

**Declining bivalve species and functional diversity along a coastal
eutrophication-deoxygenation gradient in the northern Gulf of Mexico**

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Abstract: Coastal eutrophication and hypoxia are growing challenges globally, yet their impacts can be difficult to evaluate because of limited biomonitoring that typically postdates the onset of these stressors. We address this limitation by investigating how the taxonomic and functional diversity of marine bivalve communities vary with primary productivity, dissolved oxygen, temperature, and seafloor sediment properties across the northern Gulf of Mexico, a region that includes one of the world's largest dead zones. We hypothesized that taxonomic and functional richness would decline in eutrophic and hypoxic coastal environments. Live bivalve mollusks were sampled at 15 stations, spanning more than 600 km of continental shelf habitat. Individuals were identified to species and characterized based on feeding, mobility, fixation, life position relative to the sediment-water interface, and body size. Alpha and beta species and functional diversity were computed using Hill numbers and linear models used to assess their covariation with regional environmental conditions. Species and functional diversity were highest in less eutrophic environments characterized by normoxic conditions, and lowest in more eutrophic environments where oxygen was more limited. Community-level differences were underlain by functional shifts, with abundant shallow-infaunal, deposit and mixed feeders in more eutrophic settings, in contrast with less eutrophic settings where suspension feeders were more abundant. Median body size increased with eutrophication, possibly as a result of hypoxia-induced declines

in predator and competitor populations. These results suggest that intensifying nutrient loading and deoxygenation in the coastal zone will cause declines in multiple dimensions of benthic biodiversity with implications for ecosystem function.

Keywords: Functional diversity; Species richness; Coastal eutrophication; Hypoxia; Space-for-time; Gulf of Mexico; Benthic; Bivalve mollusk; Continental Shelf

1. INTRODUCTION

Ocean deoxygenation is a global challenge. Since the 1960s dissolved oxygen concentrations have decreased by approximately 2% on average, and up to 30% regionally, due to a combination of anthropogenic nutrient loading and climate change (Schmidtko et al. 2017, Deutsch et al. 2024). Nutrient-rich runoff from agricultural and urban development enhances coastal primary productivity, and the aerobic decomposition of phytoplankton and algal blooms depletes dissolved oxygen leading to the formation of coastal dead zones (Rabalais et al. 2007, Levin et al. 2009, Breitburg et al. 2018, Deutsch et al. 2024). Warmer waters also hold less oxygen and thermal stratification can reduce mixing, thereby isolating oxygen-limited bottom waters (Breitburg et al. 2018, Deutsch et al. 2024). Warming may also result in greater runoff due to more frequent and intense precipitation events, which is projected to increase nutrient loading in some coastal regions (Sinha et al. 2017, Laurent et al. 2018). Understanding the impacts of current and future changes in oxygen availability on coastal fauna requires integrative approaches that consider the combined effects of interacting environmental stressors on different levels of biological organization.

Reductions in oxygen have been shown experimentally to inhibit the growth and abundance of marine benthos and to increase their mortality rates (Villnäs et al. 2012, Sampaio et al. 2021). Experimental approaches allow one to isolate the unique effects of oxygen versus temperature or other environmental factors; however, scaling observed responses up to ecosystems in which multiple stressors act in tandem is challenging (Breitburg et al. 2019, Woods et al. 2022). Observational data can be used to evaluate experimental predictions at broader scales (e.g., Karlson et al. 2002, Kendzierska & Janas 2024), and have documented mass mortality of marine fauna in response to hypoxia, often in combination with warming events which accelerate metabolic rates, increase biological oxygen demand, and reduce aerobic scope (Breitburg et al. 2018, Deutsch et al. 2024). The extent of biological monitoring in most marine ecosystems is exceptionally limited though and, where available, tends to postdate the onset of many causes of anthropogenic environmental change, including ocean deoxygenation (Finnegan et al. 2024). Space-for-time approaches can help address the dearth of historical observational data by focusing on biotic response to interacting environmental drivers along present-day geographic gradients. Previous studies have used this approach to investigate changes in species richness with oxygen concentration along depth transects and across oxygen minimum zones

(Rhoads & Morse 1971, Levin et al. 2009, Sperling et al. 2016, Gallo et al. 2020), but the corresponding impacts of these changes on ecosystem function are understudied and/or have tended to focused on select species (though see Fajardo et al. 2018 and Bon et al. 2021, among others). Taxonomic and functional responses to environmental stress can be highly divergent (Edie et al. 2018, Pimiento et al. 2020, Moyes et al. 2023), depending on species functional redundancy, which limits any attempt to use taxonomic data to predict ecosystem functional responses to ocean deoxygenation or other types of environmental change.

Pronounced gradients in dissolved oxygen, primary productivity, and seafloor properties exist today across the northern Gulf of Mexico (Mendelssohn et al. 2017). Watershed size varies markedly across the region, and greatly affects environmental conditions on the adjacent continental shelf (Van der Zwaan 2000, Krause et al. 2023). Primary productivity is highest offshore of Louisiana, which is influenced by the Mississippi River watershed which drains 3.3×10^6 km² (roughly 40%) of the contiguous United States (Mendelssohn et al. 2017, Krause et al. 2023). Decomposition of phytoplankton and algal blooms in coastal Louisiana result in the annual development of one of the most extensive dead zones globally (Rabalais et al. 2007, Levin et al. 2009, Osterman et al. 2009). The Mobile Bay and Apalachicola watersheds are 3.5% and 1.6% the size of the Mississippi watershed, and consequently primary productivity is more constrained offshore of Alabama and north Florida (Harnik et al. 2017, Krause et al. 2023, Calderaro et al. 2024). Hypoxic conditions are also more spatiotemporally variable in Alabama than Louisiana (Brunner et al. 2006, Harnik et al. 2017, Dzwonkowski et al. 2018, Calderaro et al. 2024), and have not been observed on the north Florida continental shelf (Rabalais 1992, Santema et al. 2015). Seafloor properties also vary geographically, from abundant fine-grained sediments proximal to the Mississippi delta to coarser grains offshore of Alabama and north Florida where sedimentation rates are slower (Davis 2017). In contrast, regional differences in mean annual sea surface temperature are modest, and less than the observed seasonal variation (Mendelssohn et al. 2017, Calderaro et al. 2024).

Using the northern Gulf of Mexico as a model system, we investigate how the taxonomic and functional alpha and beta diversity of marine bivalve communities vary along these present-day environmental gradients on the continental shelf. We hypothesize that bivalve taxonomic (i.e., species) diversity will be lower in more productive and more oxygen-limited environments consistent with previous studies of other macrobenthic fauna (Rhoads & Morse 1971, Levin et al.

2009, Sperling et al. 2016, Gallo et al. 2020). We also expect corresponding declines in bivalve functional diversity in areas of lower oxygen concentration, with the magnitude of decline mediated by the extent of functional redundancy among bivalve species. We expect greater reductions in both species and functional diversity in areas where warmer ocean temperatures coincide with eutrophic conditions (Deutsch et al. 2024). Such changes in species and functional composition along environmental gradients should also result in increasing beta diversity with increasing geographic distance between communities. We investigate these hypotheses using bivalve mollusks, because of (i) their role in ecosystem functioning in aquatic, soft-sediment habitats (Norkko et al. 2013, Vaughn & Hoellein 2018, Lockwood & Mann 2019), (ii) their species richness and abundance on the continental shelf relative to other groups of macrobenthic invertebrates (e.g., Kokesh et al. 2022), and (iii) because their compositional variation along human and non-human environmental gradients is often congruent with other marine macrobenthos (Tyler & Kowalewski 2017, Kokesh et al. 2022).

