



Contrasting patterns of α - and β -diversity in deep-sea bivalves of the eastern and western North Atlantic



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ABSTRACT

We analyzed patterns of α - and β -diversity in deep-sea bivalves collected by epibenthic sleds from the western North Atlantic south of New England, and from the eastern North Atlantic in the Rockall Trough, Porcupine Seabight and Porcupine Abyssal Plain. In the western North Atlantic, species diversity, measured as the normalized expected number of species, shows a unimodal bathymetric trend peaking at mid-bathyal depths. In the eastern North Atlantic, diversity increases monotonically with depth reaching a maximum at abyssal depths. We used Baselga's (2010) metrics to distinguish two separate components of β -diversity along depth gradients, species dissimilarity among sites due to spatial replacement (turnover) and species loss leading to nestedness. We also examined the rank order of nestedness with depth using Rodríguez-Gironés and Santamaría's (2006) BINMATNEST. The primary difference in β -diversity between west and east centers on the composition of abyssal communities. In the western North Atlantic, abyssal assemblages are nested subsets of bathyal assemblages. In the eastern North Atlantic, turnover dominates at all depths. These very fundamental differences in community structure between the basins may be attributable to differences in food supply, which is greater in the eastern North Atlantic region sampled. POC-flux to abyssal depths in the east may not reach levels low enough to depress species diversity as it does in the west. In the west, the abyssal fauna is largely an impoverished nested subset of the bathyal fauna that shows less endemism and may be maintained partly by source–sink dynamics.

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1. Introduction

Since the inception of modern deep-sea sampling technology (Hessler and Sanders, 1967; Sanders, 1968), geographic patterns of α -diversity have become fairly well established in the Atlantic Ocean. Their causes are scale-dependent and complex, involving both contemporary environmental drivers and evolutionary–historical processes (Rex and Etter, 2010). Patterns of β -diversity are less well described and understood (Carney, 2005; Wei et al., 2010). As in other areas of ecology, it has been much simpler to explain how many species coexist than which species coexist. Unlike α -diversity, β -diversity has no coherent and widely accepted theoretical underpinnings. Rather, interpretations of β -diversity have rested mainly on known habitat associations for a minority of species. For example, sessile zooplankton feeders like coral occur in depth zones where there is hard substrate for

attachment and sufficient downwelling of food (De Mol et al., 2002; Howell et al., 2002), opportunistic holothurians occur where there is periodic heavy deposition of phytodetritus (Billett et al., 2001), surface deposit feeding polychaetes that can tolerate low oxygen concentration dominate in narrow oxygen minimum zones (Levin et al., 2000), and so on. For most of the fauna arrayed along depth gradients in soft sediment environments, several vague generalizations can be made (Rex and Etter, 2010): (1) faunal change is continuous and gradual, (2) the rate of change in species composition correlates with the rate of change in depth reflecting the strength of the environmental gradient, (3) larger organisms and predators are lost more rapidly than smaller deposit feeders presumably because they are more vulnerable to the exponential decrease in food supply with increasing depth.

Beta-diversity in the deep sea has been interpreted almost exclusively as spatial replacement of species either along depth gradients (Carney, 2005) or horizontally (McClain et al., 2012a). Recently, it has become clear that β -diversity can have two distinct components with different causes, species turnover and

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species loss leading to nestedness (Baselga, 2010, 2012). A nested pattern is when smaller communities form ordered subsets of the species composition of larger communities. For example, in deep-sea neogastropods some abyssal assemblages are mostly impoverished nested subsets of the bathyal fauna and exhibit little evidence of endemism (Rex et al., 2005; Brault et al., in press). In other words, the abyssal assemblage represents primarily the loss of bathyal species, rather than species turnover. These nested abyssal communities typically represent highly attenuated range extensions of bathyal species that have larval dispersal ability. One explanation for this phenomenon is that abyssal populations are maintained by source–sink dynamics (Holt, 1985; Pulliam, 1988). Many abyssal populations may be so rare that they suffer chronic local extinction from vulnerabilities to Allee effects, a density-dependent effect where low numbers reduce population growth (Courchamp et al., 2008), and are maintained by dispersal from larger bathyal sources (Rex et al., 2005). However, nested depauperate abyssal assemblages are not universal. Some abyssal communities receive sufficient food supply to not experience depressed diversity (Smith et al., 1997; Glover et al., 2002), and some taxa are highly adapted to abyssal conditions and thrive there (e.g. Wilson, 1991, 1998; Billett et al., 2001). The species turnover component of β -diversity in deep-sea neogastropods dominates on the steeper continental margin (Brault et al., in press), we suppose because species are adapted to conditions or prey resources at restricted depths along a steep selective gradient; but, the details of how this might operate are almost completely unknown.

There are few directly comparable among-basin studies of both α - and β -diversity. A new Pan-Atlantic database on deep-sea bivalves (Allen, 2008) makes it possible to examine both aspects of diversity using the same samples and collecting methods, and consistent taxonomy. In this paper, we analyze diversity in the eastern and western North Atlantic, the most well-sampled region, using this database. Eastern and western faunas are fundamentally different in both α - and β -diversity, and these differences suggest a common underlying cause for both α -diversity and the species loss component of β -diversity.

2. Material and methods

We base the analysis on the deep-sea bivalve faunas of the western North Atlantic (North American Basin south of New England, Fig. 1), and eastern North Atlantic (Rockall Trough, Porcupine Seabight and Porcupine Abyssal Plain, Fig. 2). The data include all three subclasses of the Bivalvia, the Protobranchia, Lamellibranchia and Septibranchia (the latter now included in the subclass Anomalodesmata). The assemblage is very mixed trophically; the three subclasses in the deep sea represent predominantly deposit feeders, suspension feeders, and carnivores respectively. Modes of larval development and dispersal in deep-sea bivalves are less well known than in the other major macrofaunal molluscan taxon, the Gastropoda (e.g. Rex et al., 2005). The protobranchs, which typically dominate at abyssal depths (Allen, 2008), have swimming lecithotrophic larvae that disperse demersally (Zardus, 2002). The largest family of lamellibranchs, the Thyasiridae, have planktotrophic larvae (Payne and Allen, 1991). The majority of species in the abyssal bivalve assemblage appear to have dispersing larvae.

