

INCREASED ENERGY PROMOTES SIZE-BASED NICHE AVAILABILITY IN MARINE MOLLUSKS

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Variation in chemical energy, that is food availability, is posited to cause variation in body size. However, examinations of the relationship are rare and primarily limited to amniotes and zooplankton. Moreover, the relationship between body size and chemical energy may be impacted by phylogenetic history, clade-specific ecology, and heterogeneity of chemical energy in space and time. Considerable work remains to both document patterns in body size over gradients in food availability and understanding the processes potentially generating them. Here, we examine the functional relationship between body size and chemical energy availability over a broad assortment of marine mollusks varying in habitat and mobility. We demonstrate that chemical energy availability is likely driving body size patterns across habitats. We find that lower food availability decreases size-based niche availability by setting hard constraints on maximum size and potentially on minimum size depending on clade-specific ecology. Conversely, higher food availability promotes greater niche availability and potentially promotes evolutionary innovation with regard to size. We posit based on these findings and previous work that increases in chemical energy are important to the diversification of Metazoans through size-mediated niche processes.

KEY WORDS: Morphological evolution, variation.

Seventeen orders of magnitude in body size separate the smallest from the largest animals (McClain and Boyer 2009). As size dictates many facets of an organism's internal and external characteristics (Peters 1983; Calder 1984; Blackburn and Lawton 1994; Brown 1995; Gaston and Blackburn 1996; Kerr and Dickie 2001; Brown et al. 2004; White et al. 2007), great variation in these can be expected as well. Indeed, size may be the primary determinant of niche requirements such that diversity within a clade reflects its body size range (McClain and Boyer 2009). Yet, despite its importance, factors driving extreme diversification in body size are poorly resolved. This especially holds true in nonamniotic animals, which represent the greatest wealth of diversity on earth.

Chemical energy availability (Clarke and Gaston 2006), that is, food, is often invoked to explain hard limits on

maximum obtainable body size (Bruness et al. 2001; Boyer and Jetz 2010), geographic and temporal gradients in size (Blackburn and Gaston 1996; McClain et al. 2005, 2006; Rex et al. 2006; Allen 2008; Olson et al. 2009; Terribile et al. 2009; Finnegan et al. 2011), and optimal sizes within clades (Brown et al. 1993; Marquet et al. 1995; Rex and Etter 1998; Ritchie and Olf 1999; Aava 2001; Sebens 2002). Several well-known body size "rules," including Cope's and Bergmann's rules, may reflect availability and heterogeneity in chemical energy (McNab 2010). However, and perhaps surprisingly given the numerous studies hypothesizing links between size and food availability, studies actually documenting this relationship are uncommon and focused on two disparate groups, amniotes (e.g., Blackburn and Gaston 1996; Aava 2001; Olson et al. 2009; Terribile et al. 2009; Boyer

and Jetz 2010) and zooplankton (Stemberger and Gilbert 1985; Gliwicz 1990).

On the surface, the hypothesis relating body size to chemical energy availability should be simple. Larger body sizes have a greater metabolic demand, despite per unit mass efficiencies, and require greater food resources (McNab 1971). Thus, all else being equal, greater food availability would allow for larger sizes. Likewise, evolution should proceed toward energetic efficiency where optimal size should reflect a balance of trade-offs that maximize energy intake and minimize output (Brown et al. 1993; Rex and Etter 1998; Sebens 2002).

However, the relationship between body size and energy availability could be more interesting than a simple more energy/bigger size relationship. Optimal size should vary with environmental influences on intake and costs (Rex and Etter 1998; Ritchie and Olff 1999). For example, cost functions with body size may increase as greater energy is required to search for scarcer food supplies (Rex and Etter 1998). Clade-specific requirements, physiology, ecology, and constraints could potentially lead to a multitude of optimal sizes (e.g., the left-skew body size distribution in bivalves Roy et al. 2000). For example, cost functions would be different among organisms with different motilities and energetic demands of movement. Because body size correlates with a multitude of other ecological features of an organism, these balances may be increasingly complex (Peters 1983; Calder 1984). For example, lower food availability may actually select against smaller sizes despite their lower food requirements because of associated decreases in foraging area and starvation resistance (Millar and Hickling 1990; McClain et al. 2006). Increased energy availability may also not occur equitably among individual species or guilds, that is, interspecific competition (McClain and Barry 2010).

Thus, considerable work remains to both document patterns in body size over gradients in food availability and understand the processes potentially generating them. Here, we examine the functional relationship between body size and chemical energy availability over a broad assortment of marine mollusks varying in habitat and mobility. We utilize a developed dataset for 1578 species of bivalves from the Northeast Pacific and Northwest Atlantic oceans and 3350 species of gastropod from the Northwest Atlantic.

Methods

DATASETS

Data for bivalves from the Northeast Pacific and Northwest Atlantic were collected through an extensive search of the primary literature and online databases resulting in complete information for 1578 species from 75 families. Substantial information came from Desbruyeres et al. (2006), Malacolog version 4.1.1

(Rosenberg 2009), and Coan et al. (2000). The data collected included: taxonomic information from the subclass to species; synonymies; maximum and minimum water depth in meters; maximum and minimum latitude; maximum reported shell length, width, and height in millimeters; habitat type; ocean basin; and images of the species. Habitat type was broken into fine grain, coarse grain, sediment generalist, hard substrate, hydrothermal vent, methane seep, seamount, wood fall, whale fall, reducing generalist (a generalist on vents, seeps, wood falls, or whale falls) and other, which were primarily made up of commensal bivalves. The bivalve dataset with carbon flux values is available at <http://datadryad.org/>.

Data for gastropods of the Northwest Atlantic were derived from Malacolog version 4.1.1 (Rosenberg 2009) resulting in data for 3350 species from 112 families. The data collected included: taxonomic information from the subclass to species; maximum and minimum water depth in meters; maximum and minimum latitude; and maximum reported shell length. The gastropod dataset with carbon flux values is available at <http://datadryad.org/handle/10255/dryad.37167>.