2. MATERIALS & METHODS

2.1. Study area and datasets

We sampled live bivalve mollusks at 15 stations that span more than 600 km of continental shelf habitat in May and June 2018 (Fig. 1a, Table 1). All samples were collected in U.S. Federal Waters in the northern Gulf of Mexico in accord with federal policies for collecting marine invertebrates that are not listed as at risk. Stations were distributed along the -20 m isobath on the inner shelf in order to investigate regional variation in environmental conditions while controlling for water depth; shallower, more inshore locations can be strongly influenced by point source nutrient enrichment and salinity variation which were not the focus of the current study. Five stations were sampled in each of three regions (Louisiana, LA; Alabama, AL; Florida, FL), and stations within each region were spaced 10 km apart. Benthic samples were collected using a Grey O'Hara-type box corer (LA and AL) and Van Veen sediment grab (FL); the size (area) of each of these sampling devices was 0.1 m². Multiple samples were collected at each station and processed using a 2 mm sieve, with the goal of collecting 100 or more live individuals per station (median = 105 individuals/station) (Table 1). We used a 2 mm sieve because previous work has shown that molluscan biodiversity data (species composition and

relative abundance) generated using finer mesh sizes (< 2 mm) consist primarily of recent recruits, many of whom die before reaching adult size (> 2 mm) (Kidwell 2001). As a result, fine mesh (< 2 mm) molluscan datasets are particularly sensitive to census timing. Sample size (i.e., number of living individuals) varied among stations and regions (Table 1), and consequently we used coverage-based diversity metrics to control for varying sampling effort in our subsequent analyses (see 2.2. *Data analysis*). We focused on diversity comparisons at a consistent sampling coverage estimated using numerical abundance data (i.e., the number of live individuals per site), rather than a fixed number of sediment grabs per site, because the current study is part of a broader-scale effort focused on reconstructing molluscan biodiversity change over time in the northern gulf using a combination of live censuses and historical data generated from molluscan skeletal remains (shells). The density of historical shells sampled at a given station is affected not only by the density of living individuals, but also by sedimentation rates among other factors, and consequently paleoecologists generally analyze relative versus absolute abundance and have shied away from comparisons of population density over time. The low densities of living bivalves in these settings (median = 3 live individuals per benthic sample; Fig. S1), in conjunction with the costs involved in offshore fieldwork, limited the number of stations (15 in total) that could be sampled. Live individuals were separated offshore, frozen for transport, and air-dried prior to data collection.

Individuals were identified to species using regional monographs (Mikkelsen & Bieler 2008, Tunnell Jr. et al. 2010) and taxonomically standardized following the World Register of Marine Species (WoRMS Editorial Board 2023). Individuals were categorized functionally based on their body size, feeding, mobility, fixation, and life position relative to the seafloor (i.e., tiering) (Fig. 1b). The body size of each individual was calculated using shell area, as approximated by an ellipse (Calderaro et al. 2024); shell length (the anterior-posterior dimension of the shell parallel to the hinge) and height (the dorsal-ventral dimension perpendicular to the length measurement) were measured using a Leica M125 stereomicroscope. Other functional categories were determined based on a literature review (Mikkelsen & Bieler 2008, Huber 2010, 2015, Rocha & Matthews-Cascon 2015, Audino & Marian 2018, Taylor & Glover 2021). The degree of phylogenetic conservatism of these functional traits varies across the Bivalvia, and most of these assignments were made at the genus or family level; a dearth of inter- and

intraspecific studies makes it challenging to assess variation in bivalve functional traits at finer taxonomic scales.

Environmental measurements for each station were compiled using a combination of openly-available gridded climate data analyzed in a previous study (Calderaro et al. 2024), and new sediment measurements that we generated from our field samples (Table 1). We focused on temporally-averaged climate data rather than measurements of environmental variables made at the time of each benthic census (e.g., via CTD casts) in order to summarize the environmental conditions that bivalves encounter over their multi-year lifespans. Gridded climate data were downloaded from the Ocean Productivity Project (Oregon State University 2022) and Gulf of Mexico Regional Climatology (ver. 2) derived from the World Ocean Database (Garcia et al. 2018, Seidov et al. 2020), and used to calculate net primary production (NPP, in $\text{mgC}/\text{m}^2/\text{day}$), sea surface temperature (SST, in $^{\circ}\text{C}$), and dissolved oxygen (DO, in $\mu\text{mol}/\text{kg}$). Mean NPP values were calculated by averaging data for each month from 2003 through 2018 and then calculating the mean across months. [NPP values were generated from MODIS data that are available from 2002 onwards; we began with the first full year of NPP data in 2003.](#) The mean and standard deviation of SST and mean DO were calculated for bottom waters (15 m depth) for summer months (July, August, and September) from 1955 through 2017. DO data are only available as a single climatology that spans 1955-2017, and we chose a similar temporal range for the SST data that are available from the same data source. We analyzed northern hemisphere summer climate using July-August-September climatology in order to minimize the geographic distance between gridded environmental data and our sampling stations and because of our interest in investigating the combined impacts of SST, DO, and NPP on bivalve biodiversity; low DO is generally associated with higher NPP and warmer SST, conditions generally encountered in particular shelf environments in the late summer. Each station was matched to the nearest grid point with climate measurements, based on the shortest geographic distance using the World Geodetic System of 1984 . The mean distance between our stations and grid points with NPP, DO, and SST data was NPP = 5.5 km, DO = 77.9 km, and SST = 6.74 km, respectively. Spatial resolution varies among these three environmental measures, from 0.1° for SST, 0.16° for NPP, to 1° for DO. Due to the lower spatial resolution of the DO data in the World Ocean Database, a total of four unique DO values were retrieved for the 15 studied stations. Additional details regarding the compilation of gridded climate data at these 15 sampling stations are available in Calderaro et al.

(2024). Seafloor sediment properties were characterized by measuring the weight percent of silt and clay (i.e., particles < 63 microns) in bulk sediment that we collected at each station (mean sample size was 350 g dry weight). Sediment samples contained a mixture of carbonate, siliciclastic, and organic grains. Sediment samples were stored at room temperature prior to grain size analysis. Geochemical data (e.g., total organic carbon, total nitrogen) were not collected for this study.