All material was collected with epibenthic sleds (Hessler and Sanders, 1967), as part of the Woods Hole Oceanographic Institution's Benthic Sampling Program (Sanders, 1977), or the Joint French and British INCAL 1976 Expedition in the Rockall Trough. Complete data, including stations of the Porcupine Seabight, for localities, species identifications, and relative abundances in

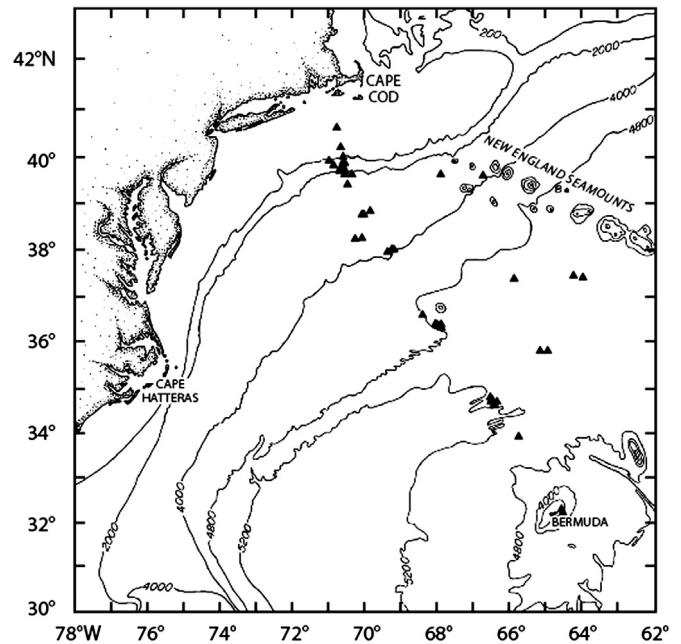


Fig. 1. Map of the sampling area for the western North Atlantic (North American Basin south of New England). Triangles indicate the sites of stations for all samples used in the analysis, including non-rarefied samples.

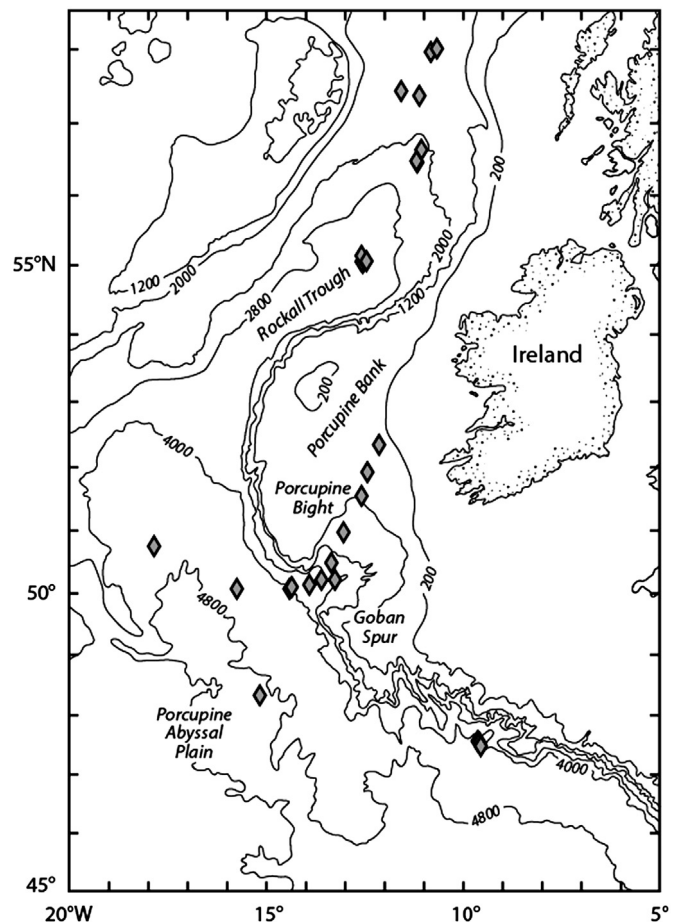


Fig. 2. Map of the sampling area for the eastern North Atlantic (Rockall Trough, Porcupine Seabight and Porcupine Abyssal Plain). Diamonds indicate the sites of stations for all samples used in the analysis, including non-rarefied samples.

samples can be found in Allen (2008). Please see Gage et al. (1980) (Rockall Trough) and Rice et al. (1991) (Porcupine Seabight and Porcupine Abyssal Plain) for background on sampling programs. Locations of stations in this analysis are noted in Fig. 1 for the western North Atlantic and in Fig. 2 for the eastern North Atlantic. In total, 190 species distributed among 53,693 individuals from 48 samples were recovered in the west, and 175 species distributed among 60,417 individuals from 27 samples in the east. Eighty-four species (23%) are shared between the west and east.

Because sample size differed so much among stations (1–34,580 individuals), and diversity is sample-size dependent, we normalized samples to 50 individuals [Hurlbert's (1971) expected number of species, $E(S_{50})$] to estimate α -diversity, and plotted $E(S_{50})$ against depth to show the bathymetric trends. This rarefaction process eliminated 7 stations in the west, leaving 41 for our analysis, and 1 station in the east, with 26 stations remaining for analysis. For the analysis of β -diversity, we used the same normalization which selected the most abundant species included in the rarefied samples; presence-absence data for these species were used in the analysis. Species ranges and raw data for the number of species per sample (i.e. not normalized) are provided as Supplementary material.

Baselga (2010, 2012) pointed out that overall beta diversity measured as Sørensen's (1948) dissimilarity index β_{SOR} could be decomposed mathematically into dissimilarity due to turnover measured as Simpson's (1943) index β_{SIM} and a new index of dissimilarity due to species loss leading to nestedness β_{NES} . We examine all three metrics within two broad depth intervals of bathyal and abyssal zones, 1000–3800 m and 3800–5000 m respectively, to determine their relative importance with depth. We initiated the analyses at 1000 m because there is a small increase in nestedness at upper bathyal depths. This is associated with a decrease in diversity and shared species makeup with mid-bathyal depths and is not the focus of this paper (see Brault et al., in press). We computed dissimilarity between pairs of sites against the difference in depth for each pair (Baselga, 2010). We used a Mantel test with 1000 replicates (Pearson correlation) to assess whether the components of β -diversity changed among sites along the bathymetric gradient. Baselga also derived composite multiple-site metrics (β_{SOR} , β_{SIM} , and β_{NES}) to compare whole regions, such as the bathyal and abyssal depth intervals used in this study for the among-site analyses. The multiple-site comparisons have no statistics associated with them, but should be consistent with the general outcome of the pair-wise site analysis. It is important to stress that β_{NES} is not strictly speaking nestedness, but reflects that part of dissimilarity that can be attributed to the effects of nestedness rather than turnover.

