



Nestedness and species replacement along bathymetric gradients in the deep sea reflect productivity: a test with polychaete assemblages in the oligotrophic north-west Gulf of Mexico

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ABSTRACT

Aim To test the hypothesis that low productivity drives the nestedness component of β -diversity in polychaetes at the deep-sea floor.

Location Western Gulf of Mexico.

Methods We used A. Baselga's (2010, *Global Ecology and Biogeography*, **19**, 134–143) metrics of species replacement and nestedness to assess their overall significance with differences in depth and particulate organic carbon (POC) flux to the seafloor. We used M. A. Rodríguez-Gironés & L. Santamaría's (2006, *Journal of Biogeography*, **33**, 924–935) BINMATNEST to calculate the significance and direction of nestedness with depth and POC flux.

Results Nestedness was the most significant part of β -diversity with depth and POC flux. The rank order of nestedness increased significantly with increasing depth, and decreased significantly with increasing POC flux. There was little endemism below 2000 m.

Main conclusion The polychaete fauna in the deepest western Gulf of Mexico is largely a nested subset of the shallower upper to mid-bathyal fauna. While the causes of β -diversity in the deep sea are undoubtedly multivariate, the relative importance of turnover and nestedness appears to be modulated by productivity in the form of POC flux to the seafloor. Under circumstances of extremely low POC flux and animal density in the deepest reaches of the Gulf, nestedness may be caused by some populations being maintained by immigration from larger populations upslope, or by biogeographic filtering for tolerance to abyssal conditions. Resources at great depths in regions of exceptionally low productivity may be too limited to permit adaptation resulting in endemism and continued downslope turnover. If productivity helps to explain the nestedness part of β -diversity, this may lead to a more unified theory of deep-sea biodiversity.

Keywords

deep sea, Gulf of Mexico, nestedness, niche requirements, POC flux, polychaetes, source-sink dynamics, β -diversity

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INTRODUCTION

The last decade has seen important advances in the study of β -diversity including its relationship to α -diversity (Jost, 2007), new analytical methods (Soininen *et al.*, 2007; Tuomisto, 2010; Gotelli & Chao, 2013; Baselga & Leprieur,

2015), and expanding the concept to include phylogenetic affinity (Chiu *et al.*, 2014), functional traits (Ricotta & Burrascano, 2008) and scale dependence (Zhang *et al.*, 2015). However, patterns and causes of β -diversity in the deep-sea benthos remain poorly documented and understood. Traditionally, β -diversity has been interpreted exclusively as spatial

replacement of species (turnover) either along bathymetric gradients (Carney, 2005) or horizontally among basins (Wei *et al.*, 2010; McClain *et al.*, 2012a; McClain & Rex, 2015). However, recently β -diversity as a concept has been shown to be composed of two distinct components: species replacement (turnover) and nestedness resulting from species loss (Baselga, 2010, 2012). Nestedness is when smaller communities are ordered subsets of the species makeup of larger communities. Turnover is when the species composition along an environmental gradient involves the substitution of new and different species. Nestedness and turnover are processes with different causes.

In previous papers, we have analysed bathymetric trends of turnover and nestedness in gastropods of the eastern North Atlantic (Brault *et al.*, 2012), bivalves in the eastern and western North Atlantic (Brault *et al.*, 2013), and echinoderms in the eastern North Atlantic (Wagstaff *et al.*, 2014). In the eastern and western North Atlantic, the relative importance of nestedness and species replacement in shaping β -diversity in molluscs appears to be related to food supply to the seafloor in the form of particulate organic carbon (POC) flux (Brault *et al.*, 2012, 2013). POC flux decreases exponentially with depth as sinking organic matter is remineralized in the water column creating a steep environmental gradient of food supply with depth at the seafloor. Higher surface production results in higher flux at depth (Rex & Etter, 2010). On continental margins (the bathyal zone), where flux is relatively high because of proximity to productive coastal systems and moderate depth, turnover dominates β -diversity in all cases examined by us (Brault *et al.*, 2012, 2013; Wagstaff *et al.*, 2014). If high surface production extends seaward over the abyss (> 4000 m), turnover continues downward in the abyss resulting in significant abyssal endemism (Brault *et al.*, 2013; Wagstaff *et al.*, 2014). Where POC flux is severely low at abyssal depths, population densities and species diversity become depressed (Rex & Etter, 2010). The abyssal community is essentially a progressively reduced and nested bathyal assemblage of species that have larval dispersal ability (Brault *et al.*, 2012, 2013). There is little abyssal endemism. Food supply to some impoverished abyssal plains simply may be too low to support a diverse community, or to permit adaptation to abyssal conditions.