SIZE MEASUREMENTS

Approximate biovolume for each species was calculated as length \times height² of the shell, which provides robust estimates of biovolume and strongly correlates with individual soft tissue mass (Powell and Stanton 1985). Previous work suggests the choice of body size metric in mollusks is unlikely to mask ecological patterns (McClain 2004) and thus we feel confident that maximum reported shell dimensions are a robust measure for detecting size clines. In the absence of both length and height measurements, missing measurements were calculated from length:height ratios based on raw measurements from ImageJ version 1.42 (U.S. National Institutes of Health, Bethesda, MD) taken from the best available picture for each species from the literature or online collections.

CARBON FLUX

The chemical energy available to the mollusks was estimated as particulate organic carbon (POC) flux ($\text{g of C m}^{-2} \text{ year}^{-1}$) based on the Lutz et al. (2007) model. The model utilizes empirically derived sediment trap POC flux estimates compared to remotely sensed estimates of net primary production (NPP) and sea surface temperature (SST). These data were used to develop an algorithm with coefficients predicting annual POC flux at a given depth from remotely sensed data. Sediment trap data consist of estimates of flux collected over 25 years including 244 annual flux estimates and 153 subannually resolved flux time series. For the same localities of sediment traps, NPP and SST were then gathered to develop the predictive equations for POC. NPP and SST were estimated from the NOAA/NASA AVHRR Oceans Pathfinder SST,

NASA SeaWiFs surface chlorophyll concentrations, and photo-synthetically active radiation.

For each species, we quantified the mean, median, and standard deviation of carbon flux over their known latitudinal and depth ranges. Data from each species were manipulated using ArcGIS Workstation 10 (Environmental Systems Research Institute, Redlands, CA). We created a GIS coverage for each species' north–south range extent. This was overlaid upon bathymetry data (GEBCO 08, 30 arc-second grid, September 2010 release, www.gebco.org) to limit each species' distribution to their recorded depth range. To obtain the carbon flux values, each species' range was overlaid upon the Lutz et al. (2007) model, with values exported to a text file. Values from each species were compiled into a single data file.

In some cases, because of the coarseness of the depth and carbon flux GIS grids and the small biogeographic ranges of some of the bivalves here, we slightly extended species ranges to obtain carbon flux data. This ensured that matching cells in the GIS grids would be found for each species. The smallest latitudinal extent for any species with small ranges was set at 1°. Species recorded from a single depth, or very narrow depths were also expanded. All species found at depths less than 10 m were adjusted to a minimum depth range of 10 m. Species at depths up to 20 m were adjusted so that their minimum depth range was 10 m, with an equal amount added to the minimum and maximum depth. Depth ranges from 20 to 49 m were adjusted to have a 20 m minimum depth range, 50–199 m to 40 m, 200–999 to 100 m, and >1000 m to 200 m. The grade of the continental shelf is low and thus depth ranges changes were limited to shorter intervals to prevent making biogeographic ranges substantially larger.

Analyses

REGRESSION TREES AND RANDOM FORESTS

Regression trees were used to determine the extent that productivity, geography, and habitat predict variation in the size of mollusks. These types of analyses are becoming more common in ecological and evolutionary research (Boyer 2008; Davidson et al. 2009; Durst and Roth 2011). Regression trees are ideal for analyses where the dependent and multiple independent variables may be related to each other in a complex manner. Regression trees allow for the partitioning of the dependent variable by a suite of both categorical and continuous variables. Trees are “learned” by continuous splitting of the source dataset, that is, the root node, into subsets that comprise subsequent nodes. For each node, the tree-building algorithm determines which of a large number of possible splits best explains the maximum variability in the dependent variable in terms of the independent variables. After each node determination, a decision is made whether to subject

the node to further splits or terminate splitting, that is, a terminal node. This repeated process is referred to as recursive partitioning. The recursion is completed when the subset at a specific node all have the same value of the target variable, or when splitting no longer adds value to the predictions.

Because regression trees tend toward overfitting, we examined the cross-validation plot (not shown) to determine where pruning should occur. We used the one standard deviation rule (1-SE) in which we choose the left-most complexity parameter (cp) value on the plot for which the mean of the cross-validation lies below a line representing the mean value of errors of the cross-validations plus the standard deviation of the cross-validation upon convergence. Nodes with cp values less than this (bivalves: $cp < 0.027$, gastropods: $cp < 0.012$) were pruned as they were unlikely to contribute meaningful information. We used the *rpart* package in R to construct a fully grown regression tree.

Regression trees can be sensitive to small changes in data size and variables entered in the analysis. To correct for this, we used random forest models that can quantify the importance of specific variables over multiple trees from bootstrapped subsets of the dataset. From these multiple trees, the importance of predictors is calculated by aggregating (majority vote or averaging) the predictions from the ensemble of trees. Here, we ran 10,000 classification trees in the *randomForest* package in R to retrieve the relative importance of the predictors.

QUANTILE REGRESSION

Quantile regression was utilized to examine whether patterns differed among size classes with respect to gradients in carbon flux. This method has proven robust in detecting constraints on both minimum and maximum size in previous studies (McClain and Rex 2001; McClain et al. 2005) because it estimates varying quantiles (τ) of the response variable to certain values of the predictor variables. For each value of τ , a regression intercept and slope were calculated. Quantile regression was implemented with the *quantreg* in R. Further explanations of the method can be found in Cade et al. (1999), Cade and Guo (2000), McClain and Rex (2001), and Cade and Noon (2003).

PHYLOGENETIC GENERALIZED LEAST SQUARES

To control for the influence of shared evolutionary history on body size and carbon flux relationships, we also fit a phylogenetic generalized least-squares (PGLS) model to our data (Revell 2010). This method builds on basic generalized least-squares models by adding an additional independent variable that represents a covariance matrix derived from the phylogenetic relationships of the species in the analysis. Accounting for this covariance matrix allows for the fact that individual species are not independent due to their varying levels of phylogenetic relatedness. Our model

included a covariance structure derived from a Brownian motion model calculated with the *corPagel* function in the *ape* package of R. Multiple examples are provided and worked through in Revell (2010). Analyses were conducted with the *gls* function in the *nlme* package in R. We also used a weight function in the generalized least-squares model to account for the heterogeneity in variance (see Figs. 3 and 4) of molluscan size over carbon flux.