In addition to the dissimilarity metrics, we used Rodríguez-Gironés and Santamaría's (2006) BINMATNEST algorithm to determine whether there was significant nestedness among sites, and the rank order of nestedness with depth. BINMATNEST is an improved version of the classic Atmar and Patterson's (1993) calculator for determining whether there is significant nested order among sites in a species presence-absence vs. site matrix. The procedure packs the positive observations of the matrix optimally into the upper left triangle by permuting the rows and columns. The packed matrix is compared to a set of null matrices (1000 in this analysis) in which the observations are randomized to determine whether there is significant nested order overall among sites. The packed matrix also establishes the rank order of nestedness among sites, which we plotted against depth to determine how the degree of nestedness changed bathymetrically. Both the dissimilarity metrics and the BINMATNEST analysis are based on species presence-absence data rather than relative abundance data. We feel this is the most conservative way to consider very large-scale patterns of biogeography, especially in a remote environment where there is an

indeterminate but potentially large amount of sampling error. Please see Brault et al. (in press) for a fuller account of the application of these methods to deep-sea communities. The analyses do not assume that the ranges are fully occupied, but were conducted only on the actual stations occupied by species along the ranges.

3. Results

Bathymetric patterns of α -diversity $E(S_{50})$ are fundamentally different between the western and eastern North Atlantic. In the west (Fig. 3), diversity is a significant unimodal function of depth that peaks at mid-bathyal depths. In the east (Fig. 4), diversity is a significant monotonic positive function of depth with a maximum at abyssal depths. Species ranges and species richness derived

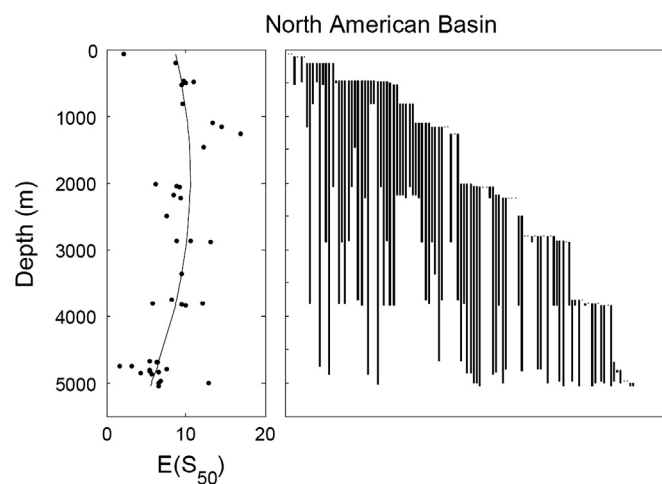


Fig. 3. Species diversity measured as Hurlbert's (1971) expected number of species $E(S_{50})$, and depth ranges of deep-sea bivalves in the western North Atlantic. Ranges are based on species occurrences that are included in the normalized samples. Based on data from Allen (2008). The regression equation for the relationship of $E(S_{50})$ to depth (D) is: $E(S_{50}) = 8.6301 + 0.0020D - 5.2192e^{-7}D^2$ ($N=41$, $F=8.98$, $P=0.00064$, $R^2=0.29$).

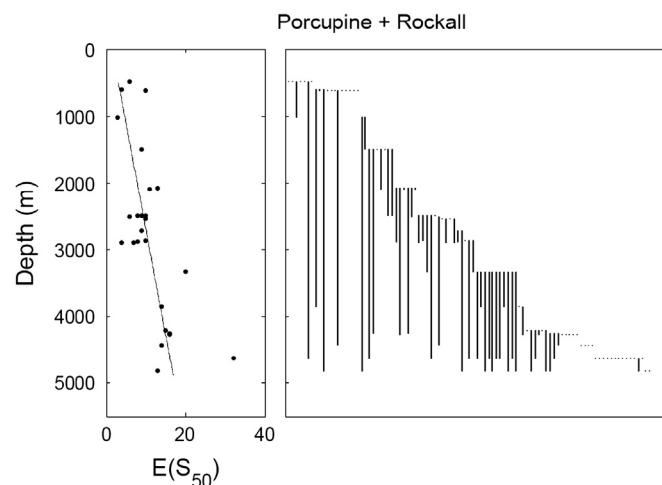


Fig. 4. Species diversity measured as Hurlbert's (1971) expected number of species $E(S_{50})$ and depth ranges of deep-sea bivalves in the eastern North Atlantic. Ranges are based on species occurrences that are included in the normalized samples. Based on data from Allen (2008). The regression equation for the relationship of $E(S_{50})$ to depth (D) is: $E(S_{50}) = 1.5547 + 0.0031D$ ($N=26$, $F=20.82$, $P=0.0001$, $R^2=0.46$).

from raw data (Figs. S1 and S2), although compromised by large discrepancies in sample size, essentially show the same patterns. In the west, number of species is a significant unimodal function of depth, and abyssal samples appear to be nested subsets of the bathyal assemblage. In the east, the number of species reaches its highest level in the abyss, but the diversity–depth trend, although positive, is not significant, probably owing to fewer and un-normalized samples.

