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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.

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

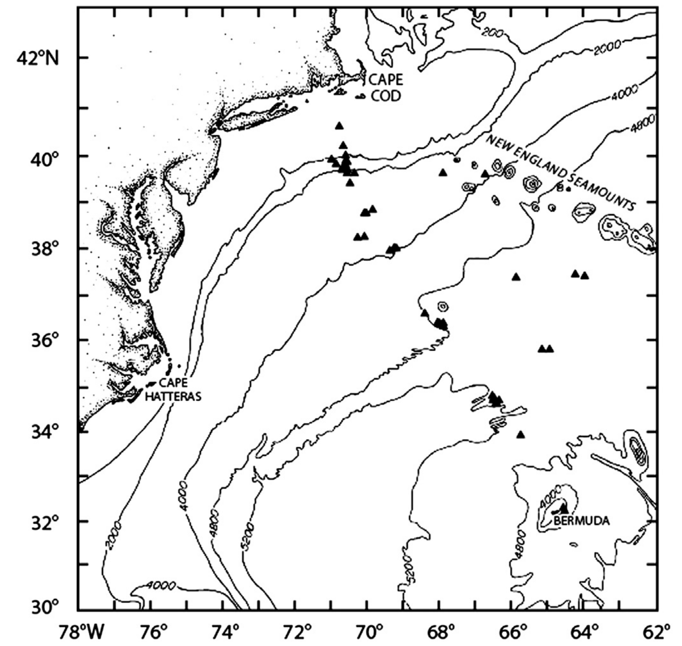

Fig. 1. Map of the sampling area for the western North Atlantic (North American Basin south of New England). Triangles indicate the sites of stations for all samples used in the analysis, including non-rarefied samples.

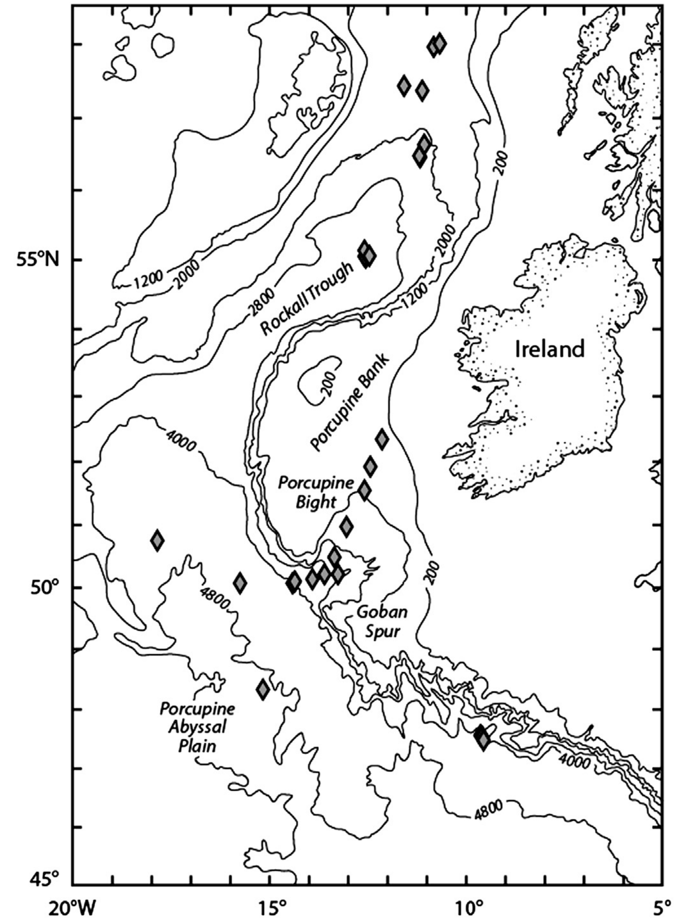

Fig. 2. Map of the sampling area for the eastern North Atlantic (Rockall Trough, Porcupine Seabight and Porcupine Abyssal Plain). Diamonds indicate the sites of stations for all samples used in the analysis, including non-rarefied samples.