There are few tests of the role of productivity in shaping β -diversity. Here, we extend our earlier studies of β -diversity to the polychaete fauna in a highly oligotrophic region of the north-west Gulf of Mexico that experiences much lower POC flux than the eastern and western North Atlantic. We hypothesize that extremely low food supply will cause extensive nestedness with depth, and permit less endemism at greater depths compared to upper and mid-bathyal depths.

MATERIALS AND METHODS

This study focuses on the two most western sampling transects (Fig. 1) of the Deep Gulf of Mexico Benthos

(DGoMB) Study in the northern Gulf (Rowe & Kennicutt, 2008; Wei *et al.*, 2010). The transects include 13 sampling stations extending from 213 to 3146 m across the bathyal zone, and three deeper stations at 3526–3732 m in the Sigsbee Abyssal Plain. The Gulf basin is bordered to the south by the Yucatan sill at 2000 m. The seafloor of the Gulf descends only to 3800 m, *c.* 1200 m shallower than the abyssal plains of the North Atlantic. We focus on the western Gulf because of its very low productivity and relatively simple topography. In contrast, the eastern Gulf is a more complex environment that is influenced by the Mississippi River outflow. Samples were collected from years 2000 to 2002 with a 0.20 m² box corer, and sieved on a 300 μ m screen.

Surface productivity in the Gulf is generally lower than in the North Atlantic (*cf.* Johnson *et al.*, 2007; Biggs *et al.*, 2008), and decreases by half westward across the Gulf making the western region impoverished (Biggs *et al.*, 2008). We estimated POC flux to the seafloor by using the algorithm of Lutz *et al.* (2007), which integrates satellite-derived surface chlorophyll concentration with sediment trap data taken in the deep water column. This reduces the potential effect of lateral advection of phytodetritus by currents as it settles through the water column. POC flux was estimated at the seafloor using the latitude and longitude coordinates of the benthic sampling stations. Earlier (Brault *et al.*, 2013), we used this method to estimate POC flux in the eastern and western North Atlantic, to which we compare the Gulf here. Over depth ranges that can be compared (*c.* 400–3800 m), POC flux at depth averages 1.85 mg C m⁻² day⁻¹ in the western Gulf, in contrast to 10.93 mg C m⁻² day⁻¹ in the western and 11.64 mg C m⁻² day⁻¹ in the eastern North Atlantic. A comparison of POC flux ranging from 0.5 to 45.0 mg C m⁻² day⁻¹ over the full depth ranges of the three regions is shown in Fig. 2. The abundance and biomass of the benthos in the western Gulf are *c.* 20% and an order of magnitude lower respectively than in the North Atlantic, and species diversity is about a third at 3800 m (Rex & Etter, 2010). Hence, food supply, benthic standing stock, body size and biodiversity of the benthos are all considerably depressed compared to those found in the North Atlantic at similar depths.