Superficially, the depth range distributions of both regions look similar (Figs. 3 and 4), with many abyssal populations being range extensions of conspecific bathyal populations. However, their internal structures differ. In the west, overall beta diversity increases throughout the depth ranges (Fig. 5). Turnover dissimilarity is positively and significantly related to depth difference in both zones. Nested dissimilarity shows no relationship with depth separation in either depth zone, but values of nestedness reach higher levels > 3800 m (medians are significantly higher > 3800 m, Wilcoxon rank sum test $P < 0.001$). Multiple-site metrics show relatively little difference between depth zones either < 3800 m or > 3800 m (0.889 vs. 0.875 for β_{SOR} and 0.862 vs. 0.807 for β_{SIM}), but β_{NES} , while generally quite low, is considerably higher > 3800 m (0.027 vs. 0.069). In the east (Fig. 6), overall dissimilarity and turnover dissimilarity are significantly and positively related to depth difference < 3800 m, and are not significant, but remain fairly high > 3800 m. None of

the other relationships is significant, and nested dissimilarity remains low in both depth zones. Multiple-site metrics are very similar < 3800 m and > 3800 m for β_{SOR} , β_{SIM} , and β_{NES} (0.774 vs. 0.786, 0.711 vs. 0.724, and 0.064 vs. 0.062 respectively).

BINMATNEST, which measures nestedness *per se* provides clearer and more definitive results. In both the west and east the packed matrix is significantly more ordered than the null matrices ($P < 0.000001$) indicating some degree of nestedness among sites in both regions. However, the direction of nestedness is completely different (Fig. 7). In the west below about 1000 m, there is a significant increase in the rank order of nestedness with depth with highest values attained in the abyss. In complete contrast, in the east, the rank order of nestedness is highest at mid-bathyal depths, and decreases significantly toward the abyss where it reaches its lowest levels (Fig. 7). In other words, the abyssal samples in the west are highly nested subsets of the bathyal assemblage, and abyssal samples in the east are not.

Abyssal endemism (> 4000 m) using rarefied data is concomitantly higher in the east (26 species vs. 7 species in the west). We stress that what we call abyssal endemism is regional endemism, and is slightly underestimated by 3–6 species (see below) because some locality records are lost by rarefaction. Using raw data, abyssal endemism remains higher in the east (28 vs. 13 species in the west, Figs. S1 and S2). Again, this is a regional, rather than global, estimate; species that are regional

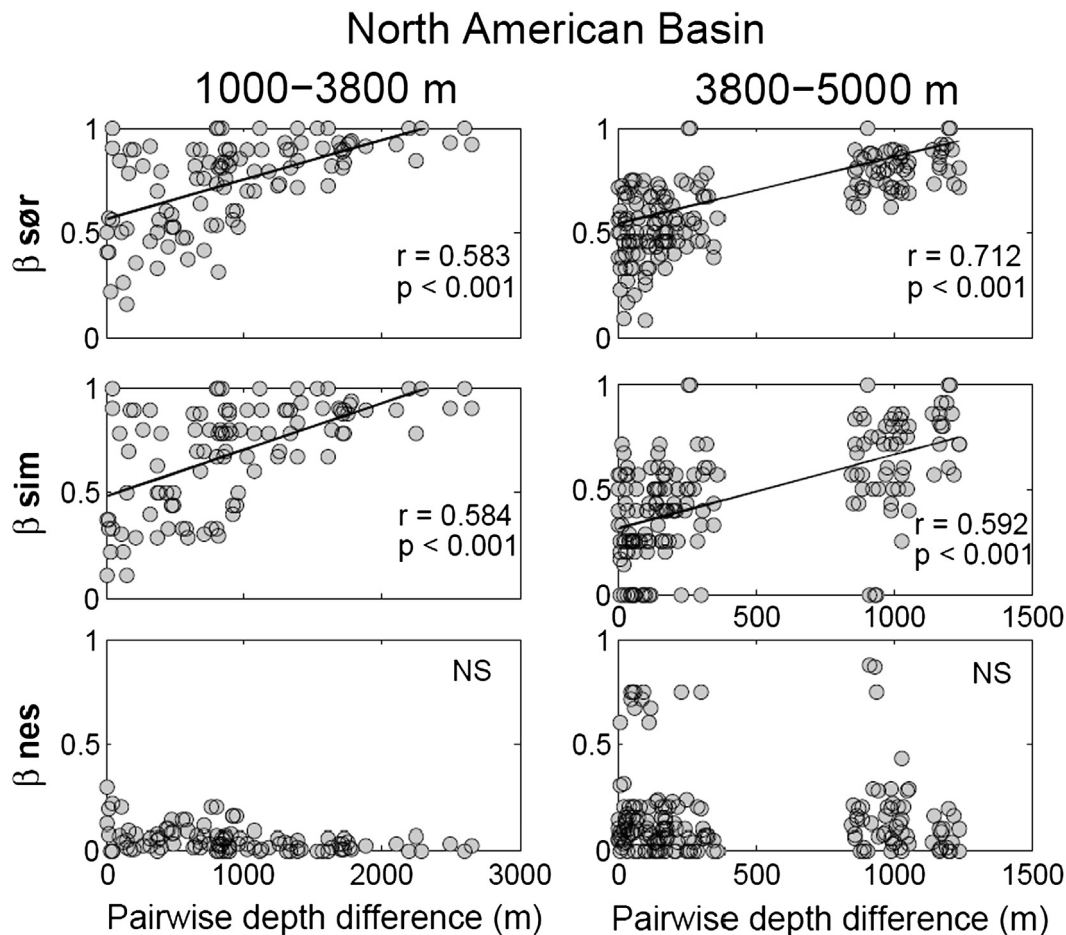


Fig. 5. Baselga's (2010) pair-wise dissimilarity of deep-sea bivalve assemblages as a function of depth separation for comparisons among sites in the western North Atlantic in two depth regions 1000–3800 m and 3800–5000 m. Dissimilarity ranges from 0 (identical species composition) to 1 (completely different species composition). The breach in depth separation is a sampling gap between 3800 m and 4600 m. P values indicate significance of Pearson r resulting from a Mantel test with 1000 replicates. Regression lines are shown only when r values are significant. Sørensen's dissimilarity (β_{sor}) reflects overall dissimilarity in species makeup. Turnover (β_{sim}) and nestedness (β_{nes}) dissimilarities are two components of beta diversity.