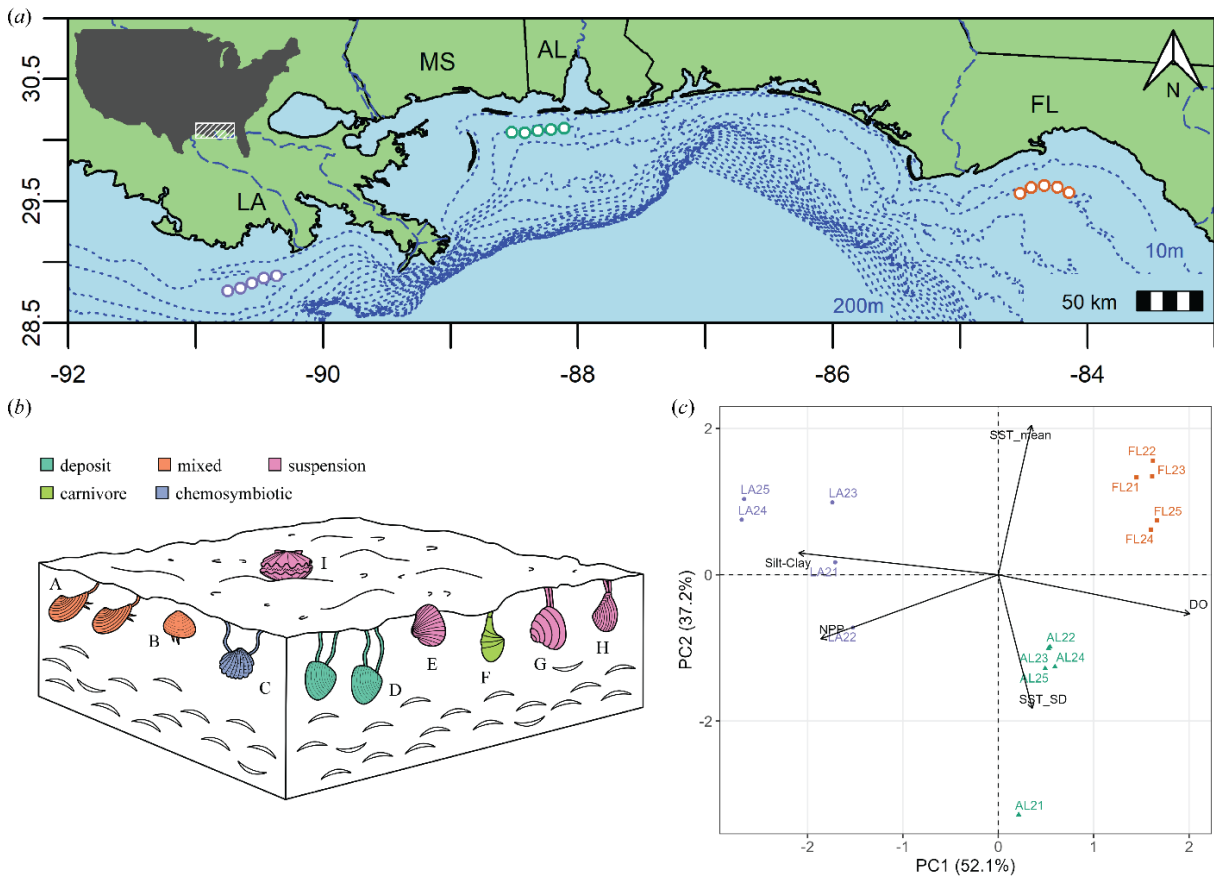


Fig. 1. (a) Map of sampling stations in the northern Gulf of Mexico. LA, Louisiana, MS, Mississippi, AL, Alabama, and FL, Florida. (b) Illustration using select bivalve species from the northern gulf to show that taxonomic and functional richness measure unique dimensions of benthic biodiversity. Species are denoted by capital letters: A, *Nuculana acuta*; B, *Nucula proxima*; C, *Radiolucina amianta*; D, *Abra lioica*; E, *Noetia ponderosa*; F, *Cardiomya costellata*; G, *Lirophora oblitterata*; H, *Caryocorbula swiftiana*; I, *Argopecten gibbus*. Species vary in functional similarity (e.g., feeding mode, denoted by color). H and I, for example, both suspension feed, yet are infaunal and epifaunal respectively, whereas D and G are both infaunal, but D deposit feeds and G suspension feeds. (c) Principal Components Analysis of environmental variation across all 15 sampling stations; DO = dissolved oxygen concentration; NPP = net primary productivity; Silt-Clay = weight percent silt and clay; SST_Mean and SST SD = mean and standard deviation of summer sea surface temperature. Panel 1b was drawn by Lena Harnik.

Region	Station	Latitude	Longitude	Depth (m)	Collection Date (D/M/Y)	Sample Size (N)	Number of benthic samples	Taxonomic diversity			Functional diversity			DO	NPP	Silt-Clay	SST_Mean	SST_SD
								q=0	q=1	q=2	q=0	q=1	q=2					
Louisiana	LA21	28.76715	-90.752	20.3	20/05/2018	78	20	7.86	4.26	3.19	2.42	1.9	1.76	103.7	3128	0.59	28.18	1.47
	LA22	28.79128	-90.6526	20.6	22/05/2018	105	30	3.79	3.21	2.84	1.9	1.69	1.57	103.7	3043	0.55	27.81	1.97
	LA23	28.83182	-90.5609	20.4	23/05/2018	101	25	3.33	2.84	2.52	2.08	1.91	1.78	103.7	3043	0.6	28.46	1.01
	LA24	28.87188	-90.4687	20.8	18/05/2018	99	40	2.36	1.84	1.59	1.66	1.44	1.33	103.7	3864	0.84	28.45	1.03
	LA25	28.8926	-90.3686	20.9	19/05/2018, 24/05/2018	58	28	2.94	2.47	2.16	1.88	1.69	1.57	103.7	3864	0.79	28.37	0.74
Alabama	AL21	30.06492	-88.5216	20.5	31/05/2018	125	25	10.66	7.68	5.84	3.1	2.7	2.46	198.7	3071	0.24	26.31	2.71
	AL22	30.06112	-88.418	20	31/05/2018	37	40	15.26	8.43	5.29	2.94	2.28	1.94	198.7	2910	0.02	27.14	1.37
	AL23	30.07827	-88.3165	20.5	01/06/2018	124	40	14.79	8.53	5.64	3.01	2.16	1.8	198.7	2946	0.02	27.16	1.39
	AL24	30.08993	-88.2138	19.8	30/05/2018	121	50	11.77	5.03	2.83	2.65	1.75	1.47	198.7	2946	0.03	27.35	1.71
	AL25	30.0985	-88.1101	20.7	01/06/2018	162	20	13.38	7.15	4.99	3.27	2	1.69	198.7	3028	0.06	27.36	1.72
Florida	FL21	29.56453	-84.5318	20.5	21/06/2018	109	20	21.97	12.6	7.81	4.21	3.18	2.68	202.7	1654	0	28.66	0.78
	FL22	29.61222	-84.4438	19	25/06/2018	85	30	19.4	11.59	8.04	5.13	3.35	2.85	195.9	1485	0	29.40	1.12
	FL23	29.62953	-84.3423	20.5	22/06/2018	118	25	23.95	14.41	10.11	5.32	3.52	2.93	195.9	1485	0.01	29.29	1.23
	FL24	29.61475	-84.2404	18.2	24/06/2018 25/06/2018	102	20	16.02	8.91	6.06	5.16	3.28	2.69	195.9	1428	0.03	28.72	1.48
	FL25	29.57232	-84.1495	19.5	24/06/2018	115	15	22.22	14	9.61	5.76	3.87	3.19	195.9	1486	0.01	29.09	1.59

Table 1. Information regarding the location, water depth, collection date, sample size (# of live individuals), number of benthic samples, taxonomic and functional diversity, and environmental conditions at 15 stations on the continental shelf that are distributed across the northern Gulf of Mexico from Louisiana to north Florida. Diversity order $q = 0$ is the effective number of rare species or functional groups; $q = 1$ is the effective number of common species or functional groups; $q = 2$ is the effective number of highly abundant species or functional groups. DO, dissolved oxygen concentration ($\mu\text{mol/kg}$); NPP, net primary productivity ($\text{mg C/m}^2/\text{day}$); Silt-Clay, weight percent silt-clay; SST, sea-surface temperature ($^{\circ}\text{C}$), mean and standard deviation (SD). Note, the data at three stations (LA24, LA25, and AL22) were too sparse to accurately estimate sample coverage (see 3. *Results*) and these stations were excluded from subsequent diversity analyses.

2.2. Data analysis

Ecologists have long recognized that observed diversity measurements depend on sampling effort and sample completeness and thus cannot be directly compared across stations and regions without standardization. Proper standardization can be achieved by comparing samples at the same level of sample coverage, where sample coverage is the proportion of individuals in a community that belong to the species represented in a given sample. Sample coverage can be accurately estimated from the observed data, and provides an objective measure of sample completeness for standardizing diversity comparisons. We used Hill numbers to compute alpha and beta diversity from our station-level taxonomic and functional data at a standardized sample coverage of 90% (Hill 1973, Ellison 2010, Chao et al. 2014, Chao et al. 2019, Chao et al. 2020). Hill numbers describe the effective number of species, and functional groups, with diversity order (q) controlling the sensitivity of these measures to species abundance; $q = 0$ measures the effective number of rare species (i.e., species richness), whereas increasing q -values weight abundance more heavily, with $q = 1$ and $q = 2$ being the effective number of common (i.e., Shannon diversity) and highly abundant (i.e., Simpson diversity) species, respectively. Hill numbers are increasingly used in marine ecology to investigate geographic variation in diversity and their associations with environmental factors (e.g., Kusumoto et al. 2020, Hong et al. 2022, Mamo et al. 2023). Species alpha diversity at varying q -values was calculated using the iNEXT.3D standardization (Chao et al. 2021). Functional alpha diversity at varying q -values was computed from species-pairwise Gower distances based on one continuous (shell area) and four categorical traits (feeding, mobility, fixation, and life position relative to the substrate) (Fig. 1b) (Chao et al. 2019). Standardized functional diversity measures were then generated from the resulting pairwise distance matrix using iNEXT.3D (Chao et al. 2021).

We investigated the association between taxonomic and functional diversity using linear models. These diversity measures are not independent because functional diversity was calculated using both species (e.g., feeding mode) and individual-level (e.g., body size) traits, which may bias estimated slope coefficients upward. We determined if the observed association between taxonomic and functional diversity was greater than expected using a bootstrap procedure in which we resampled, with replacement, taxonomic and functional diversities from the 12 stations with robust diversity estimates (see 3. *Results*). To address the potential

dependence of functional diversity on taxonomic diversity, we required that each taxonomic diversity value was greater than or equal to the resampled functional diversity value. We then fit a linear model to the bootstrap sample and repeated this process 10,000 times in order to generate a null distribution of slope coefficients that were used to determine whether the observed coefficient value was significantly greater (one-tailed test).