The fauna analysed here is the polychaete worm fraction of the box-core samples. Polychaetes are the most abundant and diverse macrofaunal elements in the deep-sea benthos (Gage & Tyler, 1991; Rex & Etter, 2010). Since sampling was entirely quantitative, there was no need to rarefy samples to a common sample size, a standard practice when using qualitative trawl data (Rex & Etter, 2010). We report density and diversity as the number of individuals per square metre (hereafter inds m⁻²) and number of species respectively per core (Fig. 3).

In total, 1361 polychaete individuals distributed among 163 species were collected in the western Gulf. Ninety-nine of the species were identified to genus and species. An additional 63 belonged to known genera, and were given species

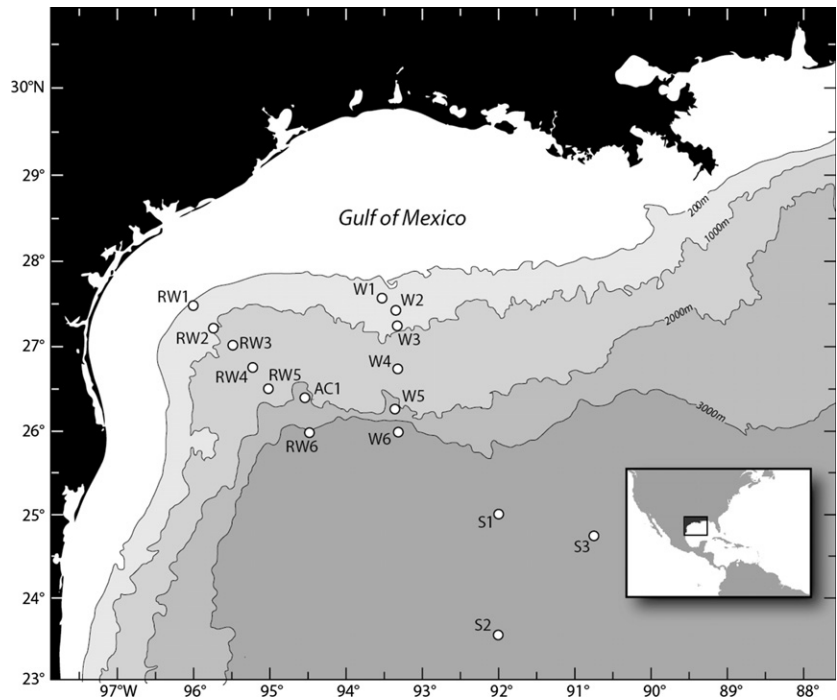


Figure 1 Station localities of 16 box-core samples of polychaetes collected from 213 to 3732 m in the north-west Gulf of Mexico, during the Deep Gulf of Mexico Benthos (DGoMB) study from 2000 to 2002 (Rowe & Kennicutt, 2008).

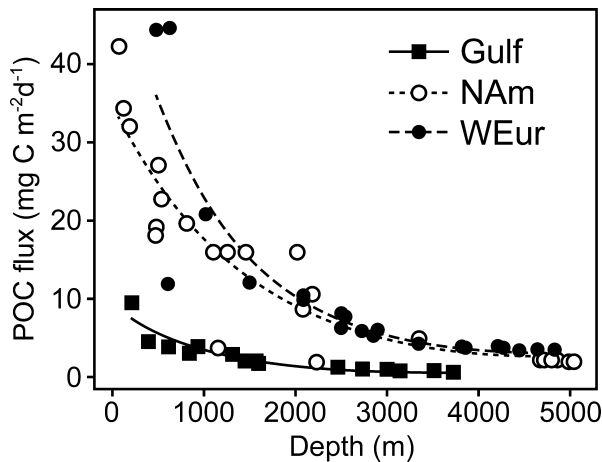


Figure 2 A comparison of particulate organic carbon (POC) flux at the seafloor over depth ranges from 213 to 3732 m in the north-west Gulf of Mexico, and in the western (65–5042 m) and eastern (485–4823 m) North Atlantic (North American and West European Basins respectively) (Brault *et al.*, 2013). The Gulf has much lower productivity than the North Atlantic. Over the depth ranges that can be compared (400–3800 m), POC flux averages 1.85 mg C m⁻² day⁻¹ in the Gulf, compared to 10.92 mg C m⁻² day⁻¹ in the western and 11.64 mg C m⁻² day⁻¹ in the eastern North Atlantic. Estimates of POC flux at the seafloor were determined by the algorithm of Lutz *et al.* (2007) using the latitude and longitude coordinates of the benthic sampling stations.