A species-level phylogeny is unavailable for the 1000s of mollusks in the analyses here, especially among the undersampled deep-sea clades. Likewise, family-level phylogenies that would include the diverse families in these analyses are also absent for both gastropods and bivalves, especially among deep-sea families. For both groups, we use a tree topology for our analyses based on the most current system of taxonomy (Bouchet and Rocroi 2005; Bouchet et al. 2010). This results in polytomies at each taxonomic level. For both trees, arbitrary branch lengths were calculated based on the method of Nee et al. (1994). We also assigned branch lengths through several other methods, for example, assigning all branch lengths to one or the method of Grafen (1989). The results were consistent across these methods and we only show those results based on Nee et al. (1994).

Results

BIVALVES

The pruned regression tree (Fig. 1) explained 42.4% and the random forest model explained 47.2% of the variation in bivalve body sizes. The first split was tied to habitat differences separating smaller bivalves associated with fine grain sediment, other (largely commensal relationships), and woodfalls from large bivalves in coarse grain, hard substrate, and reducing habitats. Similarly, the 10,000 runs of the random forest model also denoted habitat differences as the most important factor determining bivalve body size (Fig. 2A). These habitat-based size differences can be more clearly seen in Figure 3. The largest average sizes were present in species occurring in hydrothermal vents, methane seeps, generalist species occurring across reducing habitats, and to a lesser extent whale fall communities. Hard substrate bivalves were of intermediate sizes. The smallest bivalves occurred in sediment (e.g., fine grain, coarse grain, or sediment generalists), wood fall habitats, and among the other category dominated primarily by commensal bivalves.

Among those bivalves found in fine grain, other, and wood habitats, the amount of carbon flux was an important determinant of size (Fig. 1). This split distinguished between species experiencing greater or less than a mean of 4.8 g of carbon per meter per year over their entire known geographic range. The random forest model also selected both log mean carbon flux and log median carbon flux as important relative to body size (Fig. 2A). Conducting an analysis separately for bivalves living in sediment identi-

fied log mean flux as the most important variable for predicting size (Fig. 2B). Of course, these analyses assumed a relationship with the conditional mean of body size and therefore would not indicate constraints on minimum and maximum size (McClain and Rex 2001). Among sediment species, the relationship between mean carbon flux and body size was represented by triangular constraint space with a greater range of sizes at increasing carbon flux values (Fig. 3 and 4). For sediment bivalve species, quantile regression analysis exhibited a pattern of increasingly positive slopes with increasing quantiles (Fig. 4). To restate, the relationship between size and carbon flux was strongest among the largest bivalves. Interestingly, a weak but significant positive relationship also existed among the smallest bivalves.

Several other variables were of note. Depth among the coarse grain, hard substrate, and reducing habitat groups was important. The relevant split occurred at a depth of 1.25–1.5 m and separated larger subtidal and intertidal from smaller and deeper bivalves (Fig. 1). Depth was also significant in the random forests models when the analysis was constrained to sediment bivalves (Fig. 2A and B). In certain bivalve clades in coarse grain, hard substrate, and reducing habitats, size also appeared greater in the Pacific Ocean (Fig. 1), but was a weak predictor compared to other variables (Fig. 2A and B). Likewise, latitudinal extent was of moderate importance compared to the other variables (Fig. 2A and B).

Several splits in the pruned regression tree related to taxonomic order (Fig. 1). The first split (Fig. 1, split 1) under larger size species in coarse grain, hard substrate, and reducing habitats separated the larger bivalves in the orders Mytiloidea (mussels), Ostreoida (scallops and oysters), and Pterioidea (winged oysters) in the subclass Pteriomorpha, from smaller bivalves distributed among families of the subclasses Pteriomorpha, Anomalosdesmata, Heterodonata, and Protobranchia. A further split (Fig. 1, split 4) in this habitat group distinguished the smaller Nuculoidea from the other orders. Clade splits (Fig. 1, splits 2 and 3) were also evident in fine grain, other, and woodfall habitat groups. Both of the splits separated smaller species in orders among the Heterodonts (Myoidea and Veneroidea) and Prosobranchs (Nuculoidea). Random forests models also indicated the importance of broad clade differences in size (Fig. 2).

Bivalves continued to demonstrate a positive relationship between biovolume and carbon flux when we accounted for phylogenetic relatedness in a PGLS model ($\lambda = 1.0009$, biovolume = $0.45 + 0.33$ carbonflux, $P < 0.0001$, AIC = 2908.45). A null model without consideration of phylogeny ($\lambda = 0$) produced the worst fit (AIC = 3957.87). Incorporating a term to account for heterogeneity in variances decreased the relative support for the model (AIC = 3171.57). Thus, the increased size variance at greater carbon fluxes reflected a diversification in the size/flux

