

DEEP-SEA BIVALVES OF THE NORTH AMERICAN AND ARGENTINE BASINS: A COMPARISON OF SPECIES DIVERSITY AND FUNCTIONAL DIVERSITY USING JOHN ALLEN'S (2008) DATABASE

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Abstract We analyzed bathymetric trends in species diversity and feeding types in deep-sea bivalves of the North American and Argentine Basins in the western Atlantic using Allen's (2008) taxonomic database, and related these trends to energy availability. Chemical energy was assessed as particulate organic carbon (POC) flux to the seafloor, and kinetic energy by bottom water temperature. POC flux and temperature show significant and highly regular exponential declines with depth, the Argentine Basin having higher POC flux and lower temperature across most of the depth range sampled (upper bathyal to abyss). Both basins show unimodal diversity-depth patterns. Peak diversity is deeper and abyssal diversity higher in the Argentine Basin. POC flux was the primary predictor of species diversity. Bivalve taxa were classified as deposit feeders, filter feeders, or carnivores as an indication of functional diversity. In both basins, deposit feeders increased with depth and filter feeders decreased, probably as a function of sediment and suspended food resources respectively. Carnivores were a minor constituent throughout the depth range. POC flux was the most effective predictor of feeding categories.

Key words Deep-sea, bivalves, North American Basin, Argentine Basin, diversity

INTRODUCTION

In this paper, we analyze the species diversity and functional diversity of bivalve assemblages of the North American and Argentine Basins using John Allen's (2008) monumental data set "The Bivalves of the Deep Atlantic." The data represent the largest existing compilation of species' relative abundance information collected from deep-sea basins in the Atlantic Ocean, and have permitted the first Pan-Atlantic syntheses of biogeographic patterns in a major taxon (Allen, 2008; McClain *et al.*, 2012a). The faunas of the North American and Argentine Basins make an interesting comparison. Both occupy the western corridor of the Atlantic at about the same latitude (~35°), north and south respectively. However, they are separated by nearly 5000 mi (~8000km), a distance that would correspond to nearly complete faunal turnover in the coastal environment, especially because of the intervening tropical Caribbean Sea.

There are undoubtedly many biotic and abiotic causes of biodiversity in the deep sea (Rex & Etter, 2010). Here, we are particularly interested in how energy is related to community structure in the two basins. Energy has emerged as a key factor in regulating biodiversity. In the deep sea,

energy availability assumes two main forms. Kinetic energy, reflected by temperature, can have a potentially important influence on evolutionary rates, metabolic rates and physiological tolerances (Allen *et al.*, 2002; Yasuhara *et al.*, 2014; Yasuhara & Danovaro, 2016). Chemical energy from sinking particulate organic carbon (POC) acts as an important food supply to the benthos that can control population growth, and consequently biotic interactions (Rex & Etter, 2010; McClain *et al.*, 2012b; McClain & Rex, 2015). The exact mechanisms through which kinetic and chemical energy affect biodiversity are still not entirely clear, and their impact may vary across biological scales (McClain *et al.*, 2012b; Woolley *et al.*, 2016). Documenting new patterns of species diversity as functions of temperature and POC flux at large spatial scales broadens our understanding of energy-diversity relationships in the deep ocean, and in general.

MATERIAL AND METHODS

We base the analysis on the deep-sea bivalve fauna of the western North Atlantic (North American Basin, Fig. 1) and western South Atlantic (Argentine Basin, Fig. 2). All material was collected as part of the Woods Hole Oceanographic Institution's Benthic Sampling