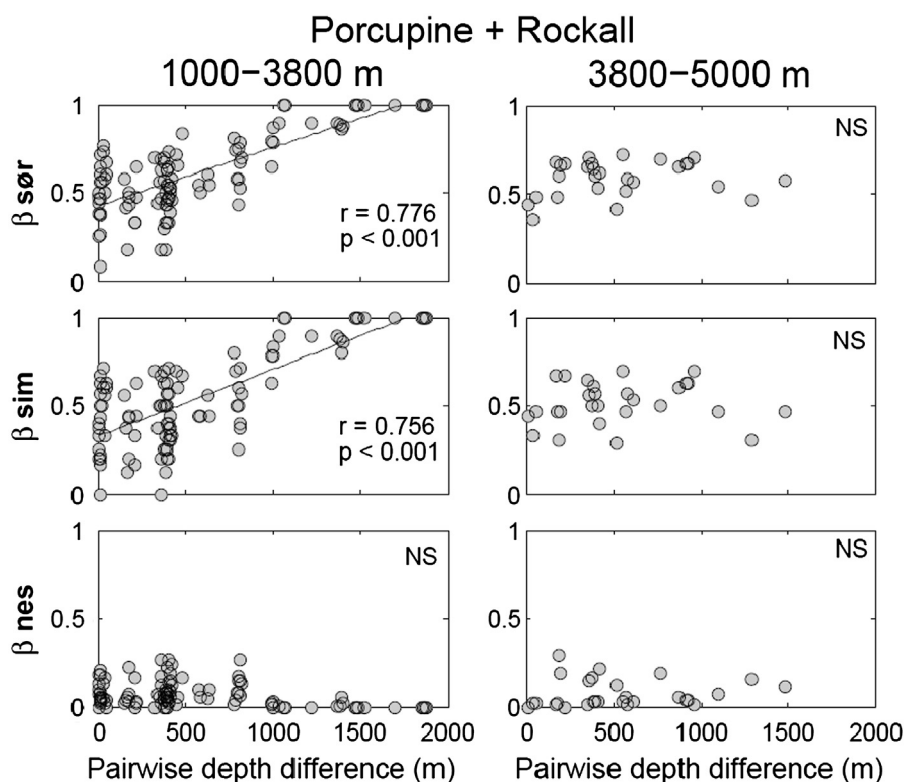


Fig. 6. Baselga's (2010) pair-wise dissimilarity of deep-sea bivalve assemblages as a function of depth separation for comparisons among sites in the eastern North Atlantic in two depth regions, 1000–3800 m and 3800–5000 m. Dissimilarity ranges from 0 (identical species composition) to 1 (completely different species composition). *P* values indicate significance of Pearson *r* resulting from a Mantel test. Regression lines are shown only where *r* values are significant. Sørensen's dissimilarity ($\beta_{sør}$) reflects overall dissimilarity in species makeup. Turnover (β_{sim}) and nestedness (β_{nes}) dissimilarities are two components of beta diversity.

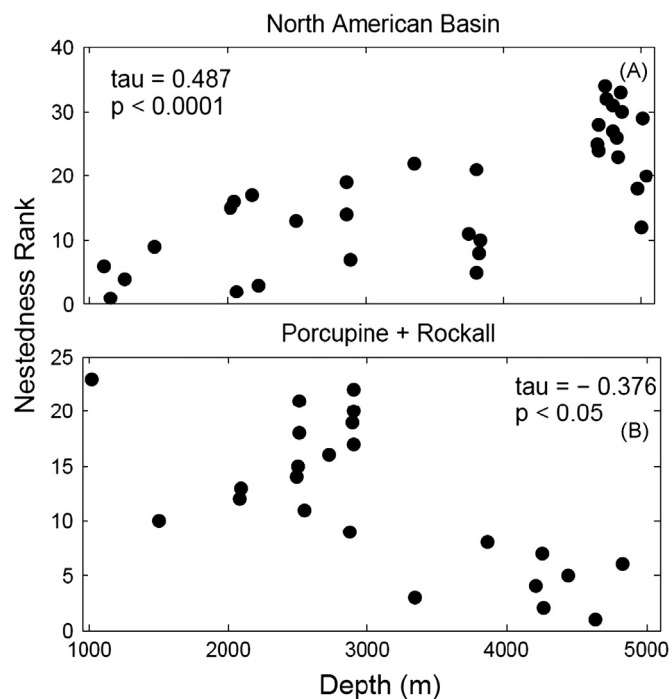


Fig. 7. The rank order of nestedness for deep-sea bivalve assemblages in (A) the western North Atlantic and (B) the eastern North Atlantic determined by Rodríguez-Gironés and Santamaría's (2006) BINMATNEST.

abyssal endemics can occupy bathyal depths in other basins (Rex and Etter, 2010), and some abyssal endemics might have been missed in sampling.

4. Discussion

Western and eastern assemblages of deep-sea bivalves in the North Atlantic display contrasting patterns of biodiversity. The primary difference concerns abyssal communities. In the west, abyssal α -diversity is depressed and β -diversity represents a nested subset of the bathyal fauna. In the east, abyssal α -diversity remains quite high, β -diversity is characterized by species turnover rather than nestedness, and endemism is greater.

The causes of deep-sea biodiversity are undoubtedly multivariate (Rex and Etter, 2010). But recently, energy in the form of POC-flux has emerged as the primary determinant of α -diversity in molluscs (Tittensor et al., 2011; McClain et al., 2012b). Several kinds of evidence suggest that food supply to the benthos is greater in the eastern region (Fig. 2) than in the western region (Fig. 1). High surface phytoplankton production and export flux of POC extend much farther out to sea off the Rockall Trough, Porcupine Seabight, and Porcupine Abyssal Plain than south of New England (see e.g. Behrenfeld and Falkowski, 1997; Sun et al., 2006; Lutz et al., 2007). POC-flux, measured by the Lutz et al. (2007) algorithm at our sampling stations, decreases with depth in both the eastern and western regions (linear regressions both with negative slopes significant at $P < 0.0001$), the usual trend throughout the deep sea. But, below 3800 m, POC-flux is 56 percent higher in the eastern basin (median 3.65 vs. 2.06 $\text{g C m}^{-2} \text{yr}^{-1}$, $P < 0.01$, Fisher-Yates test). Estimates of POC-flux at depth in a larger dataset from the eastern and western North Atlantic (McClain et al., 2012b) show similar decreasing trends between the two regions to 3800 m, and then a complete dichotomy > 3800 m with consistently higher values in the east (Fig. S3). The Porcupine Abyssal Plain is a site of episodic heavy deposition of phytodetritus (Billett et al., 1983), probably as a consequence of high and variable downward particle flux (Lampitt et al., 2010).