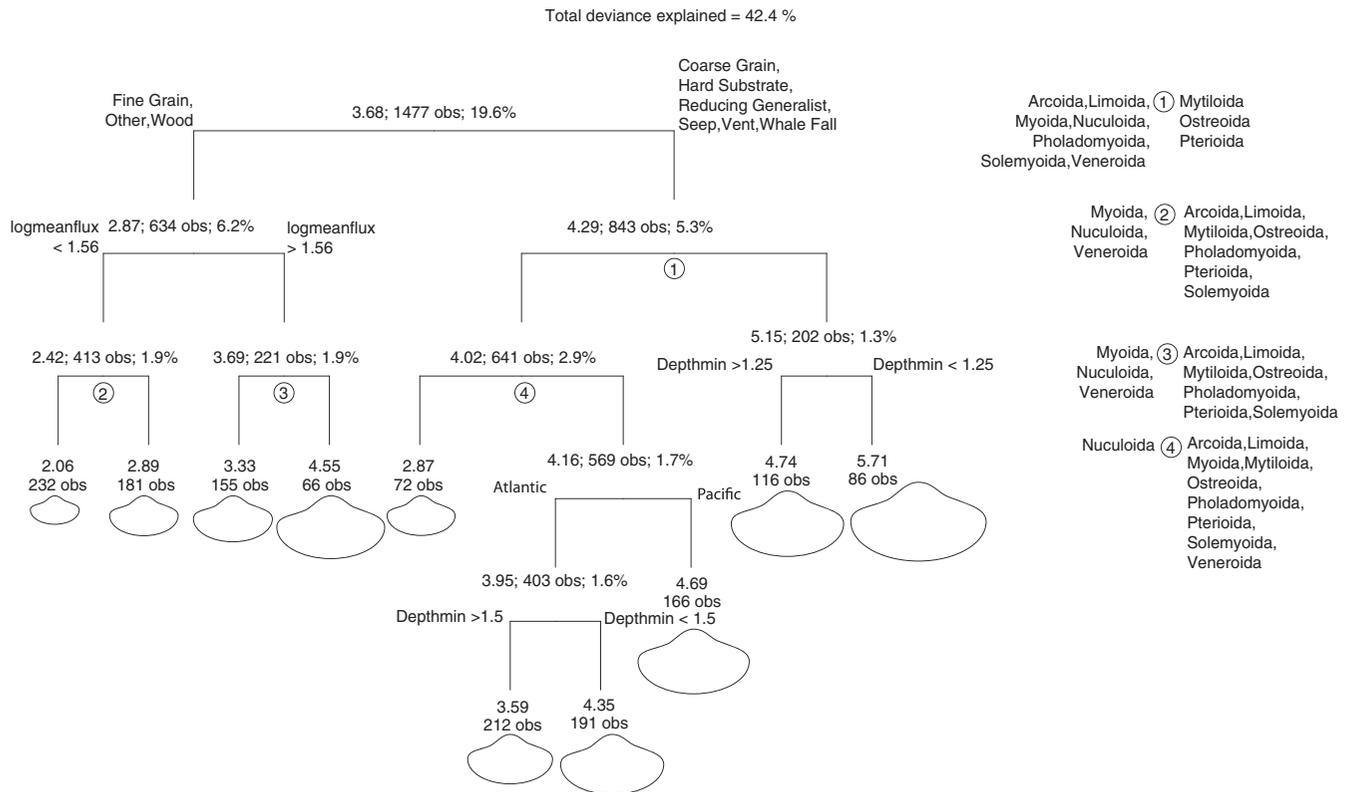


Figure 1. Regression tree showing predicted direction of size change for marine bivalves. Bivalve outlines of varying size represent terminal nodes and the size of the bivalve after the splitting process. Text at right angles represent the split variables, for example, the first split represents a division between fine grain/other, and wood versus coarse grain, hard substrate, etc. Number in circles represent a split in taxonomic order. Body size increases to the right of each branch point. Values at splits show splitting body size, number of observation in the branch, and percent variation described by the branch.

space. This is also supported when visualizing the relationship between biovolume and carbon flux among bivalve families (Fig. 5). Individual families exhibited varying relationships between biovolume and carbon flux and occupied different regions of the biovolume and carbon flux bivariate space. Several families inhabiting a wide range of carbon flux exhibited little variation in biovolume, for example, Cuspidariidae.

GASTROPODS

Among gastropods, latitudinal range, depth range, and carbon flux were all significant predictors of body size in the random forests model (Fig. 2C, total model explains 32.65% of the variance). Clade differences were also seen at the level of superorder. In the regression tree (not shown), the first split was also on superorder, distinguishing the, on average, larger sized species of Caenogastropoda from the smaller Vetigastropoda. Similar to bivalves, gastropods exhibited a greater variation in size at higher carbon flux values (Fig. 4). This relationship occurred in both the Caenogastropoda and Vetigastropoda (not shown). In contrast to bivalves, the relationship between carbon flux and body size among the smallest sizes was negative, that is, the smallest

gastropods were found at the highest carbon fluxes. This pattern among larger body sizes and carbon flux was positive.

As with bivalves when accounting for phylogenetic relationships, gastropods continued to demonstrate a positive relationship between biovolume and carbon flux ($\lambda = 0.981$, biovolume = $1.83 + 0.21$, carbon flux, $P < 0.0001$, AIC = 3037.21). The null model without consideration of phylogeny ($\lambda = 0$) produced worse fits (AIC = 3712.39). Incorporating a term to account for heterogeneity in variances also decreased the relative support for the model (AIC = 3683.35), again indicating that clades occupied distinctive regions of the size and flux bivariate space (Fig. 6).

Discussion

Overall, we find that nearly half of the variation in molluscan body size can be described by variation in carbon flux, habitat differences, clade-specific ecology, and geography likely correlated with gradients in unmeasured abiotic variables. A large percentage of this explained variance in the model was accounted for by variation in carbon flux or habitat differences likely reflecting shifts in energy availability. For bivalves and to lesser extent gastropods, chemical energy availability emerged as a factor of great