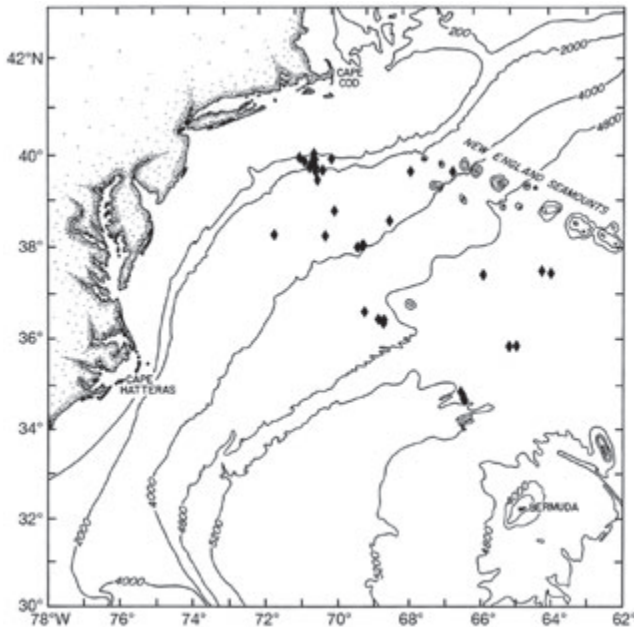


Figure 1 Map of the sampling area for the North American Basin. Diamonds indicate the sites of epibenthic sled stations that yielded the bivalve faunas analyzed here. For locality data, and species lists see Allen (2008). Map modified from Stuart & Rex (2009).

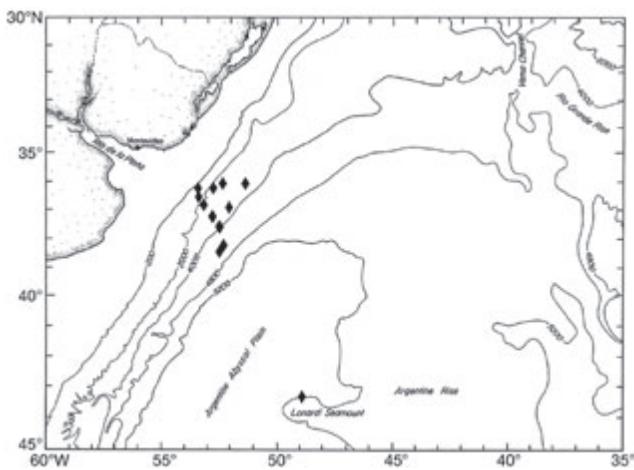


Figure 2 Map of the sampling area for the Argentine Basin. Diamonds indicate the sites of epibenthic sled stations that yielded the bivalve faunas analyzed here. For locality data and species lists see Allen (2008). Map modified from Stuart & Rex (2009).

Program (Sanders, 1977). Samples were dredged using an epibenthic sled (Hessler & Sanders, 1967), a non-quantitative device that covers roughly 1000 linear m² of seafloor. The taxonomy was carried out by John Allen, Howard Sanders, and their colleagues, and reported in a long series of systematic monographs summarized

by Allen (2008). The sampling was more intense in the North American Basin (cf. Figs 1 & 2). It represents 37 sampling stations from 196–5042m. There were 14 stations from 293–5223m sampled in the Argentine Basin. Allen (2008) presented the raw data (Appendix 3, pp 88–105 and pp 114–120) including sampling station localities, species identifications, and relative abundance of species. In total, the samples comprised 52,426 individuals distributed among 180 species in the North American Basin, and 14,429 individuals among 134 species in the Argentine Basin. Remarkably, there are 67 species shared between the two basins. In the Argentine Basin 58 percent of the shared species are found at depths greater than 3000m, which is in contrast to the North American Basin where the majority of the species (64 percent) are in depths above 3000m.

We estimated species diversity by using Hurlbert's (1971) expected number of species with all sample sizes normalized to 50 individuals $E(S_{50})$. We plot $E(S_{50})$ against depth to show bathymetric trends in diversity. We calculated POC flux at the seafloor by using the Lutz *et al.* (2007) algorithm, which integrates satellite-derived surface production with a global database of sediment trap results. The latter helps reduce the distorting effects of lateral advection of sinking phytodetritus. The POC flux estimates were made at the longitude, latitude and depth of the sampling stations. We used data on bottom water temperature from the NOAA database (www.nodc.noaa.gov/cgi-bin/OC5/WOA05/woa05.pl). We regressed POC flux and bottom temperature against $E(S_{50})$ to explore the relationships of diversity as a response variable to the proxies of kinetic energy (temperature) and chemical energy (POC flux) as explanatory variables.