Macrofaunal density and the trophic make-up of abyssal bivalve assemblages also suggest greater food supply in the east. Quantitative data on macrofaunal density for the two regions are sparse, but values in the east are significantly higher in the vicinity of our samples (North American Basin compared to Porcupine Abyssal Plain and Goban Spur, Mann–Whitney U test, $U=81$, $z=2.35$, $P<0.01$, data and references in Rex and Etter, 2010). Unfortunately, density data are unavailable for bivalves per se. However, the composition of bivalve feeding modes differs markedly between the regions. In the west >3800 m, deposit feeders (protobranchs) comprise 40.3% of species and 88.5% of individuals. In the east, protobranchs are reduced to 30.7% of species and 49.2% of individuals. Carnivores (septibranchs) show the opposite trend, increasing from 19.4% of species and only 1.1% of individuals in the west to 29.5% and 13.3% respectively in the east. The proportion of suspension feeding (lamellibranch) species is about the same between regions (40.3% vs. 39.8%), but the representation of individuals increases from 10.4% in the west to 37.5% in the east. This pronounced shift to more suspension feeders and carnivores in the east could reflect more energy availability in the form of sinking phytodetritus for suspension feeders and more prey resources to support carnivores. The order of magnitude increase of carnivorous individuals is particularly indicative of more energy availability because of their susceptibility to the significant energy loss that occurs between trophic levels. While this evidence is certainly not conclusive, it is all consistent with the east having higher abyssal α -diversity than the west because of greater productivity. However, while elevated abyssal diversity in the east occurs at higher POC-flux than in the west, eastern abyssal POC-flux is still lower than at bathyal depths (see e.g. Fig. S3). In addition to more food supply at abyssal depth in the east, which supports greater trophic complexity and more species, the higher level of endemism there suggests that historical–evolutionary processes may augment diversity as well. Greater diversity may partly result from improved adaptation to abyssal conditions.

In regions where there is a broad range of POC-flux, such as the North American Basin in the western North Atlantic, diversity increases with depth to the mid-bathyal zone (between 1000 and 3000 m), and then decreases in the highly oligotrophic abyss (Rex and Etter, 2010; Tittensor et al., 2011). Species diversity is a unimodal function of POC-flux, consistent with the productivity–diversity theory (Rosenzweig, 1995). Diversity may be depressed in the abyss because food supply is insufficient to support populations large enough to be reproductively viable. Many abyssal populations may act as sinks that suffer chronic local extinction from Allee effects, and are maintained by continued immigration from more abundant bathyal source populations. Where abyssal POC-flux is greater, abyssal population density and α -diversity remain high (Smith et al., 1997; Glover et al., 2002, and this paper for the eastern basin). Where regional surface production is lower than in the western North Atlantic, the productivity–diversity curve shifts predictably toward lower levels of productivity (Rex and Etter, 2010) and the productivity–diversity curve becomes entirely negative, as it does, for example, in the Mediterranean (Tselepidis et al., 2000). This negative relationship is similar in form to the lower bathyal–abyssal segment in the western North Atlantic (Fig. 3). Depressed α -diversity coupled with a nested pattern of β -diversity provides geographic evidence that source–sink dynamics may help regulate abyssal community structure in the western North Atlantic.

In the eastern North Atlantic, α -diversity increases with depth to a maximum at abyssal depths. β -diversity is dominated by turnover throughout the depth range, and there is, as a consequence, more abyssal endemism than in the west. There is really no *a priori* reason to expect that source–sink dynamics maintain

abyssal biodiversity. It seems more likely that POC-flux to the abyss remains sufficiently high in the east to support a rich community and provide opportunities for adaptation to abyssal conditions. This is a very simplified and qualitative view of productivity–diversity relationships in the deep sea, but at least one that is consistent for North Atlantic bivalves at very large biogeographic scales. All of these relationships could be compromised, of course, by other drivers of diversity that were not measured.

The most important finding is that β -diversity in the deep sea can include both species replacement and species loss (also in Brault et al., *in press*), and that the latter appears to be ultimately a function of productivity in the form of POC-flux. Put simply, as POC-flux decreases with depth, particularly at the extremely low values experienced in some abyssal plains, species drop out because of insufficient food supply. The general notion that β -diversity is somehow connected to POC-flux is not new. For example, Rex (1977, 1981) showed that depth-related rates of change in species composition in megafaunal elements, and in macrofaunal gastropods, bivalves and polychaetes correspond to their relative positions in the trophic structure, being greater at higher trophic levels. This suggested that competition for prey at higher trophic levels may restrict ranges resulting in greater rates of turnover. Haedrich et al. (1980) proposed that differences in turnover rates between megafaunal fishes and invertebrates are related to mobility and breadth of diet. Carney (2005) attributed turnover rates to how the balance between food supply and sediment oxygen concentration limited microhabitat space, and hence vertical ranges (the TROX model of Jorissen et al., 1995). Wei et al. (2010), in an elegant analysis, showed convincingly that faunal boundaries characterized by rapid rates of change in species composition, coincided with shifts in POC-flux. Rex and Etter (2010) pointed out that part of the change in species composition with depth is a simple consequence of how the exponential decrease in POC-flux with depth enforces the progressive loss of larger organisms and secondary consumers, which have greater energy demands. McClain et al. (2012a) showed that horizontal oceanic-scale turnover in deep-sea bivalves was also linked to energy availability.

