid-bathyal zones taken together, where species turnover was rapid and diversity attained high values. The 1900 m boundary was marked by changes in the rate of species turnover and diversity. (3) A lower bathyal zone from ~1900 to 2900 m was characterized by a gradual rate of species succession and the addition of only four species; many species reached their maximum abundances in the ~2600–2800 m depth band. (4) A transition zone from ~2900 to 4100 m was marked by a very rapid rate of succession and a loss of about 35% of species; diversity reached maximum values at ~4100 m. In this region the bathyal fauna met and overlapped with the abyssal fauna. The ~4100 m boundary marked the lower...
The patterns of zonation identified in this study departed, to an extent, from those identified in the Porcupine Seabight by other workers (Billett 1991; Howell et al., 2002). However, the suggested boundaries at about 750, 1900 and 2900 m were similar to those proposed for asteroids in the same area (Howell et al., 2002). Similar boundaries have also been reported by other authors elsewhere. The boundary at ~750 m was comparable with faunal boundaries at ~800–1000 m for echinoderms from the Rockall Trough (Gage, 1986), at ~700–800 m for fish species (Pearcy et al., 1982; Moranta et al., 1998) and megafauna (Hecker, 1990), at ~626–694 m for decapod crustaceans (Maynou and Cartes, 2000), at ~500 m for elcerianth anemones (Shepard et al., 1986), and at ~530 m for protrobranch bivalves (Allen and Sanders, 1996). The boundary at ~1900 m has been previously reported at ~1900–2200 m for fish species (Pearcy et al., 1982), echinoderms (Gage, 1986), megafauna (Hecker, 1990) and decapod crustaceans (Cartes and Sardà, 1993). The discontinuity observed at ~2900 m is comparable to that found at about 2800 m, i.e. abyssal rise, for gastropods (Rex, 1977) and seastars (Howell et al., 2002). Finally, the boundary placed around 4100 m, i.e. the bathyal to abyssal transition, might be comparable to a shallower boundary (~3300 m) found for megafauna in the Porcupine Seabight (Billet, 1991; Howell et al., 2002).

Causes of zonation in the deep sea are complex and several factors, i.e. physical and/or biological, may act together to produce the observed patterns. Physical factors such as geological and topographical features, pressure, temperature, water masses structure or currents (e.g. Rowe and Menzies, 1969; Rex, 1977; Pearcy et al., 1982; Gage, 1986; Hecker, 1990; Cartes and Sardà, 1993; Abelló et al., 2002) may play an important role in patterns of zonation. Apart from the local heterogeneity in environmental conditions (e.g. temperature, currents, pressure, water masses), differences in patterns of zonation have been related to biological factors such as the trophic level of the taxon considered (Rex 1977, 1981; Cartes and Carrasson, 2004) and life-history characteristics (Sanders and Grasse, 1971; Rex, 1981).

The bathymetric distribution of fauna in the Porcupine Seabight and adjacent Abyssal Plain has been related to diverse factors, although hydrographic conditions have been invoked as being most important factors (Rice et al., 1990; Billett, 1991; Howell et al., 2002). For example, Billett (1991) suggested that the main factors driving the holothurian zonation were physiological constraints and hydrographic factors affecting the deposition and concentration of organic matter. Howell et al. (2002) indicated the importance of the permanent thermocline and water mass structure in determining the zonation patterns of seastars. Furthermore, Flach and Thomsen (1998) indicated that physical and chemical factors such as flow velocities and organic matter supply could be very important parameters structuring macrofauna. Although water mass structure and temperature might have an effect on the bathymetric distribution of bivalves in Porcupine Seabight (see detailed description of these physical factors in Howell et al., 2002), biological factors could also play a more important role. The reduced strength of zonation shown by bivalves, compared to other faunistic groups in the Porcupine Seabight and adjacent Abyssal Plain (Rice et al., 1990; Billett, 1991; Flach and Thomsen, 1998; Howell et al., 2002), has also been reported in other studies elsewhere (e.g. Sanders and Grasse, 1971; Rex, 1981; Allen and Sanders, 1996).

The bathymetric distribution of bivalves in the area of study could be explained by a combination of biological and physical factors. In deep-sea fauna, rates of zonation differ because of the biological interactions among species (Cartes and Carrasson, 2004). In general, zonation rates increase with trophic level (or size) (Rex, 1977; Cartes and Carrasson, 2004). Thus, faunal replacement with depth is more rapid among predators and croppers than infaunal deposit-feeders such as polychaetes and bivalves (Rex, 1977). Although the mode of larval development and degree of
mobility have been reported as some of the causes affecting the rate of species replacement (Sanders and Grassle, 1971; Haedrich et al., 1980; Allen and Sanders, 1996; Cartes and Carrason, 2004), recent studies have indicated that developmental mode is not the only factor determining zonation and dispersal distance (see Young et al., 1997). In fact, some of the most widespread species in deep sea present non-planktotrophic development and several planktotrophic species are confined to regions with high food availability (Young et al., 1997). Thus, other variables related with dispersal abilities such as egg size and fecundity should be taken into account to explain intensity of zonation (Cartes and Carrason, 2004). Despite the variability in reproductive patterns of deep-sea bivalves and echinoderms (seastars and holothurians) many of species present lecithotrophic development (Billet, 1991; Gage and Tyler, 1991; Le Pennec and Beninger, 2000; Ramirez-Llodra et al., 2002). It is possible that bivalves present a higher dispersal ability than echinoderms with the same type of larval development. Therefore, the lower trophic level and a higher dispersal ability of bivalves compared to seastars and holothurians might in part explain differences in rates of zonation among these groups. In contrast, sponges, which belong to a low trophic level, i.e. suspension-feeders, and present planktotrophic development (Witte, 1996), were more heavily zoned than bivalves in the Porcupine Seabight (Rice et al., 1990). This distribution, however, seemed to be related to specific hydrographic conditions in the area (Rice et al., 1990).