To examine functional diversity, we regressed the proportion of feeding types against depth. Bivalves have three basic feeding types that correspond to their higher taxonomy at the subclass level. We used the classic taxonomy, which is more familiar to ecologists and follows Allen's (2008) usage. Lamellibranchs are filter feeders; protobranchs are deposit feeders; and members of the septibranch clade of Anomalodesmata are carnivores. One genus of pectin lamellibranch, *Propeamussium*, is also a carnivore (Knudsen, 1970), and is represented by a single species in this study. One common genus of lamellibranch,

Thyasira, deserves special mention. Some thyasirids have symbiotic associations with chemoautotrophic bacteria (Cavanaugh, 1985), which may supply nutrition to supplement filter feeding. Reliance on symbiotic bacteria in *Thyasira* varies among species and even among populations of individual species (Dufour, 2005; Batstone *et al.*, 2014). Payne & Allen (1991, p 558) in their monograph of the deep-sea Thyasiridae of the Atlantic note that "Some of the species described here may have these [chemoautotrophic bacteria] in the abfrontal filamentary tissue of the gill but many others, particularly the smaller species, have no bacteria within the gills and the abfrontal region is not extended." Most deep-sea macrofaunal thyasirids are small. We have scored all thyasirids as filter feeders, which they are, but readers should be aware that some species may also have symbiotically associated chemoautotrophic bacteria. We plotted the proportion of taxonomically inferred feeding types against depth as an indication of how functional ecology changes bathymetrically in the two basins.

RESULTS

The energy environment

Relationships of POC flux to depth are similar in both basins (Fig. 3a). POC flux decreases exponentially with depth, a nearly universal trend through the deep water column as sinking phytodetritus is consumed and remineralized. Both relationships are highly significant ($P < 0.0001$). We assessed differences between the curves according to whether their confidence bands overlapped (not shown; available from the authors). The POC-depth curves begin to converge in deeper water, but POC flux remains lower in the North American Basin throughout most of the bathyal zone and then becomes very similar in the abyss.

The Argentine Basin shows higher POC flux at upper bathyal depths, possibly because near-shore production is augmented by outflow of organic material from the Rio de la Plata River. In the central basin there is a single remotely located sample at 5223m. This is a region of organic-rich mud waves and sediment drifts where chemical energy may be enriched by organic material carried in bottom currents. Here the number of species (14) and individuals (1,253) are two times and 20 times higher respectively than at a similar