The α -diversity patterns in North Atlantic bivalves accord fairly well with those found in other taxa. In the western North Atlantic, other major macrofaunal taxa (gastropods, polychaetes, cumaceans, protobranch bivalves) have unimodal diversity–depth trends (Rex and Etter, 2010). Megafaunal invertebrates and fish also have unimodal diversity–depth patterns in the west (Rex and Etter, 2010). However, isopods reach their highest diversity in the abyss, evidently because they have evolved reproductive adaptations which allow them to live at low population densities (Wilson, 1991, 1998). In the east Atlantic, Olabarria (2005), using a completely independent dataset collected from the Porcupine Seabight and Porcupine Abyssal Plain, showed that bivalve diversity measured as $E(S_{50})$ reached its highest level in the abyss, as found here. Prosobranch gastropods (Olabarria, 2006) and gastropods as a class (Stuart and Rex, 2009), both of which contain mixed feeding types, also showed elevated diversity at abyssal depths. Neogastropod diversity in the eastern North Atlantic shows a unimodal pattern with depth (Brault et al., *in press*). All neogastropods are carnivores, and the largest family, the Turridae, is composed of highly specialized predators. Higher trophic levels are more susceptible to reduced energy because of the loss of energy between trophic levels, and this may be responsible for their depressed abyssal diversity. Similarly, demersal fish show depressed abyssal diversity in the Porcupine Abyssal Plain (Priede et al., 2010), perhaps because they are secondary consumers and large animals with high energetic demands. Megafaunal asteroids, many of which are large carnivores,

also show depressed abyssal diversity at regional scales in the Porcupine Abyssal Plain (Howell et al., 2002; Rex and Etter, 2010). Holothurians, which are deposit feeders some of which are specialized to rapidly exploit phytodetrital deposits at the seafloor, predictably do not experience reduced abyssal diversity (Billett, 1991; Rex and Etter, 2010). Overall, the relationships of diversity to productivity, body size and trophic mode seem reasonably consistent.

If the nestedness portion of β -diversity (species loss) toward the abyss and depressed abyssal α -diversity in the west are both attributable to severe decreases in energy, this may lead to a more unified explanation of deep-sea biodiversity. The greatest remaining challenge is to develop a general theory to account for the species turnover component of β -diversity

Earlier studies of diversity in the deep sea have treated α - and β -diversity as separate features of community structure. They are, in fact, inextricably connected as shown here. The potential for species dissimilarity, the primary measure of β -diversity, is limited by differences in α -diversity. Differences in community composition revealed by β -diversity, including species distributions, endemism, trophic makeup, and life history, can reveal much about the causes of α -diversity that simple differences in the number of species cannot. And, α - and β -diversity are based essentially on the same data, the only difference being that β -diversity requires information on species identity; so, in relating these two dimensions of diversity, we must eventually resolve both causality and the difficult problem of statistical redundancy.

Acknowledgments

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr2.2013.01.018>.