designation by number. Only one specimen was completely unknown. All species were identified by the same taxonomist, G. Fain Hubbard, at Texas A & M University. The full dataset can be found on the Biological and Chemical

Oceanography Data Management Office website (<http://www.bco-dmo.org/dataset/565318>).

Plots of worm abundance and species diversity with depth and POC flux are provided in Fig. 3. POC flux is the ecologically meaningful explanatory variable of interest here as it is predicted to affect β -diversity; but, we also show depth to make the analysis comparable to earlier studies in which depth was assumed to be a surrogate for food supply.

We used Baselga's (2010, 2012) metrics to assess the relative importance of turnover and nestedness. He showed that overall β -diversity measured as Sørensen's (1948) dissimilarity index (β_{sor}) can be broken down into dissimilarity resulting from turnover (β_{sim} , Simpson, 1943), and a new dissimilarity metric attributable to nestedness (β_{nes}). We used the R (R Development Core Team, 2008) package 'betapart' (Baselga & Orme, 2012) for this analysis. Plotting these three components against differences in depth and POC flux for all pairs of sampling stations allows a general impression of their relative significance. As we are comparing matrices of species dissimilarity to differences in POC flux or depth, we tested for relationships by using Mantel tests with 1000 replications (Pearson correlation). More importantly, for our interests here, we used BINMATNEST (Rodríguez-Gironés & Santamaría, 2006) and R package 'bipartite' (Carsten *et al.*, 2008) to determine the nested rank order of sampling stations with depth and POC flux. The application of BINMATNEST to β -diversity in the deep-sea benthos is described by Brault *et al.* (2012, 2013). The analysis establishes whether there is a significant depth-related or productivity-related trend of nestedness per se, and the direction of that trend. If productivity regulates the degree of nestedness, we predict that the rank order of nestedness in the western

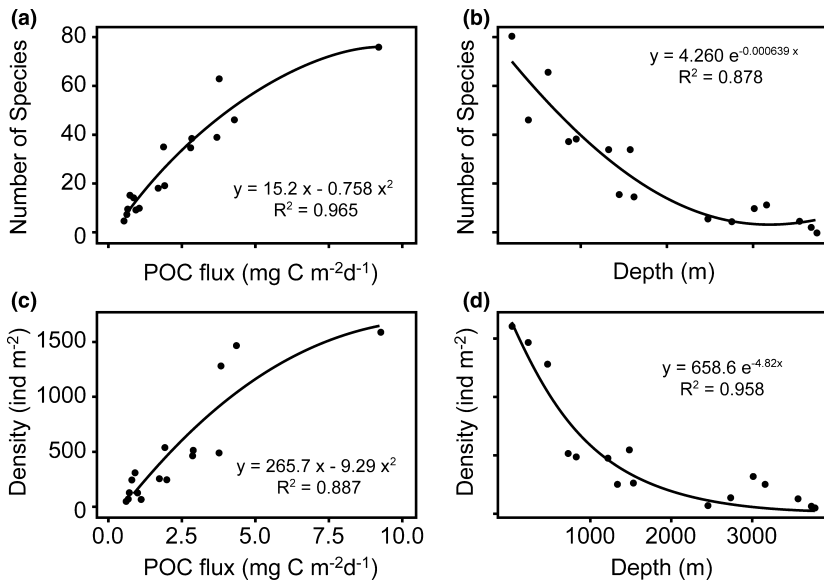


Figure 3 Polychaete diversity and density as functions of particulate organic carbon (POC) flux and depth in the north-west Gulf of Mexico. Diversity is the number of species per box core. Density is the number of individuals per box core standardized to metre squared. All are $p < 0.001$.