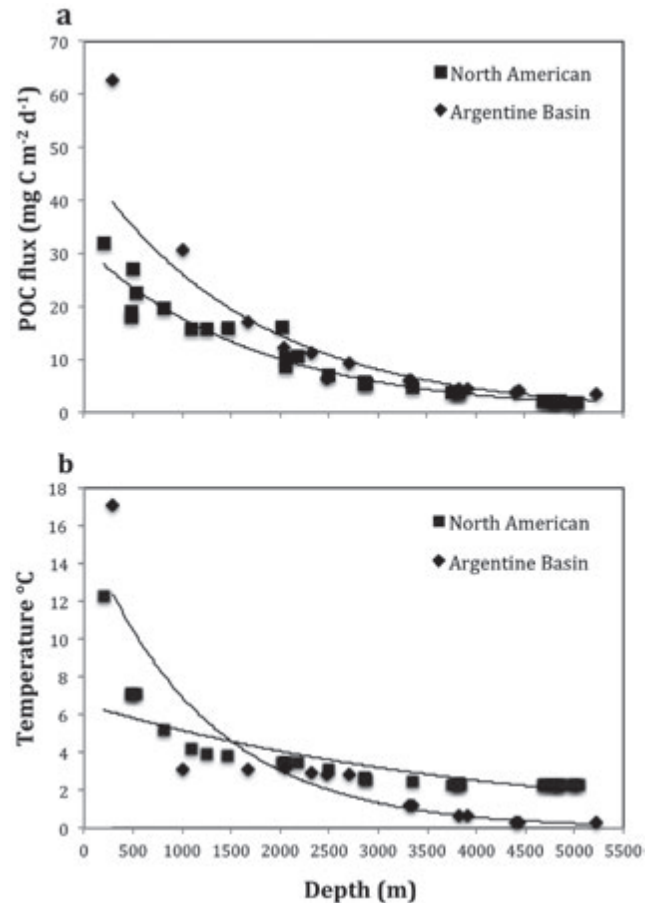


Figure 3 (a) Particulate organic carbon flux (POC flux) calculated using the Lutz *et al.* (2007) algorithm as a function of depth (m) in the North American Basin. The equation for the line is: $Y = 31.19e^{-6E-04X}$, $N = 37$, $R^2 = 0.983$, $P < 0.0001$; and Particulate organic carbon flux (POC flux) as a function of depth (m) in the Argentine Basin. The equation for the line is: $Y = 47.03e^{-6E-04X}$, $N = 14$, $R^2 = 0.909$, $P < 0.0001$. (b) Temperature ($^{\circ}\text{C}$) as a function of depth (m) in the North American Basin. The equation for the line is: $Y = 6.57e^{-2E-04X}$, $N = 37$, $R^2 = 0.819$, $P < 0.0001$; and temperature ($^{\circ}\text{C}$) as a function of depth (m) in the Argentine Basin. The equation for the line is $Y = 15.77e^{-8E-04X}$, $N = 14$, $R^2 = 0.908$, $P < 0.0001$.

depth (5042m) in the North American Basin (7 species, 62 individuals). This may possibly be a reflection of increased productivity; however, we have no specific data on these potential energy sources. Stuart & Rex (2009) provide a more detailed summary of environmental conditions in the Argentine Basin.

Temperature relationships are more complicated (Fig 3b). Temperature decreases exponentially with depth in both basins. Again, both regressions are highly significant ($P < 0.0001$).

Temperature is significantly higher at upper bathyal depths in the Argentine Basin than in the North American Basin. Then at mid-bathyal depths the curves cross so that temperature is significantly colder in the deep Argentine Basin. In summary then, across most of the deep-sea (>200m) floor, POC flux is higher, and temperature lower in the Argentine Basin.

Bathymetric trends of species diversity

Species diversity $E(S_{50})$ in the North American Basin shows a highly significant ($P < 0.0006$) unimodal relationship to depth, with peak diversity at upper bathyal depths (Fig. 4a). Diversity in the Argentine Basin (Fig. 4b) also evinces a best fit to a polynomial regression (i.e. a unimodal pattern), but the relationship is just marginally insignificant ($P < 0.068$), probably owing to the smaller number of samples, and high variability of diversity values. The amount of variance in diversity accounted for by depth is about the same in both basins ($R^2 = 0.35$ and 0.39 respectively). The level of maximum diversity is nearly the same in the two basins, about 17 species at normalized sample size (26 actual number of species). Peak diversity in the Argentine Basin is shifted to lower bathyal depths at around 3000m, and average diversity in the abyss (>4000m) is about 30% higher.

POC flux is a significant predictor of species diversity in the North American Basin ($P < 0.002$). Again, the relationship is unimodal, as might be expected since POC flux declines with depth (Fig 3a).

In the North American Basin, temperature is a significant predictor of diversity ($P < 0.04$) at a lower level than for POC flux, and again the relationship is unimodal. However, when POC flux, temperature, and their quadratic terms (to adjust for the polynomial relationship) are added to a multiple regression, POC flux remains significant ($P < 0.01$), but temperature is no longer significant ($P = 0.25$). There is no relationship between either temperature and diversity ($P = 0.20$) or POC flux and diversity ($P = 0.16$) in the Argentine Basin.