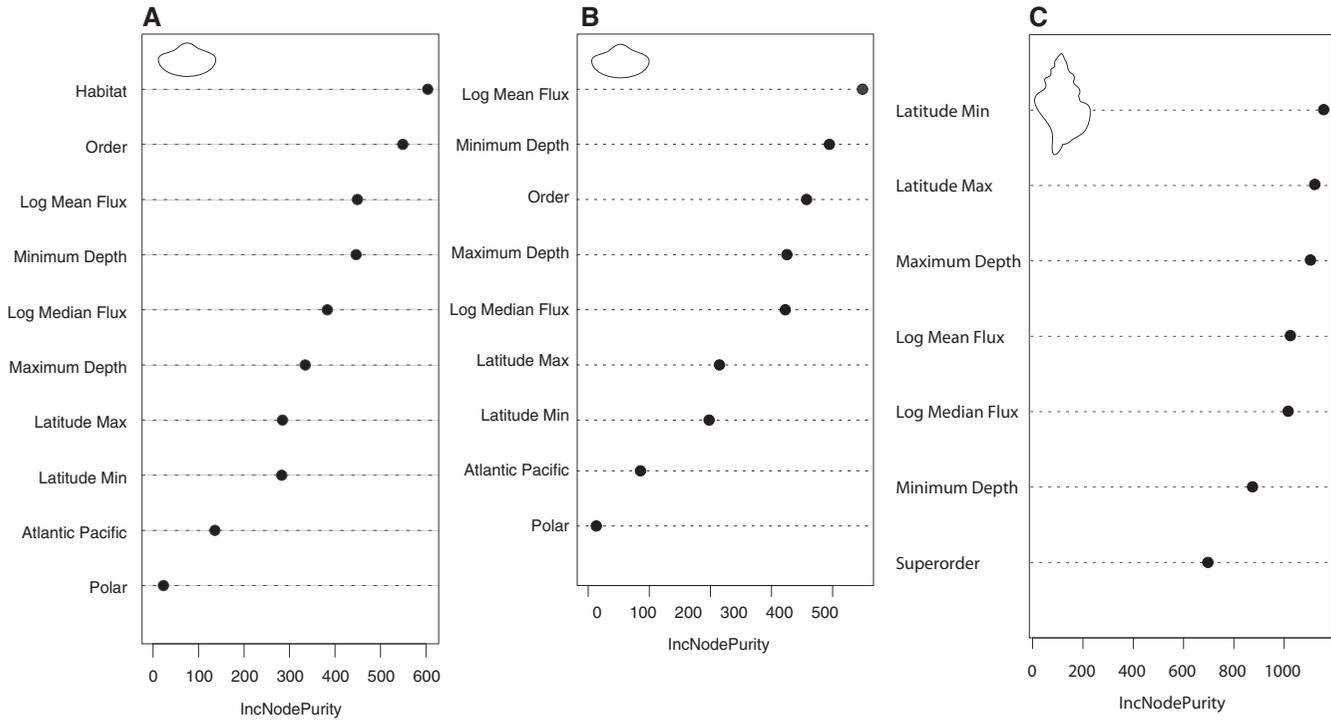


Figure 2. Node purity of predictor variables from the random forest analysis of molluskan size for (A) bivalves, (B) sediment inhabiting bivalves, and (C) gastropods. Node purity measures the similarity of responses at a node across regression trees in the runs of the random forest model with the highest node purity reflecting the greatest identical responses at a node across trees.

importance in driving geographic size clines in mollusks. For example, results from the random forest models indicated that carbon flux is the most important predictor of size for sediment-dwelling bivalves and the third most important predictor for all bivalves after habitat and order (Fig. 2). Among gastropods, log mean flux in the random forest model was deemed only marginally less important, based on node purity, than the higher ranking latitude and depth variables (Fig. 2). Likewise, in the PGLS model, AIC values were the lowest when carbon flux was included in the model. Although previous work has linked the overall miniaturization of marine invertebrates to reductions in carbon flux (Thiel 1975; Olabarria and Thurston 2003; McClain et al. 2006; Rex et al. 2006; reviewed in McClain et al. 2009), this provides the first direct evidence of a correlation between the two.

Of course not all size variation is explained by the factors in our analysis and many of the geographic variables allude to missing but important factors. For example, variation in oxygen with depth and latitude is known to limit body sizes among metazoans including deep-sea gastropods (McClain and Rex 2001). Although temperature is hypothesized to be an important factor determining size in marine invertebrates (e.g., Timofeev 2001), studies have failed to recover temperature-related size clines in mollusks (Roy et al. 2000; McClain and Rex 2001). Indeed, the greater sizes occurring at high temperature hydrothermal vents

would argue against these traditional size–temperature hypotheses predicting larger sizes in cooler environments. The latitudinal signal may also reflect variation in calcium carbonate dissolution. Solubility of calcium carbonate increases with rises in pressure and declines in temperature. This may prove a constraint on size such that larger sizes are too energetically costly to maintain in high latitude and deeper habitats (Graus 1974).

Previously one of us posited that the island rule, that is, the tendency for small mammals on islands to evolve larger sizes and large mammals to evolve smaller sizes, potentially reflects a reduction of food availability on islands compared to mainland habitats (McClain et al. 2006). This was based on a similar pattern of small trending toward large and large trending toward small occurring in marine gastropods over depth, a strong correlate of gradients in carbon flux. Because of this winnowing of sizes, both island and deep-sea faunas should exhibit less size variation than their related mainland or shallow-water faunas. Here, we demonstrate that the island-like cline and reduction in size variation in the deep-sea mollusks are related to a sharp decrease in chemical energy.

Interestingly, bivalves exhibited the same tendency toward smaller sizes and less size variation with decreased chemical energy. However, unlike gastropods, the increase in size among smaller sizes is not observed in bivalves. It might be argued that the smallest species of gastropods at remote depths and lower