Given the strong covariation among environmental variables in the northern gulf (Fig. S2), a principal component analysis (PCA) was conducted to generate composite environmental metrics that describe regional environmental conditions (Fig. 1c); all environmental variables were mean centered and scaled to the standard deviation prior to analysis. Linear regression models were used to assess the association between these composite environmental metrics (PC1 and PC2) and taxonomic and functional alpha diversity. Non-metric multidimensional scaling (nMDS) of the incidence and abundance-based distance matrices were generated in iNEXT.3D using Sørensen and Morisita-Horn dissimilarities, respectively, and these were used to visualize similarities among stations in taxonomic and functional composition. To investigate the role of geographic distance in faunal composition, pairwise taxonomic and functional beta diversities were calculated following Chao et al. (2023) and plotted against the geographic distances between stations. Differences in body size among regions were assessed using Kolmogorov-Smirnov and Mann-Whitney U (Wilcoxon Rank Sum) tests. All analyses were conducted in R, R version 4.3.3 (R Core Team 2024); all data and R code used in this study will be archived in the Dryad Digital Repository prior to publication.

3. RESULTS

Taxonomic and functional diversities of bivalve mollusks varied markedly across the northern Gulf of Mexico (Fig. 2). Diversity curves based on sample size (i.e., # of individuals) indicate that all samples are incomplete due to undetected rare species (Fig. S3), and thus the taxonomic and functional diversities of stations and regions were compared at a standardized sampling coverage of 90% (Fig. S4). Diversities were highest offshore of Florida, intermediate offshore of Alabama, and lowest offshore of Louisiana (Fig. 2). Similar geographic patterns were observed for rare ($q = 0$), common ($q = 1$), and highly abundant ($q = 2$) species and functional groups (Fig. 2). In any given region, taxonomic diversity always exceeded functional diversity when compared at the same diversity order (e.g., $q = 0$), reflecting the degree of functional

redundancy among species. Station-level differences in species and functional alpha diversity in Florida and Alabama were not geographically structured, however species diversity in Louisiana tended to increase with distance from the Mississippi Delta (Table 1). Sparse data at LA24, LA25, and AL22 limit statistical inference of diversity at these stations (Table 1). Samples from LA24 and LA25 contained only four live-collected species and insufficient frequencies of singletons and doubletons to accurately estimate sample coverage; at LA24, no singleton or doubleton species were sampled, and at LA25, there were no singletons and only one doubleton species. These two stations are located at the core of the dead zone adjacent to the Mississippi Delta; LA24 is within 0.5 km of C6B, a station where mid-summer hypoxia has been documented most years between 1985 and 2014 (see C6 in Fig. 1 of Rabalais & Baustian 2020). Consequently, dissolved oxygen concentrations likely limit species diversity estimates for this area of the Louisiana continental shelf. The number of live individuals sampled at AL22 was too limited ($N = 37$) to reliably estimate sample coverage. As a result, these three sites (LA24, LA25, and AL22) were excluded from subsequent diversity analyses. Excluding LA24 and LA25 from subsequent analyses is statistically conservative; the lack of singletons in spite of reasonable samples sizes, in conjunction with documented hypoxia in this area of the Louisiana shelf, suggest that the very low diversities at these two stations are biologically meaningful, even though coverage-based standardization was not possible.

Taxonomic and functional alpha diversity were strongly positively correlated (Fig. 2); Pearson product moment correlation values were 0.90 and 0.91, respectively, for rare and highly abundant species and functional groups at the 12 sampling stations with robust diversity estimates (Fig. S2). Taxonomic and functional diversities covaried with regional environmental gradients (Table 2, Fig. S5). Linear models explained $> 51\%$ of the variation in standardized taxonomic and functional diversities (median adjusted R^2 value = 0.72), and were more effective in describing the diversities of rare ($q = 0$) than common ($q = 1$) or highly abundant ($q = 2$) species and functional groups (Table 2, Fig. S5). PC1 scores primarily reflect differences among stations in dissolved oxygen concentration, net primary productivity, and sediment grain size, whereas PC2 scores primarily reflect differences among stations in the mean and standard deviation of sea surface temperature (Fig. 1c); cumulatively, these two components explain 89.3% of the environmental variation among stations. Species and functional diversities were highest in normoxic, less productive settings, characterized by coarser seafloor sediments (i.e.,

stations offshore of Florida) (Table 2, Fig. S5). Species and functional diversities declined with increasing primary productivity, decreasing dissolved oxygen concentration, and decreasing grain size (Table 2), and were lowest at stations offshore of Louisiana (Fig. 1c). In contrast, differences in sea surface temperature (PC2) explained relatively little additional variation in taxonomic and functional diversity across the northern gulf (Fig. 1c, Table 2). The diversities of rare functional groups tended to be higher in regions with warmer, less variable, sea surface temperatures, however, this was due to regional differences between Florida and Alabama, with stations offshore of Louisiana deviating from the trend (Table 2, Figs 1c & S5).

Differences in taxonomic and functional alpha diversity were associated with a change in bivalve community composition (Table S1). A non-metric multidimensional scaling of taxonomic and functional dissimilarity revealed distinct clusters of stations, with taxonomic differences between regions somewhat more pronounced than functional differences (Figs 3 & S6). Consistent regional differences in taxonomic and functional composition were observed across different diversity orders; $q = 0$ (Fig 3) and $q = 2$ (Fig S6) are presented to illustrate the compositional dissimilarities of rare and highly-abundant species, respectively. Taxonomic and functional dissimilarities (i.e., beta diversity) both increased with increasing geographic distance between stations (Fig. 4). Taxonomic and functional dissimilarities between sampling stations tended to be greater offshore of Florida than offshore of Alabama or Louisiana, however there was considerable overlap among regions in beta diversity (Fig. S7).

Regional differences in bivalve alpha and beta diversity across the northern gulf were underlain by shifts in functional traits (Figs 5, 6, & S8). Bivalve communities in more eutrophic environments offshore of Louisiana and Alabama contained a greater abundance of obligate deposit feeders and mixed feeders (Fig. 5); mixed feeders are individuals which may be capable of deposit or detritus feeding as well as suspension feeding. In contrast, less eutrophic environments located offshore of Florida contained many more suspension feeders, and a greater diversity of feeding types overall (Fig. 5). Other categorical functional traits (i.e., mobility, position relative to the substrate, fixation) exhibited less variation geographically (Fig. 5). Mobile bivalves comprised the bulk of individuals overall, with a slight increase in the relative abundance of immobile and swimming individuals offshore of Florida. Most bivalves in the northern gulf were siphonate and infaunal, however asiphonate infauna increased in relative abundance from Louisiana to Florida, though remained uncommon. Stations offshore of Florida

347 also contained rare epifaunal and nestling individuals. With respect to fixation, most bivalves
348 lived unattached, though rare cementing individuals were sampled offshore of Florida and
349 byssate individuals were somewhat less common offshore of Alabama than offshore of Louisiana
350 and Florida.