Functional diversity

The proportion of filter feeding, deposit feeding, and carnivorous species with depth in the North American Basin is shown in Fig. 5. Deposit feeders (protobranchs) show a clear and highly significant ($P < 0.0001$) linear increase with depth,

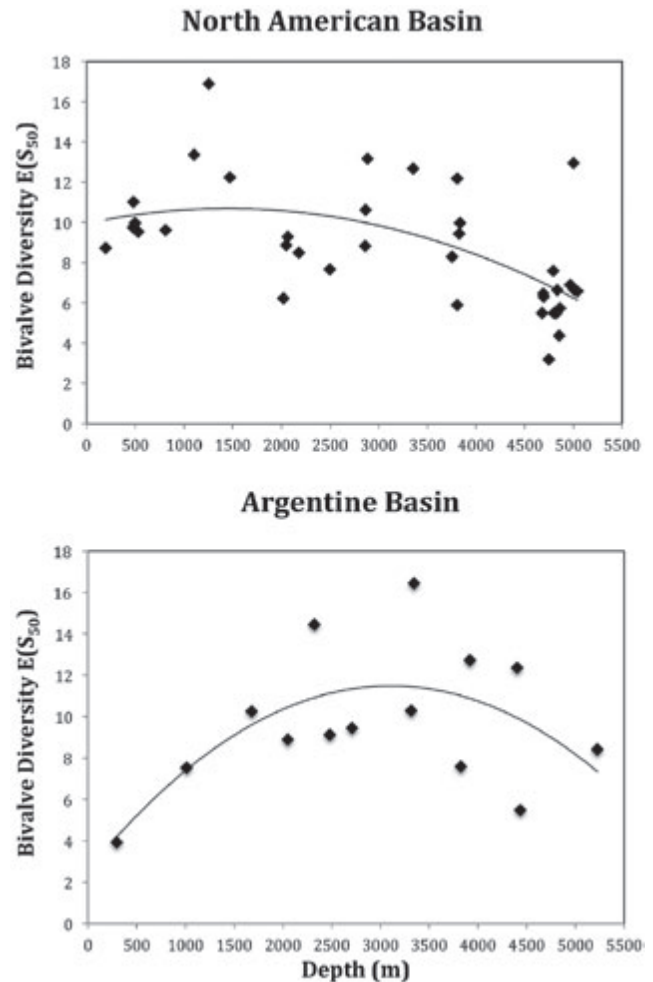


Figure 4 (Upper Panel) Bivalve species diversity measured as Hurlbert's (1971) expected number of species normalized to 50 individuals $E(S_{50})$ as a function of depth (m) in the North American Basin. The equation for the line is: $Y = 9.944 + 0.001X - 4E-7X^2$, $N = 37$, $R^2 = 0.353$, $P = 0.0006$. (Lower Panel) Bivalve species diversity measured Hurlbert's (1971) expected number of species normalized to 50 individuals $E(S_{50})$ as a function of depth (m) in the Argentine Basin. The equation for the line is: $Y = 2.578 + 0.006X - 9E-07X^2$, $N = 14$, $R^2 = 0.386$, $P = 0.068$, NS. Line is meant only to indicate general trend. See text for a discussion of diversity as a function of POC flux and temperature.

and dominate the abyssal fauna. Filter feeders (lamellibranchs) prevail at upper bathyal depths, and then decline toward the abyss ($P < 0.0001$). Carnivores have a low level of diversity throughout the depth range, and decline slightly, but significantly ($P = 0.002$), to a minimum in the abyss. All three trophic categories are predicted significantly by POC flux ($P < 0.0001$, $P < 0.0001$, and $P < 0.04$ respectively). Temperature predicts the proportion of deposit feeders and filter