Gulf will be a significant negative function of POC flux, and a positive function of depth. All analyses of β -diversity were conducted on presence-absence data, which is the most conservative approach in large-scale studies of species composition.

RESULTS

Polychaete density and diversity decrease exponentially with depth, and increase with POC flux (Fig. 3). Interestingly, functional diversity, in terms of the number of coexisting feeding guilds in worms, also decreases with depth (Carvalho *et al.*, 2013) indicating a much simpler community at great depths.

Overall β -diversity (β_{sor}) is a positive significant ($P < 0.01$) function of depth difference among sampling stations (Fig. 4d), and this relationship is largely due to the positive trend in nestedness dissimilarity (β_{nes}) with depth difference (Fig. 4f). Turnover dissimilarity (β_{sim}) is unrelated to depth difference (Fig. 4e). β_{sor} and β_{sim} are statistically unrelated to differences in POC flux (Fig. 4a,b respectively). However, β_{nes} is a positive and significant ($P < 0.01$) function of the difference in POC flux (Fig. 4c). In other words, β -diversity in the deep western Gulf is largely attributable to nestedness from species loss and not species replacement.

The most important result is the rank order of nestedness among samples (Fig. 5). The rank order of samples is a significant negative function of POC flux (Fig. 5a), and a significant positive function of depth (Fig. 5b); the highest rank (most nested sample) is the deepest as predicted. Plots of all 163 species' depth ranges (see Appendix S1 in Supporting Information) show that below 2000 m, the fauna is composed largely of range extensions of upper to mid-bathyal assemblages. There is little indication of endemism below 2000 m. Five of the 38 species (13%) found below 2000 m were endemic to this depth zone, compared to 71 of the 125 species (57%) above 2000 m.

DISCUSSION

The dominant component of β -diversity for the polychaetes in the north-west Gulf is nestedness, which is a negative function of POC flux as predicted for very low food supply (Fig. 5). The fauna of the Sigsbee Abyssal Plain and lower bathyal zone is primarily a progressively reduced ordered subset of the upper and mid-bathyal fauna (see Appendix S1). These results support an association between low productivity and the nestedness contribution to β -diversity along bathymetric gradients in the deep-sea benthos. The lower the POC flux, the more β -diversity represents nestedness.

Are there sources of organic carbon other than surface production that could influence β -diversity? The Gulf of Mexico contains numerous chemosynthetic cold seeps that could potentially export organic matter to the surrounding benthic environment (Cordes *et al.*, 2009). However, the highest concentration of seeps appears to occur east of the study area (U.S. Interior Department, 2006). While the specific effects of seeps are hard to determine, our results show no strong systematic departure from the relationships of either diversity and abundance to POC flux and depth (Fig. 3) or nestedness to POC flux and depth (Fig. 5) that would suggest additional sources of carbon flux.

The mechanistic link between POC flux and nestedness involves the effect of productivity on population size. Reduced productivity diminishes population size making rarer species more subject to chronic local extinction through increased vulnerability to Allee effects. This is also the most obvious explanation for depressed α -diversity in the abyssal communities of oligotrophic basins (Rex & Etter, 2010). Rex *et al.* (2005) and Brault *et al.* (2012) showed that under these circumstances abyssal species assemblages were largely composed of bathyal species with dispersing larvae. These two factors, low abyssal population

Figure 4 Sørensen's (1948) dissimilarity index (β_{sor}) among polychaete samples decomposed into dissimilarity resulting from turnover (β_{sim} Simpson, 1943), and a dissimilarity metric attributable to nestedness (β_{nes} , Baselga, 2010). Dissimilarity is shown as a function of particulate organic carbon (POC) flux difference (a–c) and depth difference (d–f). Dissimilarity ranges from 0 (identical polychaete assemblages) to 1 (completely different assemblages). Pearson correlation coefficients and significance levels resulting from the Mantel test are indicated.