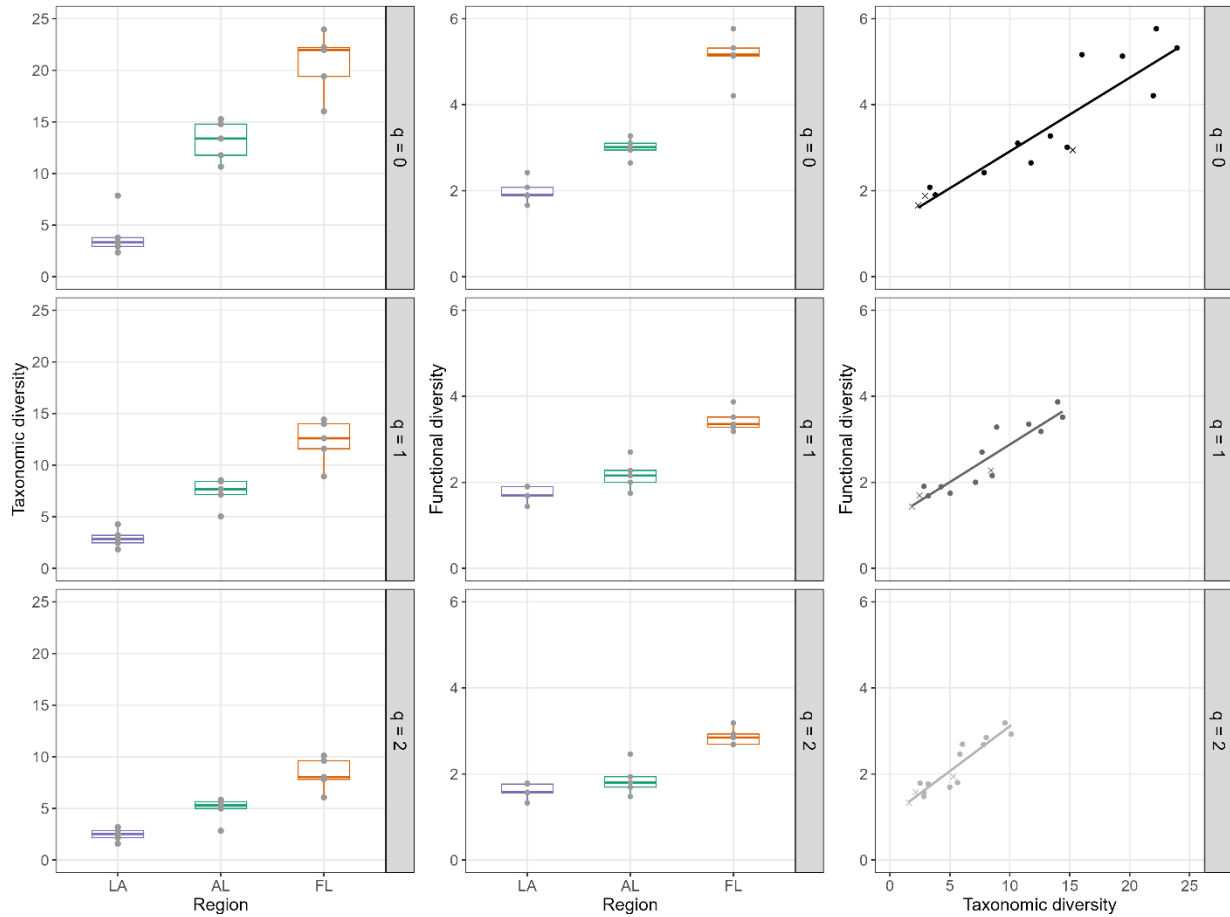


Fig. 2. Geographic trends in the taxonomic and functional alpha diversity of marine bivalves at 15 stations across the northern Gulf of Mexico, for rare ($q = 0$), common ($q = 1$), and highly abundant ($q = 2$) species and functional groups at a standardized sampling coverage of 90%. Bivalve taxonomic and functional alpha diversity are strongly positively correlated in the northern gulf. Solid lines are linear regression models for diversity orders $q = 0$, $q = 1$, and $q = 2$ at 12 stations with robust diversity estimates ($p < 0.01$ for each linear model determined using a bootstrap procedure); stations that were excluded from these models (see 3. *Results*) are indicated with an “X.” LA, Louisiana, AL, Alabama, FL, Florida.

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	Model with PC1 and PC2 as covariates		Model with only PC1 as covariate	
	$p < 0.05$	adj. R^2	$p < 0.05$	adj. R^2
TD_q0	PC1	0.87	PC1	0.84
TD_q1	PC1	0.78	PC1	0.75
TD_q2	PC1	0.68	PC1	0.66
FD_q0	PC1 + PC2	0.84	PC1	0.76
FD_q1	PC1	0.68	PC1	0.62
FD_q2	PC1	0.56	PC1	0.51

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Table 2. Linear models relating taxonomic (TD) and functional diversity (FD) to regional environmental conditions at 12 stations across the northern Gulf of Mexico. TD and FD were modeled using estimates for the diversity of rare ($q = 0$), common ($q = 1$), and highly abundant ($q = 2$) species and functional groups. Regional environmental conditions were modeled using PCA axis 1 and 2 scores based on ordination of all 15 stations as composite environmental variables; dissolved oxygen concentration, net primary productivity, and percent silt-clay contribute to variation along PC1, and sea surface temperature (mean and standard deviation) contribute to variation along PC2. PC1 scores were significant predictors of TD and FD at all q -values, whereas PC2 scores were only a significant additional predictor when modeling the diversity of rare functional groups. Overall, models that included PC2 explained relatively little additional variation over those in which PC1 was the only predictor.

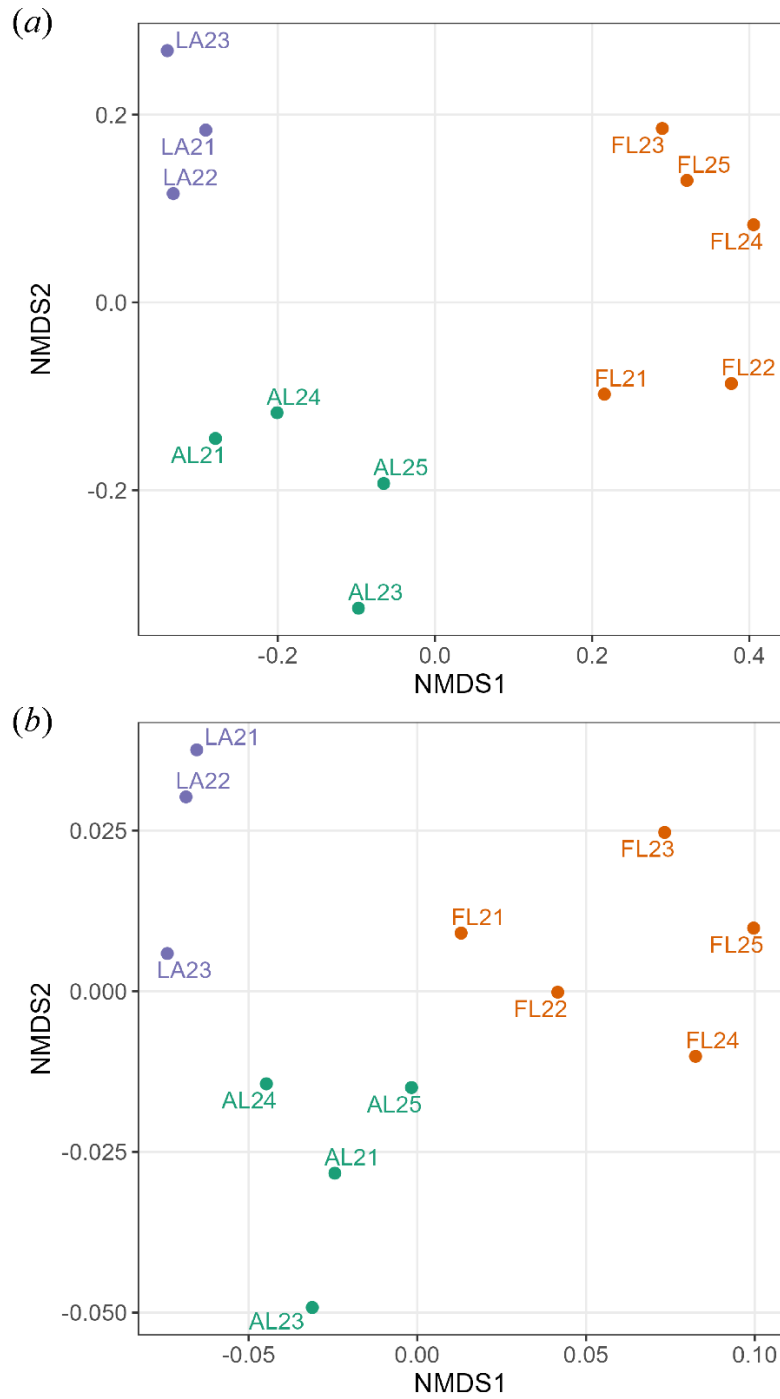


Fig. 3. nMDS ordination of (a) taxonomic and (b) functional composition at stations across the northern Gulf of Mexico, generated using Sørensen-type dissimilarities (diversity order $q = 0$ at a sampling coverage of 90%). LA, Louisiana, AL, Alabama, and FL, Florida.