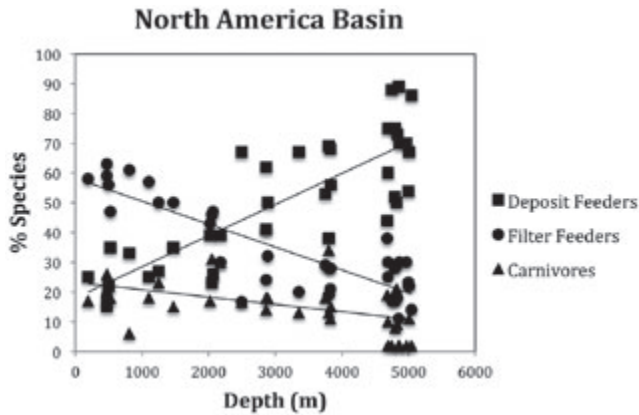


Figure 5 The proportion of species in bivalve feeding types as a function of depth in the North American Basin. Deposit feeders increase with depth, filter feeders decrease, and carnivores are a minor element that decreases slightly. Equations for the regression lines are: Deposit feeders $Y=18.008+0.0105X$, $N=37$, $R^2=0.686$, $P<0.0001$. Filter feeders $Y=58.239-0.0077X$, $N=37$, $R^2=0.726$, $P<0.0001$. Carnivores $Y=23.567-0.0027X$, $N=37$, $R^2=0.237$, $P<0.002$. See text for the proportion of feeding types as functions of POC flux and temperature.

feeders ($P<0.0001$), but not carnivores ($P=0.11$). However, when POC flux and temperature are included together in a multiple regression, POC flux remains significant, but temperature becomes insignificant ($P=0.26$, $P=0.36$, respectively for deposit and filter feeders). So, POC flux is the primary predictor of feeding types.

In the Argentine Basin, the proportions of deposit feeding and filter feeding categories also show significant relationships with depth (Fig. 6; $P<0.002$, $P<0.0015$, respectively) in the same direction (positive or negative) as in the North American Basin. The proportion of carnivores is insignificant. POC flux and temperature are unrelated to the representation of feeding types.

DISCUSSION

A major challenge in deep-sea ecology is to determine which form of energy, kinetic or chemical, is most influential in affecting biodiversity. The temperature-diversity hypothesis for the deep sea relates to either physiological tolerance or evolutionary rates (Yasuhara & Danovaro, 2016). Diversity may be limited to the number of species that are adapted to live at either warm or cold temperatures (Currie *et al.*, 2004). This may account for depressed diversity at upper

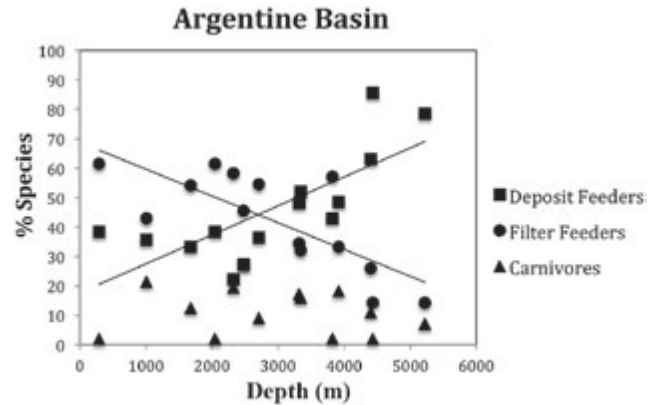


Figure 6 The proportion of species in bivalve feeding types as a function of depth in the Argentine Basin. Deposit feeders increase with depth, filter feeders decrease, and carnivores are a minor element showing no significant pattern. Equations for the significant regression lines are: Deposit feeders $Y=17.681+0.0098X$, $N=14$, $R^2=0.562$, $P=0.002$. Filter feeders $Y=68.7775-0.0091X$, $N=14$, $R^2=0.583$, $P=0.002$. No feeding category is predicted significantly by either POC flux or temperature.

bathyal (warmer) and abyssal (colder) depths. Also, higher temperatures may accelerate reproductive rates so that favorable mutations accumulate more rapidly in populations leading to higher speciation rates (Rhode, 1992) resulting in more species occupying warmer regions.