References

- Allen, J.A., 2008. Bivalvia of the deep Atlantic. *Malacologia* 50, 57–173.
- Atmar, W., Patterson, B.D., 1993. On the measure of order and disorder in the distribution of species on archipelagos. *Oecologia* 96, 373–382.
- Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. *Global Ecol. Biogeogr.* 19, 134–143.
- Baselga, A., 2012. The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecol. Biogeogr.* 21, 1223–1232.
- Behrenfeld, M.J., Falkowski, P.G., 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnol. Oceanogr.* 42, 1–20.
- Billett, D.S.M., 1991. Deep-sea holothurians. *Oceanogr. Mar. Biol. Ann. Rev.* 29, 259–317.
- Billett, D.S.M., Lampitt, R.S., Rice, A.L., Mantoura, R.F.C., 1983. Seasonal sedimentation of phytoplankton to the deep-sea benthos. *Nature* 302, 520–522.
- Billett, D.S.M., Bett, B.J., Rice, A.L., Thurston, M.H., Galéron, J., Sibuet, M., Wolff, G.A., 2001. Long-term change in the megafauna of the Porcupine Abyssal Plain, (NE Atlantic). *Prog. Oceanogr.* 50, 325–348.
- Brault, S., Stuart, C.T., Wagstaff, M.C., Rex, M.A. Geographic evidence for source-sink dynamics in deep-sea gastropods of the eastern North Atlantic: an approach using nested analysis. *Global Ecol. Biogeogr.*, <http://dx.doi.org/10.1111/geb.12005>, in press.
- Carney, R.S., 2005. Zonation of deep biota on continental margins. *Oceanogr. Mar. Biol. Ann. Rev.* 43, 211–278.
- Courchamp, F., Berec, L., Gascoigne, J., 2008. *Allee Effects in Ecology and Conservation*. Oxford University Press, UK.
- De Mol, B., Van Rensbergen, P., Pillen, S., Van Herreweghe, K., Van Rooij, D., McDonnell, A., Huvenne, V., Ivanov, M., Swennen, R., Henriët, J.P., 2002. Large deep-water coral banks in the Porcupine Basin, southwest of Ireland. *Mar. Geol.* 188, 193–231.
- Gage, J.D., Lightfoot, R.H., Pearson, M., Tyler, P.A., 1980. An introduction to a sample time-series of abyssal macrobenthos: methods and principal sources of variability. *Oceanol. Acta* 3, 169–176.
- Glover, A.G., Smith, C.R., Paterson, G.L.J., Wilson, G.D.F., Hawkins, L., Shearer, M.S., 2002. Polychaete species diversity in the central Pacific abyss: local and regional patterns, and relationships with productivity. *Mar. Ecol. Prog. Ser.* 240, 157–170.
- Haedrich, R.L., Rowe, G.T., Polloni, P.T., 1980. The megabenthic fauna in the deep sea south of New England, USA. *Mar. Biol.* 57, 165–179.
- Hessler, R.R., Sanders, H.L., 1967. Faunal diversity in the deep-sea. *Deep-Sea Res.* 14, 65–78.
- Holt, R.D., 1985. Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. *Theor. Popul. Biol.* 28, 181–208.
- Howell, K.L., Billett, D.S.M., Tyler, P.A., 2002. Depth-related distribution and abundance of seastars, (Echinodermata: Asteroidea) in the Porcupine Seabight and Porcupine Abyssal Plain, N.E. Atlantic. *Deep-Sea Res.* I 49, 1901–1920.
- Hurlbert, S.H., 1971. The nonconcept of species diversity: a critique and alternative parameter. *Ecology* 52, 577–586.
- Jorissen, F.J., de Stigter, H.C., Widmark, J.G.V., 1995. A conceptual model explaining benthic foraminiferal microhabitats. *Mar. Micropaleontol.* 26, 3–15.
- Lampitt, R.S., Salter, I., de Cuevas, B.A., Hartman, S., Larkin, K.E., Pebody, C.A., 2010. Long-term variability of downward particle flux in the deep northeast Atlantic: causes and trends. *Deep-Sea Res.* II 57, 1346–1361.
- Levin, L.A., Gage, J.D., Martin, C., Lamont, P.A., 2000. Macrobenthic community structure within and beneath the oxygen minimum zone, NW Arabian Sea. *Deep-Sea Res.* II 47, 189–226.
- Lutz, M.J., Caldeira, K., Dunbar, R.B., Behrenfeld, M.J., 2007. Seasonal rhythms of net primary production and particulate organic carbon flux describe biological pump efficiency in the global ocean. *J. Geophys. Res.* 112, C10011, <http://dx.doi.org/10.1029/2006JC003706>.
- McClain, C.R., Stegen, J.C., Hurlbert, A.H., 2012a. Dispersal, environmental niches and oceanic-scale turnover in deep-sea bivalves. *Proc. R. Soc. B* 279, 1993–2002.
- McClain, C.R., Allen, A.P., Tittensor, D.P., Rex, M.A., 2012b. Energetics of life on the deep seafloor. *Proc. Natl. Acad. Sci., USA* 109, 15366–15371.
- Olabarria, C., 2005. Patterns of bathymetric zonation of bivalves in the Porcupine Seabight and adjacent abyssal plain, NE Atlantic. *Deep-Sea Res.* I 52, 15–31.
- Olabarria, C., 2006. Faunal change and bathymetric diversity gradient in deep-sea prosobranchs from Northeastern Atlantic. *Biodiv. Conserv.* 15, 3685–3702.
- Payne, C.M., Allen, J.A., 1991. The morphology of deep-sea Thyasiridae (Mollusca: Bivalvia) from the Atlantic Ocean. *Philos. Trans. R. Soc. London B* 334, 481–562.
- Priede, I.G., Godbold, J.A., King, N.J., Collins, M.A., Bailey, D.M., Gordon, J.D.M., 2010. Deep-sea demersal fish species richness in the Porcupine Seabight, NE Atlantic Ocean: global and regional patterns. *Mar. Ecol.* 31, 247–260.
- Pulliam, H.R., 1988. Sources, sinks and population regulation. *Am. Nat.* 132, 652–661.
- Rex, M.A., 1977. Zonation in deep-sea gastropods: the importance of biological interactions to rates of zonation. *Eur. Symp. Mar. Biol.* 11, 521–530.
- Rex, M.A., 1981. Community structure in the deep-sea benthos. *Annu. Rev. Ecol. Syst.* 12, 331–353.
- Rex, M.A., Etter, R.J., 2010. *Deep-Sea Biodiversity: Pattern and Scale*. Harvard University Press, Cambridge, USA.
- Rex, M.A., McClain, C.R., Johnson, N.A., Etter, R.J., Allen, J.A., Bouchet, P., Warén, A., 2005. A source-sink hypothesis for abyssal biodiversity. *Am. Nat.* 165, 163–178.
- Rice, A.L., Billett, D.S.M., Thurston, M.H., Lampitt, R.S., 1991. The Institute of Oceanographic Sciences Biology Programme in the Porcupine Seabight: background and general introduction. *J. Mar. Biol. Assoc. UK* 71, 281–310.
- Rodríguez-Gironés, M.A., Santamaría, L., 2006. A new algorithm to calculate the nestedness temperature of presence-absence matrices. *J. Biogeogr.* 33, 924–935.
- Rosenzweig, M.L., 1995. *Species Diversity in Space and Time*. Cambridge University Press, Cambridge, UK.
- Sanders, H.L., 1968. Marine benthic diversity: a comparative study. *Am. Nat.* 102, 243–282.
- Sanders, H.L., 1977. Evolutionary ecology and the deep-sea benthos. In: Goulden, C.E. (Ed.), *The Changing Scenes in Natural Sciences 1776–1976*. Philadelphia Academy of Natural Sciences Special Publication, PH, USA, pp. 223–243.
- Simpson, G.G., 1943. Mammals and the nature of continents. *Am. J. Sci.* 241, 1–31.
- Smith, C.R., Berelson, W., DeMaster, D.J., Dobbs, F.C., Hammond, D., Hoover, D.J., Pope, R.H., Stephens, M., 1997. Latitudinal variations in benthic processes in the abyssal equatorial Pacific: control by biogenic particle flux. *Deep-Sea Res.* II 44, 2295–2317.
- Sørensen, T.A., 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content, and its application to analyses of the vegetation on Danish commons. *Biol. Skr.* 5, 1–34.

- Stuart, C.T., Rex, M.A., 2009. Bathymetric patterns of deep-sea gastropod species diversity in 10 basins of the Atlantic Ocean and Norwegian Sea. *Mar. Ecol.* 30, 164–180.
- Sun, X., Corliss, B.H., Brown, C.W., Showers, W.J., 2006. The effect of primary productivity and seasonality on the distribution of deep-sea benthic foraminifera in the North Atlantic. *Deep-Sea Res. I* 53, 28–47.
- Tittensor, D.P., Rex, M.A., Stuart, C.T., McClain, C.R., Smith, C.R., 2011. Species–energy relationships in deep-sea mollusks. *Biol. Lett.* 7, 718–722.
- Tselepidis, A., Zervakis, V., Polychronaki, T., Danovaro, R., Chronis, G., 2000. Distribution of nutrients and particulate organic matter in relation to the prevailing hydrographic features of the Cretan Sea, NE Mediterranean. *Prog. Oceanogr.* 46, 113–142.
- Wei, C., Rowe, G.T., Hubbard, G.F., Scheltema, A.H., Wilson, G.D.F., Petrescu, I., Foster, J.M., Wicksten, M.K., Chen, M., Davenport, R., Soliman, Y., Wang, Y., 2010. Bathymetric zonation of deep-sea macrofauna in relation to export of surface phytoplankton production. *Mar. Ecol. Prog. Ser.* 399, 1–14.
- Wilson, G.D.F., 1991. Functional morphology and evolution of isopod genitalia. In: Bauer, R., Martin, J. (Eds.), *Crustacean Sexual Biology*. Columbia University Press, New York, pp. 228–245.
- Wilson, G.D.F., 1998. Historical influences on deep-sea isopod diversity in the Atlantic Ocean. *Deep-Sea Res. II* 45, 279–301.
- Zardus, J.D., 2002. Protobranch bivalves. *Adv. Mar. Biol.* 42, 1–65.