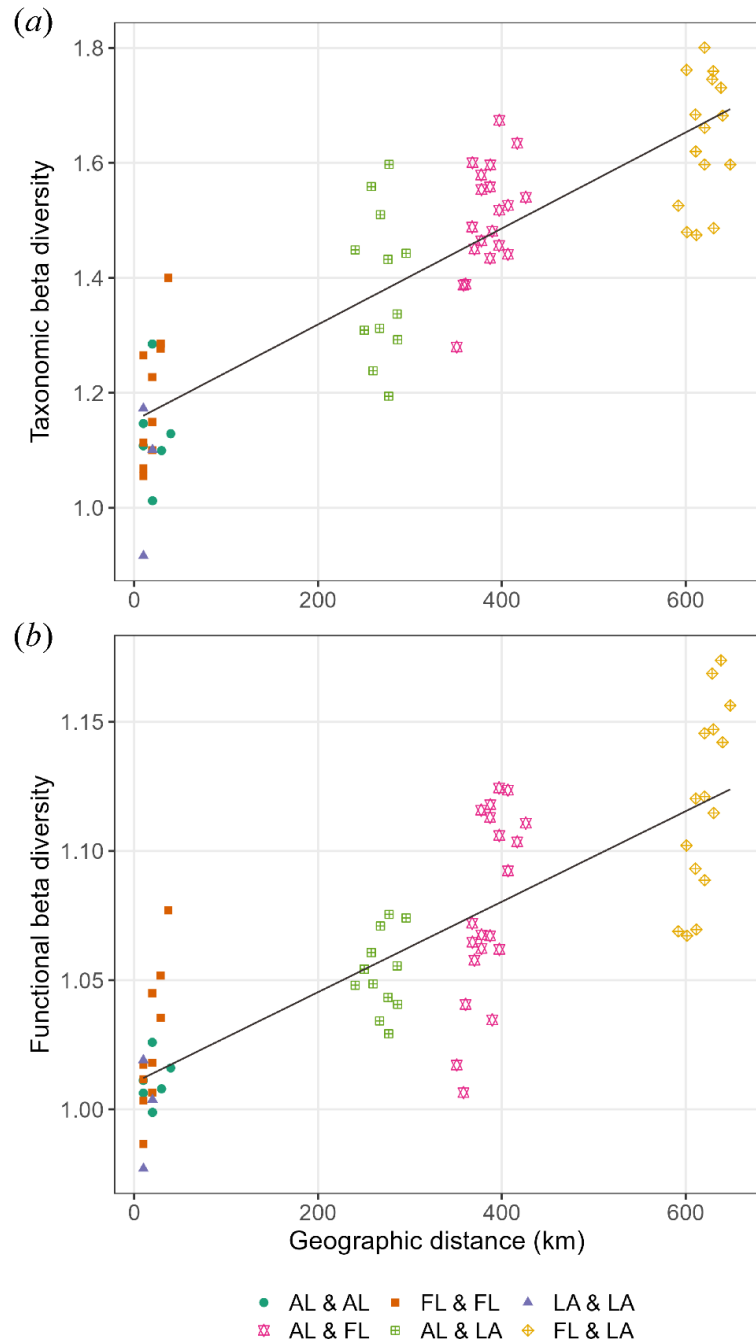


Fig. 4. (a) Taxonomic and (b) functional beta diversity vary with the geographic distance between stations. Beta diversity calculated using richness-based ($q = 0$) diversity estimates at a standardized sampling coverage of 90%. LA, Louisiana, AL, Alabama, and FL, Florida.

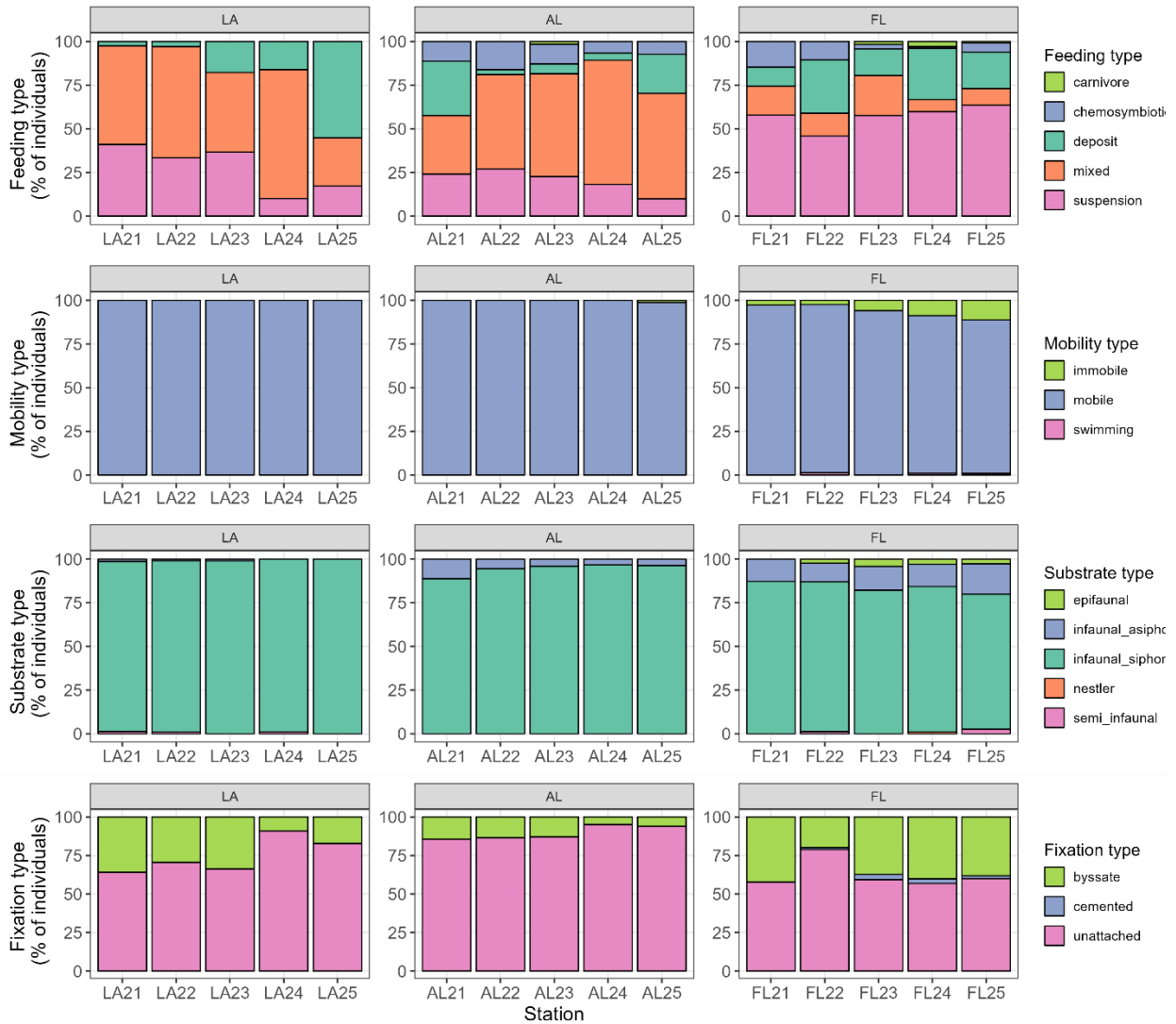


Fig. 5. Variation in bivalve categorical functional traits (rows) by region (columns) and station (individual bars) across the northern Gulf of Mexico. The relative abundance of each functional trait is plotted as the percentage of individuals with that trait that were sampled at each station. LA, Louisiana, AL, Alabama, and FL, Florida.

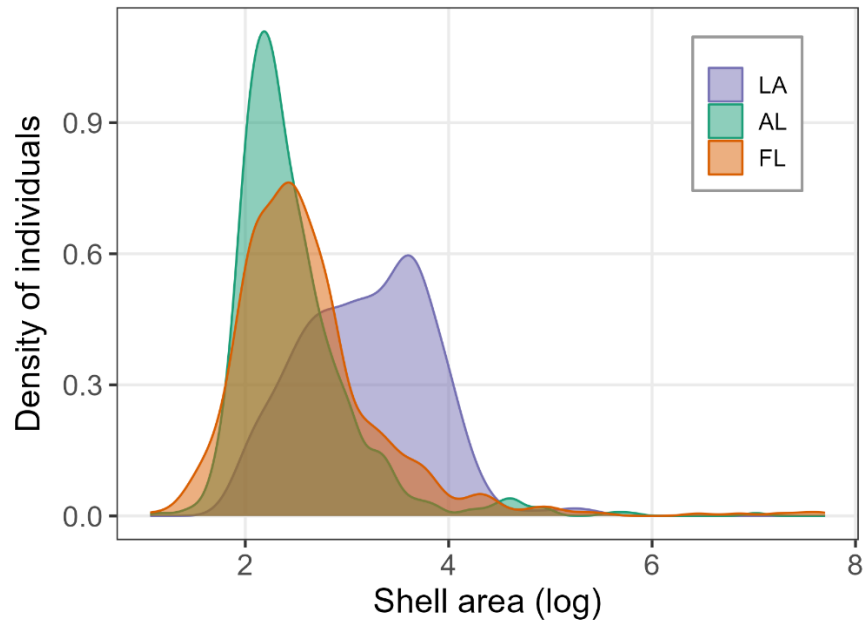


Fig. 6. Regional differences in body size for bivalves across the northern Gulf of Mexico. Individual-level body size distributions for each region are plotted using kernel density estimation. LA, Louisiana, AL, Alabama, and FL, Florida.