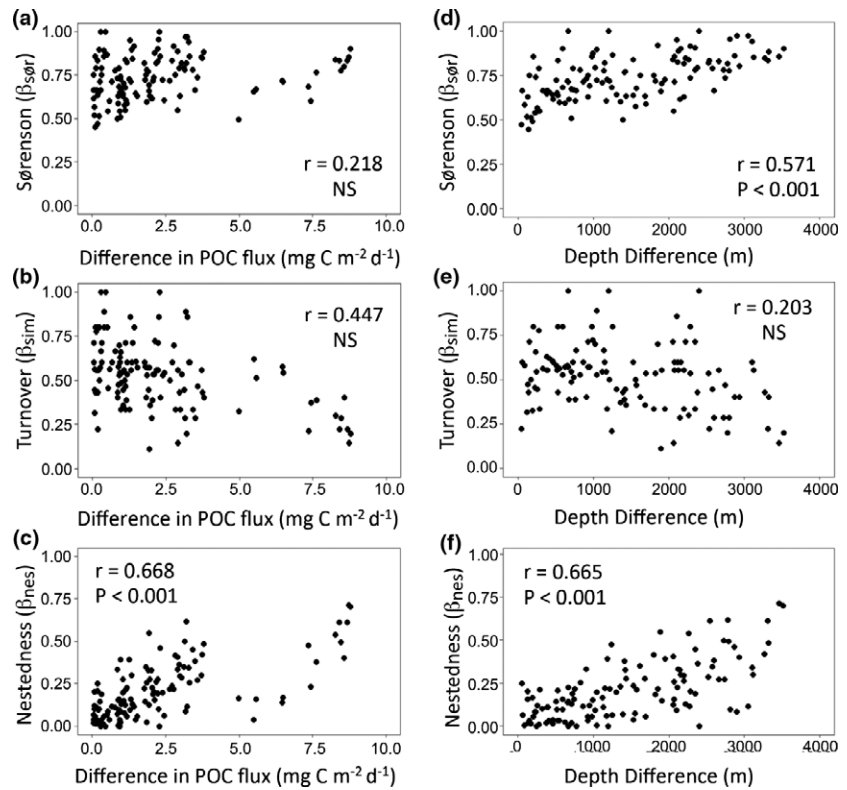
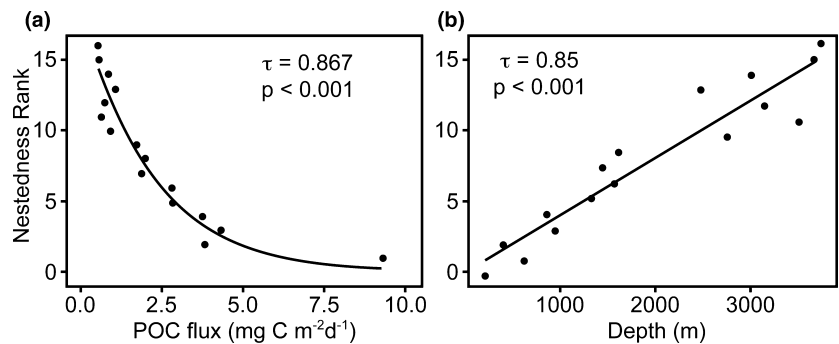


Figure 5 Nestedness rank order of deep-sea polychaete samples calculated by BINMATNEST (Rodríguez-Gironés & Santamaría, 2006) as a function of particulate organic carbon (POC) flux (a) and depth (b). Nestedness is a negative function of POC flux, and a positive function of depth. Kendall's tau and significance levels are indicated.



density and the dispersal ability of constituent species suggest that rarer abyssal species might be maintained by source-sink dynamics (Holt, 1985). Some abyssal species may live at densities so low that they are not reproductively viable, and act as sinks that depend on immigration from large bathyal source populations for their continued existence.