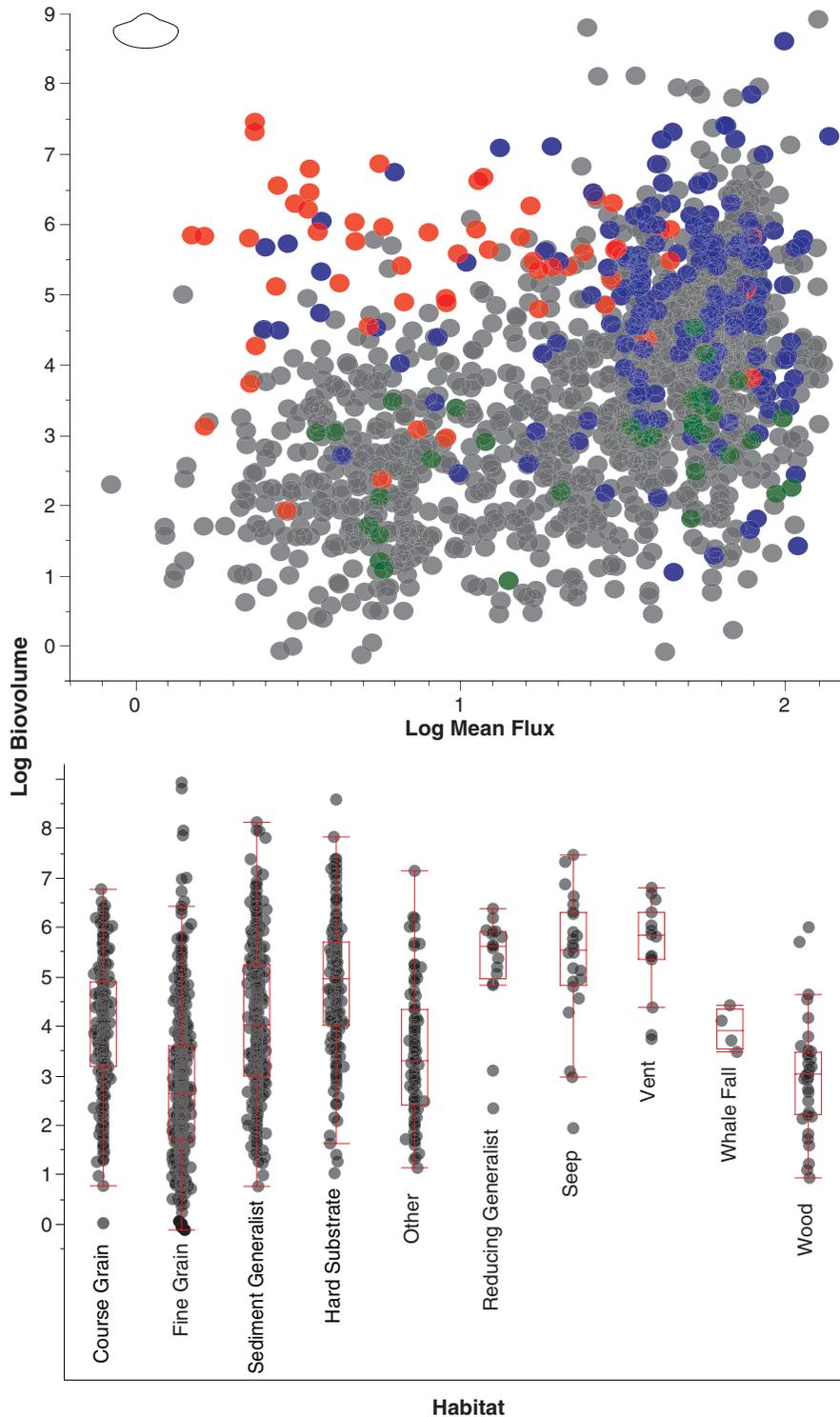


Figure 3. Log biovolume of bivalves versus log mean carbon flux (top) and habitat type (bottom). Species from sediment are denoted by gray, reducing by red, hard substrate by blue, and woodfall by green. Bottom represents box plots marking 25th and 75th quartiles (box upper and lower bounds), median (line in box), and lowest datum still within 1.5 IQR of the lower quartile and the highest datum still within 1.5 IQR of the upper quartile (whiskers).

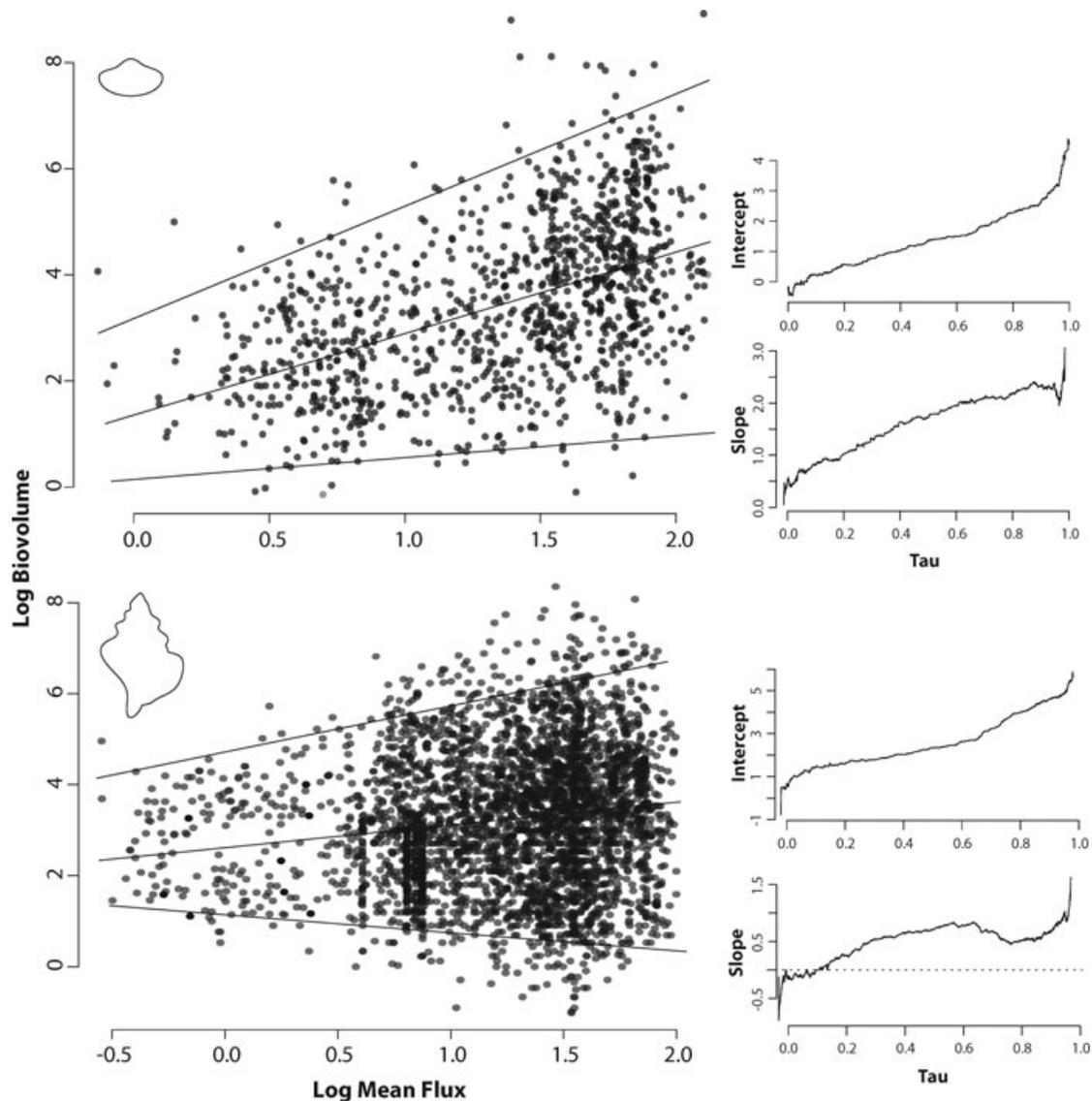


Figure 4. Log biovolume for bivalves (top) and gastropods (bottom) versus log mean carbon flux. Solid lines represent the 10th, 50th, and 90th quantiles. Small plots to the right represent how the intercept and slope change over the varying quantiles (τ).

carbon fluxes are undersampled. Although undersampling is an issue that plagues our knowledge of low productivity deep-sea systems (McClain and Hardy Mincks 2010), our understanding of gastropods and bivalves in the deep sea is garnered from the same set of samples. These samples are effective in yielding small bivalves in the analysis here and so should capture the smallest gastropods. More plausible is that ecological differences between bivalves and gastropods would yield different patterns. For example, feeding ecology can produce contrasting patterns of size in fish under similar gradients in food (Collins et al. 2005). The predominately right-skewed body size distribution in gastropods (McClain et al. 2006) versus the left-skewed in bivalves (Roy et al. 2000) over larger spatial scales argues that energetic trade-offs for the two molluscan classes may differ. McClain et al.