Individual body size also varied considerably among regions (Fig. 6). The median size of individuals offshore of Louisiana was significantly larger than in either coastal Alabama or Florida; $p < 0.05$ for all pairwise regional comparisons using Mann-Whitney U tests. Regional differences in body size reflect variation in size both within and among species (Fig. S9). Populations of relatively abundant species (Table S1) that were sampled in all three regions (e.g., *Ameritella versicolor*, *Foveamysia soror*, *Nuculana acuta*) tend to contain larger individuals offshore of Louisiana than offshore of either Alabama or Florida, though with considerable regional overlap (Fig. S9). Size differences among species sampled in only a single region also contribute to regional differences in median size (Fig. S9). For example, relatively larger bodied species such as *Lunarca ovalis* and *Agriopoma texasianum* in Louisiana, and *Noetia ponderosa* and *Eurytellina nitens* in Alabama, versus smaller bodied species like *Corbula dietziana* and *Semelina nukuloides* in Florida. The shapes of regional size frequency distributions also differed significantly; $p < 0.05$ for all pairwise regional comparisons using Kolmogorov-Smirnov tests. Size frequency distributions in Alabama and Florida are leptokurtic (i.e., more concentrated around the median), whereas the size frequency distribution in coastal Louisiana is platykurtic; kurtosis values of 10.7, 10.6, and -0.1 respectively for the three regions. Although individuals in Alabama and Florida were smaller on average than in Louisiana, a greater range of body sizes, and specifically larger body sizes, was observed in these two regions (Figs 6, S8, & S9). Larger-sized individuals in the tails of the size frequency distributions in Alabama and Florida are due to regional differences in species composition; e.g., large individuals of *Arca zebra* and *Noetia ponderosa* that were only sampled offshore of Florida and Alabama, respectively. To evaluate whether observed geographic differences in body size were associated with changes in population density (i.e., an abundance of small individuals versus few large individuals), we compared the median number of live individuals per benthic sample in each region using Mann-Whitney U tests (Fig. S1), and found no significant differences; $p > 0.05$ for all pairwise regional comparisons.

4. DISCUSSION

Bivalve species alpha diversity in the northern Gulf of Mexico declines with increasing primary productivity and decreasing dissolved oxygen. We observed broadly similar biogeographic patterns for rare ($q = 0$), common ($q = 1$), and highly abundant ($q = 2$) species,

with lowest diversities proximal to the Mississippi River delta in coastal Louisiana, a region that includes one of the world's largest dead zones (Fig 2) (Rabalais et al. 2007, Levin et al. 2009). Coastal environments that are characterized by higher dissolved oxygen concentrations (i.e., Alabama and Florida) supported a greater diversity of species, and more rare species in particular, than settings in which hypoxia occurs annually (i.e., Louisiana) (Fig. 2). Our results are congruent with previous studies of bathymetric diversity gradients and oxygen minimum zones in other regions of the global ocean (Levin et al. 2009, Sperling et al. 2016, Fajardo et al. 2018, Gallo et al. 2020, Bon et al. 2021), which have documented reduced richness of benthic and demersal species under lower oxygen conditions.

Strong covariation between primary productivity, dissolved oxygen, and seafloor sediment properties is typical in the coastal zone, and limits attempts to statistically estimate the unique effects of different environmental drivers at the regional-scale using multivariate models. Two observations, however, highlight the primary roles of eutrophication and deoxygenation in structuring observed diversity gradients on the continental shelf in the northern gulf. First, bivalve taxonomic and functional diversities decline significantly from Florida to Alabama as primary productivity increases, whereas seafloor sediment properties do not differ appreciably between these two regions (Fig. 2, Table 1). Dissolved oxygen also does not differ significantly between Alabama and Florida in the gridded environmental data (Table 1), however, previous studies have documented episodic hypoxia offshore of Alabama whereas hypoxia has not been historically observed on the north Florida shelf (Rabalais 1992, Brunner et al. 2006, Santema et al. 2015, Dzwonkowski et al. 2018). Second, of all the environmental variables considered, primary productivity has the strongest correlation with taxonomic and functional diversities across all q-values (Fig. S2). Although low diversities offshore of Louisiana may reflect the combination of high productivity, fine-grained sediment, and low dissolved oxygen that is typical of continental shelf habitats adjacent to large watersheds, diversity variation across the northern gulf as a whole is best explained by regional differences in productivity and dissolved oxygen.

Habitat heterogeneity could also contribute to these taxonomic diversity gradients in the northern Gulf, if heterogeneity is greater in less eutrophic environments on the continental shelf where terrestrial inputs of sediment, freshwater, and nutrients are reduced. Our results are qualitatively consistent with this prediction, with greater beta diversity among stations in Florida

than in either Alabama or Louisiana, though with considerable overlap among regions (Figs 3, 4, & S7).

Taken together, analyses of taxonomic alpha diversity along oxygen gradients highlight the critical role of physiology in structuring present-day biogeographical patterns, with the implication that projected declines in dissolved oxygen will reduce bivalve species richness. Species loss may be most pronounced in continental shelf environments adjacent to large terrestrial watersheds, where the combined effects of anthropogenic nutrient loading and ocean warming coincide (Deutsch et al. 2024).

Regarding functional responses to hypoxia, there is a gap between integrative studies of taxonomic and functional diversity conducted at relatively fine spatiotemporal scales (e.g., Baustian & Rabalais 2009, Rabalais & Baustian 2020) and broader space-for-time studies which have tended to focus on taxonomic diversity but not associated changes in functional diversity and trait composition (e.g., Sperling et al. 2016, though see Fajardo et al. 2018 and Bon et al. 2021). We addressed this gap by investigating gradients in bivalve species and functional diversity across the northern Gulf of Mexico and found that these two biodiversity measures were positively correlated, consistent with previous work on global diversity gradients in marine bivalves (Berke et al. 2014). Bivalve species and functional alpha diversity in the northern gulf also both covaried with regional environmental conditions. Bivalve communities in eutrophic environments that experience episodic hypoxia were characterized by an abundance of shallow infaunal deposit and mixed feeders, in contrast with less eutrophic, normoxic environments in which infaunal and epifaunal suspension feeding bivalves were most abundant and a greater diversity of feeding types was observed (Figs 5 & 1c). These functional differences, however, may be even more pronounced than reported here. There are limited data on intraspecific variation in bivalve feeding type; for some mixed feeders (e.g., tellinids such as *Ameritella versicolor*), experiments have documented individual shifts between suspension and detritus feeding (Volkenborn et al. 2012, Gadeken & Dorgan 2023), whereas for others (e.g., nuculanids such as *Nuculana acuta*) less is known, and they have been classified as obligate deposit feeders by some (e.g., Briggs et al. 2015) and capable of mixed feeding by others (Mikkelsen & Bieler 2008). The functional transition in bivalve feeding types that we documented across the northern gulf is consistent with other macrobenthic studies in the region that have documented an abundance of shallow infaunal and surficial deposit feeding polychaete worms offshore of

Louisiana (Baustian & Rabalais 2009, Rabalais & Baustian 2020) and, more broadly, with transitions from suspension feeding to deposit feeding with increasing hypoxia elsewhere in the global ocean (Levin et al. 2009). The congruent functional responses of different macrobenthic groups to increased primary production and decreased dissolved oxygen (this study, and citations therein), in combination with recent work highlighting the potential for bivalves to serve as taxonomic surrogates for other macrobenthos (Tyler & Kowalewski 2017, Kokesh et al. 2022), indicate that species and functional diversity vary predictably with primary production and dissolved oxygen in continental shelf ecosystems in the northern gulf and other locations around the world.