In addition, the hydrography and topographical features of the area may have a strong effect on patterns of species distribution (see Cartes et al., 2002). Porcupine Seabight presents an unusual canyon-like topography (see Section 2.1; Rice et al., 1991). Sedimentation (organic and inorganic fluxes) and hydrodynamics in submarine canyons help to create special habitats characterized by high abundance, biomass and diversity of species (Vetter and Dayton, 1998; Gili et al., 2000; Cartes et al., 2002). Organic matter contents have been reported to be higher in submarine canyons than over the surrounding slope areas (Danovaro et al., 1999; Gili et al., 2000; Cartes et al., 2002). Detrital material originating in the water column and on the continental shelf flows along the channels system in the Porcupine Seabight (Rice et al., 1991), and organic matter sinks along with inorganic particulate matter. Amounts of organic matter may be higher in the channel systems than surrounding areas affecting the distribution of species and assemblages in the Seabight (Figs. 3 and 7; Cartes et al., 2002). Furthermore, pulses of food arriving sporadically may tend to accumulate in this channels system that acts as trap for sediments (see Gili et al., 2000). Thus, these fluctuations in food supply can generate a high variability in patterns of abundance and distribution of species over time (see temporal variability in Section 4.1).

4.3. Diversity

Diversity trends in the deep sea are very variable. Various faunal groups have shown different depth–diversity trends (e.g. Sanders and Hessler, 1969; Rex, 1973, 1981; Carney and Carey, 1982; Cartes and Sardà, 1992; Paterson and Lambshead, 1995; Allen and Sanders, 1996; Rex et al., 1997; Howell et al., 2002). However, this large variation might in part be a result of the different collecting techniques and analytical methods used for estimating diversity (Rex et al., 1997). High diversity in the deep sea has been attributed to environmental/or biological factors (see for review Stuart et al., 2003).

A number of studies have found that gastropods and protobranches show parabolic trends in diversity, with peaks at upper rise depths (~2000–3000 m) (Rex, 1981, 1983; Rex et al., 1997). However, Allen and Sanders (1996) reported different trends in the diversity of protobranches from Atlantic basins, with diversity peaks in deeper waters (~3000–4000 m) followed by a drop to the deepest parts of the basins (~5000 m). Also, in most basins there was a dip in diversity between ~2000 and 2600 m. In the Western European basin, for example, diversity values were high with a diversity minimum at about 2500 m and a maximum at ~4400 m.

In this study, diversity did follow a concave unimodal trend (Fig. 10) similar to trends
previously shown for gastropods and bivalves (Rex, 1981, 1983; Rex et al., 1997). This diversity pattern is similar to that found for seastars in the Porcupine Seabight (Howell et al., 2002), although diversity of this group reached maximum values at ~1800 and 4700 m. Furthermore, the observed pattern matched that exhibited by protobranchs from some Atlantic basins (Allen and Sanders, 1996). Nevertheless, diversity values were not as high as those found in the West European Basin by the latter authors.

The low values of diversity between ~2100 and 2700 m were due in part to the large numbers of individuals of Kelliella atlantica in some of the samples collected at these depths. For example, this species accounted for 93% of individuals at ~2650 m. The high values of diversity found at ~4100 m were due to the large number of species recorded at this depth (16–20 species per sample). Between ~4800 and 4900 m, diversity values dropped since the number of species per sample was lower (4–9 species per sample). These results indicate high values of diversity at abyssal depths. Rex et al. (2005) proposed the “source-sink hypothesis for abyssal biodiversity” suggesting that abyssal populations might be maintained by immigration from adjacent bathyal populations of species with high dispersal ability. If so, this hypothesis, together with the low impact of predation on bivalve species at these depths (Allen and Sanders, 1996), could explain in part the high diversity values found at ~4100 m. Furthermore, several studies 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 responsible for the increase of diversity observed at 4100 m. For instance, some trophic groups such as deposit- and suspension-feeders would be favoured by this food supply. In fact, Thurston et al. (1998) and Billett et al. (2001) found that particle fluxes arriving at the sea floor on the Porcupine Abyssal Plain were very important in determining changes in the specific composition and abundance of megafaunal assemblages.

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