(2006) hypothesized that the lower constraints on size may represent selection against reduced foraging area and lower starvation resistance that would correspond with smaller sizes. Perhaps this constraint is relaxed in bivalves because motility and energetic demands are lower (Vladimirova 2001; Vladimirova et al. 2003). Indeed, increased metabolic demand may be why elasmobranchs demonstrate patterns of body size and depth similar to gastropods (Priede et al. 2006).

The size shift in deep-sea mollusks may simply reflect that small sized and predominately deposit feeding mollusks occupy soft sediments, the predominant habitat in the food-poor deep sea. Our analysis does indicate that species inhabiting soft sediment are demonstrably smaller sized. When our analysis is limited to sediment species, a strong relationship between carbon flux and

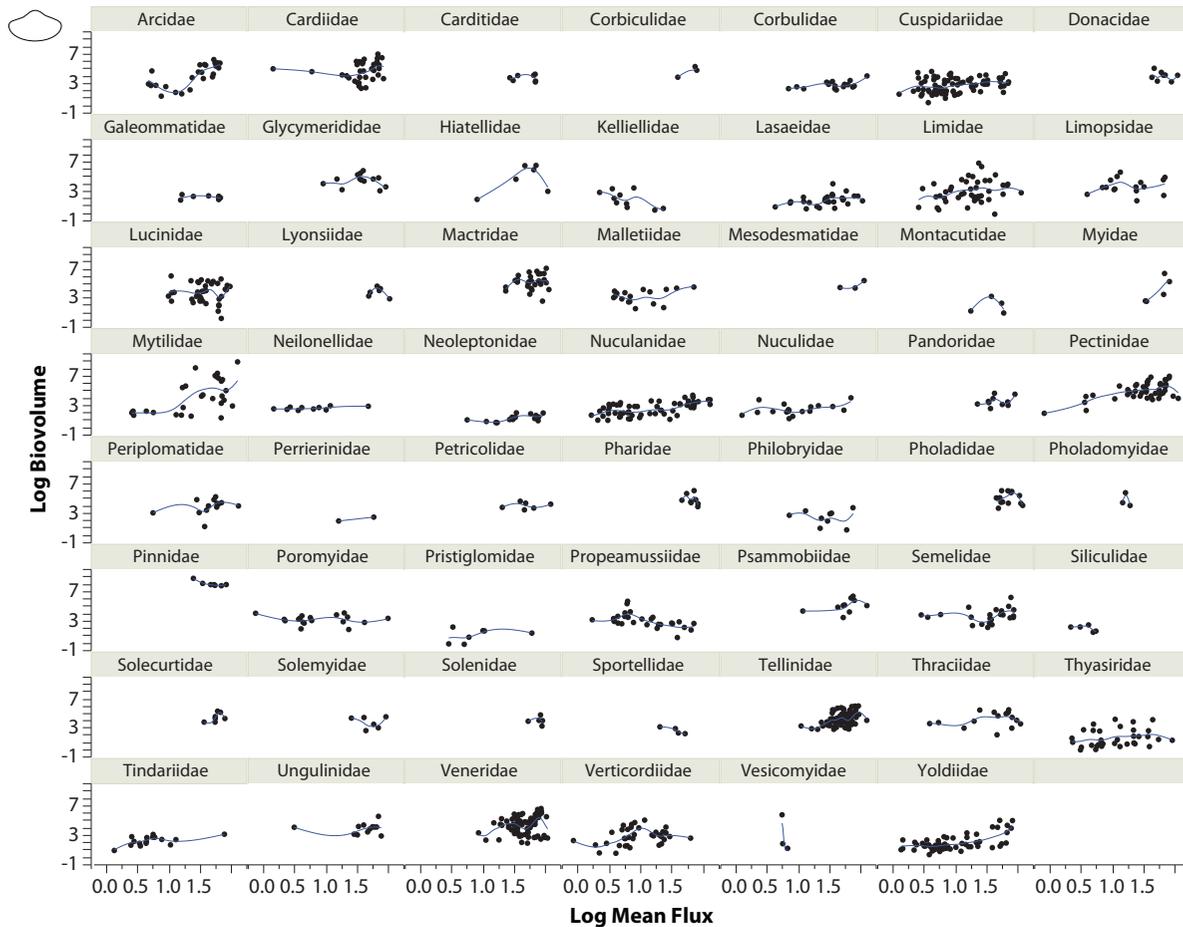


Figure 5. Log biovolume versus log mean carbon flux among bivalve families. Solid lines represent Loess fits.

body size in bivalves remains. Conversely, an increase in size is observed among mollusks in reducing environments such as methane seeps, hydrothermal vents, and whale falls. The greater size of organisms in these habitats may result from a greater input of chemical energy derived from in situ production, compared to the background abyss (Van Dover 2000). Even though wood falls represent an energy pulse to the low productivity deep, bivalve size is limited by the need to burrow into wood. The larger sized bivalves associated with hard substrates, dominated by shallow water habitats of the intertidal and subtidal, are likely to experience greater food availability due to direct primary production than captured in this study by just utilizing carbon flux. To a lesser extent, species categorized as hard substrate would also include deep-sea submarine canyon and seamounts, both noted for higher biomass and productivity input (Clark et al. 2010; De Leo et al. 2010; McClain and Barry 2010; Rowden et al. 2010). Thus, many of the habitat-based size differences may occur due to differences in chemical energy not quantified in our analyses.