The source-sink theory of abyssal diversity was originally proposed for molluscs (Rex *et al.*, 2005; Brault *et al.*, 2012). Modes of larval development and dispersal are well known for deep-sea molluscs (Bouchet & Warén, 1994; Zardus, 2002), but little is known for polychaetes (Young, 2003). Many polychaete species appear to brood, but brooded juveniles can have a dispersal phase when hatched (Young, 2003). Most coastal species do appear to have some form of long pelagic life (Thorson, 1946). So, while bathymetric patterns of animal density, α -diversity and nestedness are

consistent with source-sink dynamics, the lack of information on dispersal in deep-sea worms makes an argument for source-sink dynamics more inferential.

Certain taxa are unlikely to be maintained by source-sink dynamics in the abyss. For example, isopods have life-history attributes that allow them to live at low density (Wilson, 1991, 1998), and which should make them less susceptible to inverse density dependence. They also have direct development in a brood pouch, which would limit continuous dispersal to sinks, although perhaps some species disperse as juveniles or adults. Some abyssal holothurians can very quickly exploit sinking phytodetritus, and even experience periodic population explosions in the abyss when there is unusually high episodic surface production (Billett *et al.*, 1983, 2001). In this case, the turnover component of β -diversity is dominant (Wagstaff *et al.*, 2014).

An alternative explanation for the presence of abyssal polychaetes in the Gulf could be that niche requirements of only a small subset of species allow them to inhabit great depths. Niche requirements might involve tolerance to physical conditions like high pressure and low temperature, and biological factors like low and less labile food availability. Niches of deep-sea species are almost completely unknown. It is possible that pre-adaptation to abyssal conditions accounts for invasion of the abyss by relatively abundant species and that rare species are supported by source-sink dynamics.

Another consideration is that the depth ranges analysed here (see Appendix S1) are assumed to represent single species. The 'species' designations are based on morphology. However, recent evidence on the population genetic structure of some morphospecies distributed across broad depth ranges suggests that they actually contain distinct clades arrayed bathymetrically (e.g. Etter *et al.*, 1999; Jennings *et al.*, 2013; Glazier & Etter, 2014) that are sufficiently different to indicate cryptic species. If shallower and deeper populations of morphospecies are reproductively isolated cryptic species, then deeper populations obviously cannot be considered conspecific range extensions that are maintained by down-slope dispersal (Rex *et al.*, 2005). Why morphology is so highly conserved in some deep-sea morphospecies despite genetic differentiation remains unclear. Whether widely distributed polychaetes in the Gulf represent constellations of cryptic species is unknown because their DNA has not been sequenced.

If productivity helps to explain the nestedness part of β -diversity, this may lead to a more unified theory of deep-sea biodiversity. Recently, Wei *et al.* (2010) showed very convincingly that the overall geographic pattern of species similarity in macrofauna of the northern Gulf is linked to productivity. Transitions between major biogeographic groups coincided with shifts in POC flux independent of depth differences. Geographic variation in α -diversity is also closely related to productivity, although there are certainly other potential biotic and abiotic causes (Rex & Etter, 2010; McClain *et al.*, 2012b). Hence, it seems possible that productivity provides a promising way to integrate α - and β -diversity in deep-sea benthic systems. Recognizing the potential role of productivity in regulating deep-sea biodiversity may also help to integrate deep-sea ecology with mainstream ecology, which is based on terrestrial, aquatic and coastal systems.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Polychaete species depth ranges.

BIOSKETCH

Carol Stuart has extensive experience analyzing patterns of community structure in the deep-sea benthos including

bathymetric trends and latitudinal gradients of α - and β -diversity.

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