The productivity-diversity hypothesis in the deep sea proposes that higher and more variable food supply at upper bathyal depths drives competitive exclusion resulting in decreased diversity. Extremely low food supply in the abyss disfavors rare species through Allee effects, not allowing diversity to build (Rex *et al.*, 2005; Rex & Etter, 2010). If higher food availability persists in the abyss, diversity remains high (Brault *et al.*, 2013).

Both hypotheses allow for a unimodal diversity-depth patterns, making the task of testing alternative hypotheses difficult, especially using comparative data, proxy variables like temperature and POC flux, and the huge uncertainties involved in remote sampling. Recent global-scale analyses of energy impacts on the deep-sea benthos suggest that kinetic energy is more important at lower levels of biological organization, but that chemical energy prevails at higher levels of organization including community structure (McClain *et al.*, 2012b); and that thermal effects are more important in coastal

and upper bathyal ecosystems, but that chemical energy shapes community structure deeper in the ocean (Woolley *et al.*, 2016).

The North American Basin shows the clearest patterns of community structure. Species diversity has a significant unimodal relationship to depth. This is a common pattern in the western North Atlantic, found in several macrofaunal invertebrate taxa, and in the megafaunal invertebrates and fishes (Rex & Etter, 2010). Of the two energy-related explanatory variables, POC flux has the highest correlation with bivalve diversity suggesting that the rate of food supply is the primary driver. Temperature has a weak, but still significant correlation with diversity. However, because of the high correlation between temperature and POC flux, both of which decrease with depth, temperature becomes insignificant when both variables are entered in a multiple regression.

The increase in the proportion of deposit feeders, and concomitant decrease in filter feeders with depth probably results from a decrease in suspended phytodetrital food availability reflected by the exponential drop in POC flux. Deposit feeders dominate in the abyss where sediment is the primary remaining food resource. Carnivores are a minor part of the bivalve assemblage. Their barely significant positive relationship to POC flux in the North American Basin may result from there being greater prey resources at shallower depths than in the abyss.

Bivalves in the Argentine Basin also show a unimodal pattern of diversity with depth. The relationship is just barely insignificant, but unmistakably polynomial. Peak diversity is shifted much deeper and abyssal diversity is higher than in the North American Basin. These differences may be attributable to the higher POC flux in the Argentine Basin, which could allow higher diversity to persist at abyssal depths (Brault *et al.*, 2013). Neither POC flux nor temperature statistically explains the overall unimodal pattern. The proportions of feeding types are very similar to those in the North American Basin, suggesting that trends in functional diversity in the deep sea are conservative, irrespective overall trends of diversity with depth. None of the categories is explained by either POC flux or temperature. Trends in both basins are similar to the Pan Atlantic trends in feeding types documented by Allen (2008).

On balance, our analysis tends to support chemical energy as the primary determinant of bivalve species diversity and functional diversity in these two deep-sea basins. POC flux is more highly correlated with diversity. And, in cases where POC flux and temperature are both independently and significantly correlated with dependent variables, temperature is subordinated to insignificance in a multiple regression. Chemical energy was also found to be the best predictor of molluscan diversity in the North Atlantic (Tittensor *et al.*, 2011).

However, the results, while a useful addition of comparative evidence to the energy-diversity debate, are not definitive in identifying the relative influence of energy sources in the deep sea. We stress that the database from the Argentine Basin is smaller than that for the North American Basin, and consequently may not be adequate to accurately illustrate biogeographic trends. Also, even when relationships of energy to diversity were statistically significant, energy only accounts for about a third of the variance in diversity. The unexplained variance could be due to sampling error, or to other biological or physical variables that were not included in the analysis because they were unavailable. Diversity in the deep-sea is undoubtedly controlled by a multiplicity of factors (Rex & Etter, 2010), and we are only examining one taxon here. We also stress that POC flux and temperature are essentially proxy variables for chemical and kinetic energy, and it remains unclear exactly how accurate they represent them in natural communities.

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