Mollusk clades occupy different regions of the carbon flux and body size adaptive landscape. This is also observed in the PGLS model. When the phylogenetic relationships are accounted

for the relationship between carbon flux and variance in body size disappears. To restate, the variance in size with increased productivity reflects clade-specific responses to increasing productivity and a clade's ability to expand in the body size adaptive landscape. For example, among deep-sea gastropods, certain clades appear to respond to assumed increases in carbon flux whereas other, largely parasitic, appear buffered against gradients in chemical energy (McClain et al. 2005; McClain and Crouse 2006). Thus, our results indicate a potential vital role of chemical energy in the evolution of morphological innovation. Multiple genes influence body size (e.g., Kenney-Hunt et al. 2006; Gao et al. 2011) and therefore size can be a heritable trait (Smith et al. 2004). For example, in *Caenorhabditis elegans*, certain mutants for genes important in cellular energy conversion and transfer exhibit varying body size responses to increased food availability (So et al. 2011). Also notable is that increases in body size of mollusks through the Marine Mesozoic Revolution are tied to global increases in energy budgets (Finnegan et al. 2011).

The increased body size variation with increased chemical energy availability suggests an expansion in niche space at higher energy levels. Relationships between species richness and body

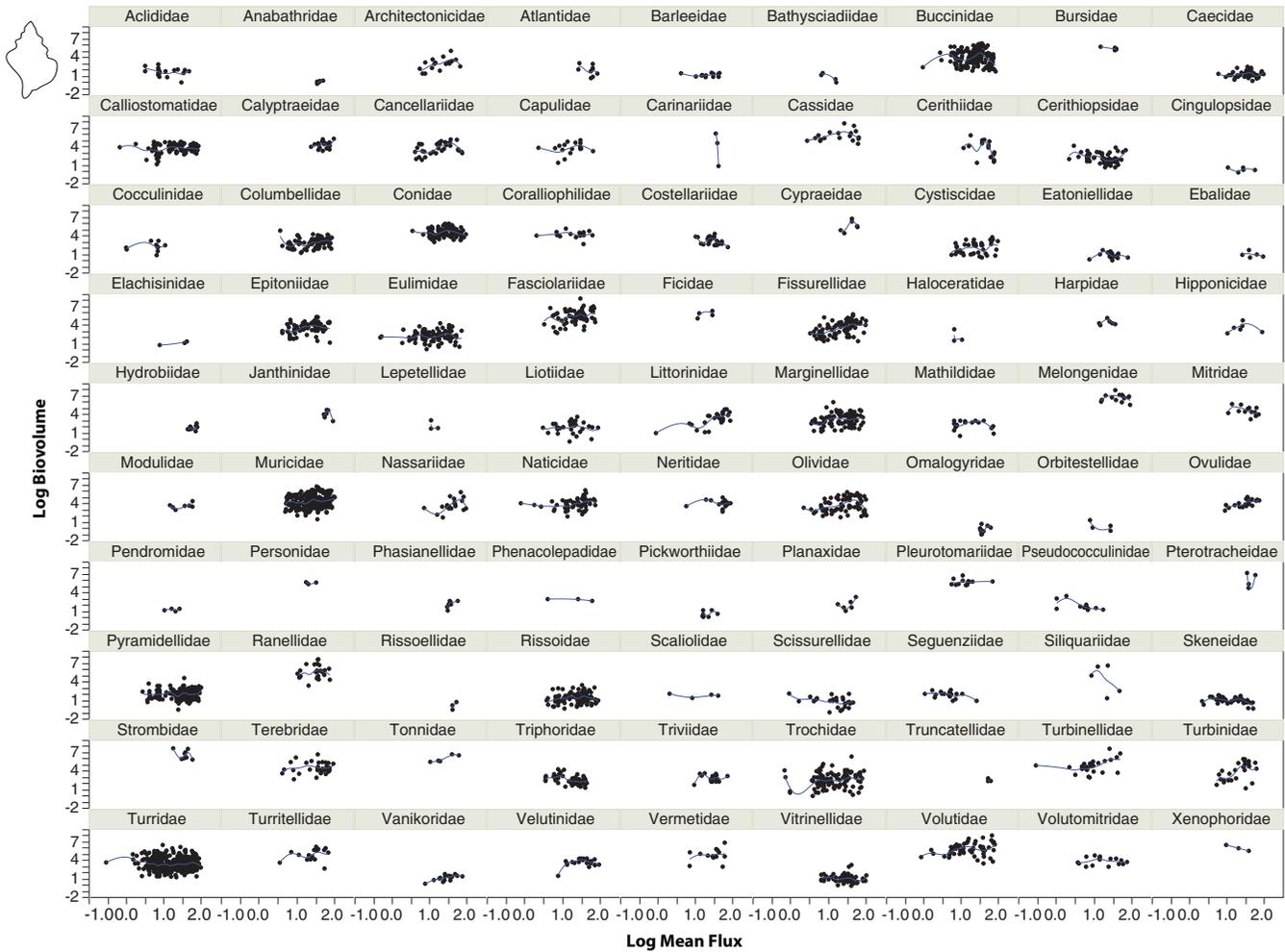


Figure 6. Log biovolume versus log mean carbon flux among gastropod families. Solid lines represent Loess fits.

size in mollusks occur at both regional and local levels (Roy et al. 2000; McClain 2004; McClain and Nekola 2008) and are potentially mitigated by chemical energy availability (McClain 2004). Strong correlations also exist between taxon richness and body size range among metazoan phyla, avian families, and mammalian families (McClain and Boyer 2009). In light of this, our findings may indicate that increases in chemical energy were important by affording more opportunity for the diversification of metazoans. This same hypothesis, that increases in chemical energy afford more opportunity and thus allowed for morphological and ecological innovation and thus increased diversity, was also posited to explain the Marine Mesozoic Revolution (Bambach 1993). It could be that greater chemical energy affording a breadth of size-based niches may in part explain rises of species richness with increased productivity (Hillebrand and Azosky 2001).

Examining if a correlation exists between heightened diversity, productivity, and size variance would provide support for these ideas. Empirical and modeling evidence from Atlantic deep-

sea bivalves suggests that at the community level there are strong ties between these factors that reflect both an ecological and evolutionary process (McClain 2011). In gastropods, low productivity abyssal communities are characterized by greatly reduced species diversity (Rex 1973) and a reduction in energetically expensive forms resulting in less variation in shell type and size (McClain et al. 2004, 2005). Future work could easily test the chemical energy/size-based niche hypothesis by examining whether rates of speciation were greatest in clades inhabiting more productive habitats and whether these were tied to concurrent expansions in size range.

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