The body sizes of macrobenthos are known to affect a variety of ecosystem services (Norkko et al. 2013, Lockwood & Mann 2019). Filtration rates and infaunal burrowing depths both positively scale with body size in marine bivalves (Stanley 1970, Lockwood & Mann 2019), with implications for water quality and carbon cycling in the coastal zone (Vaughn & Hoellein 2018). Larger bodied individuals are also more frequently subject to exploitation (Lockwood & Mann 2019, Huang et al. 2023), and are more vulnerable to ocean deoxygenation due to their higher metabolic rates (Woods et al. 2022, Deutsch et al. 2024). Regional to global studies that have considered environmental correlates of body size rarely account for intraspecific variation in size. Here we have analyzed a dataset of bivalve body size measurements for approximately 1500 individuals across the northern gulf and documented an increase in median size in the productive, lower oxygen environments that occur today in coastal Louisiana. These results reflect both intra- and interspecific size differences (Fig. S9), and are consistent with a previous study that examined body size variation in a subset of bivalve genera across the northern gulf using Holocene-age shell samples (Calderaro et al. 2024). Intraspecific increases in bivalve size in eutrophic environments have also been documented in other regions, including *Macoma balthica* from the Wadden Sea (Beukema et al. 2014) and *Varicorbula gibba* from the Adriatic Sea (Tomašových et al. 2020). In the Adriatic, increasing *V. gibba* size and abundance during the 20th century (Tomašových et al. 2018) coincided with increasing seasonal hypoxia, as evident by declines in bioturbation depth (Tomašových et al. 2021). Larger sizes in more eutrophic environments is consistent with some previous studies that have documented a positive relationship between bivalve size and growth rate and primary productivity within and among species (Kirby & Miller 2005, Carmichael et al. 2012, McClain et al. 2012, though see Berke et

al. 2013, Saulsbury et al. 2019), but runs counter to the expected reduction in body size that may occur as the severity of eutrophication increases and dissolved oxygen concentrations correspondingly decline (Pearson & Rosenberg 1978, Levin et al. 2009, Clark et al. 2013, Deutsch et al. 2024). Differences among trophic levels in aerobic scope provide a potential explanation for the differences in body size that we documented among regions. Due to their higher metabolic rates, predators may be excluded from lower-oxygen aquatic environments before their prey (Riedel et al. 2012, Sperling et al. 2013), and consequently settings that experience hypoxia may serve as a predation refuge for basal consumers such as marine bivalves (Altieri 2008, Calderaro et al. 2024). Differences in aerobic scope among bivalves may also contribute, with increased mortality and/or reduced recruitment among certain species as a result of declining oxygen concentrations resulting in competitive release of hypoxia-tolerant species and thereby their enhanced growth in oxygen-limited settings (Tomašových et al. 2020). As a result, the increase in median bivalve size we document here in eutrophic and hypoxic environments in the northern gulf may reflect greater longevity and/or faster growth of hypoxia-tolerant species due to a combination of reduced predation pressure, reduced competition, and greater food availability (Kirby & Miller 2005, Altieri 2008, Tomašových et al. 2020) (). Indirect support for the role of enhanced food supply in structuring regional differences in body size comes from our comparison of population densities across the northern gulf. Increases in median body size were not associated with declines in median population density in Louisiana or Alabama (Fig. S1), suggesting that nutrient enrichment may relax tradeoffs between individual growth and population size for some species. Although median body size was larger in the more eutrophic, lower oxygen environments offshore of Louisiana, the largest individuals in that region were smaller than those that comprise the tail of the size frequency distributions observed in Alabama and Florida (Fig. 6). This truncation of the larger-bodied end of the size frequency distribution in Louisiana is consistent with oxygen concentration limiting the maximum body size of basal consumers in that region, and is underlain by interspecific changes in community composition, specifically the absence of larger-bodied, infaunal and semi-infaunal suspension feeders, such as *Megapitaria maculata* and *Arca zebra*, in these more nutrient-rich environments. Shifts in bivalve feeding type and body size on the continental shelf going from Florida to Louisiana may signal a marked reduction in filtration rates and burrowing depth, with

corresponding impacts on rates of carbon cycling, filtration of the water column, and aeration of the seafloor.

Rising temperatures and decreasing oxygen concentrations synergistically increase the vulnerabilities of marine animals to anthropogenic environmental change (Woods et al. 2022, Deutsch et al. 2024). Warming waters speed up metabolism yet hold less oxygen which places aquatic organisms in a double bind. These covarying stressors coincide with some of the largest biotic crises in Earth's history (Penn et al. 2018, Finnegan et al. 2024), and with increasing records of marine mass mortality in recent decades (Breitburg et al. 2018, Deutsch et al. 2024). Sea surface temperatures have increased $\sim 1.0^{\circ}\text{C}$ since 1970 in the Gulf of Mexico, a rate that is approximately double that of the global ocean (Wang et al. 2023). Gridded climatological data, however, show relatively minimal differences in mean summer SST among regions of the northern gulf (Table 1). Mean summer SSTs are slightly warmer offshore of Florida and Louisiana relative to Alabama (Fig. 1c), however, these differences are modest compared to seasonal variation in each region. Consequently, the limited range of mean summer SST observed today across the northern gulf plays relatively little role in observed biogeographical patterns. Coincident changes over time in oxygen concentrations due to high nutrient discharge from the Mississippi and warming have likely contributed to the low taxonomic and functional diversities that we observed in coastal Louisiana, however testing this hypothesis will require biological and environmental timeseries that extend beyond observational records. These timeseries can be derived from studying the biomineralized tissues of bivalve mollusks and other macrobenthos which can persist for decades to millennia in seafloor sediments (Finnegan et al. 2024).

Anthropogenic nutrient loading and climate change are contributing to ocean deoxygenation globally. Here we provide baseline data on the present-day species and functional alpha and beta diversity of marine bivalve communities across the northern Gulf of Mexico. We document declines in multiple measures of biodiversity with increasing eutrophication and hypoxia. Space-for-time approaches, like those employed here, can help us better understand the biotic implications of current and future environmental change and can also serve as a basis for hindcasting historical conditions before the onset of anthropogenic eutrophication and climate change. We predict that macrobenthic communities that occur today in eutrophic and hypoxic coastal environments (e.g., Louisiana and, to a lesser extent, Alabama) were more taxonomically

and functionally diverse before the onset of anthropogenic nutrient loading, and would have contained a greater abundance of suspension feeders. In contrast, normoxic coastal environments where hypoxia has not occurred historically (e.g., Florida) would have experienced less pronounced change in species and functional diversity over time. Differing regional environmental histories in the northern gulf and elsewhere may be reflected in greater temporal beta diversity offshore larger, and more populated, watersheds like the Mississippi River (LA) and more limited spatial beta diversity along these coastlines (e.g., LA vs. FL) before anthropogenic eutrophication.

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Electronic Supplementary Material for

Harnik et al. Declining bivalve species and functional diversity along a coastal eutrophication-deoxygenation gradient in the northern Gulf of Mexico

Table S1. The relative abundance of the five most common species in each sampled region of the northern gulf. Species relative abundance was calculated using the pooled numerical abundance data for all sampling stations in each region. LA, Louisiana, AL, Alabama, and FL, Florida.

LA		AL		FL	
Species	Relative abundance	Species	Relative abundance	Species	Relative abundance
<i>Nuculana concentrica</i>	0.37	<i>Nuculana acuta</i>	0.33	<i>Caryocorbula dietziana</i>	0.19
<i>Caryocorbula swiftiana</i>	0.25	<i>Abra lioica</i>	0.15	<i>Semelina nukuloides</i>	0.15
<i>Ameritella versicolor</i>	0.17	<i>Ameritella versicolor</i>	0.13	<i>Varicorbula limatula</i>	0.12
<i>Abra aequalis</i>	0.16	<i>Caryocorbula swiftiana</i>	0.07	<i>Gouldia cerina</i>	0.07
<i>Foveamysia soror</i>	0.01	<i>Parvilucina crenella</i>	0.05	<i>Nucula proxima</i>	0.07
Cumulative abundance of top 5 ranks	0.96		0.73		0.6

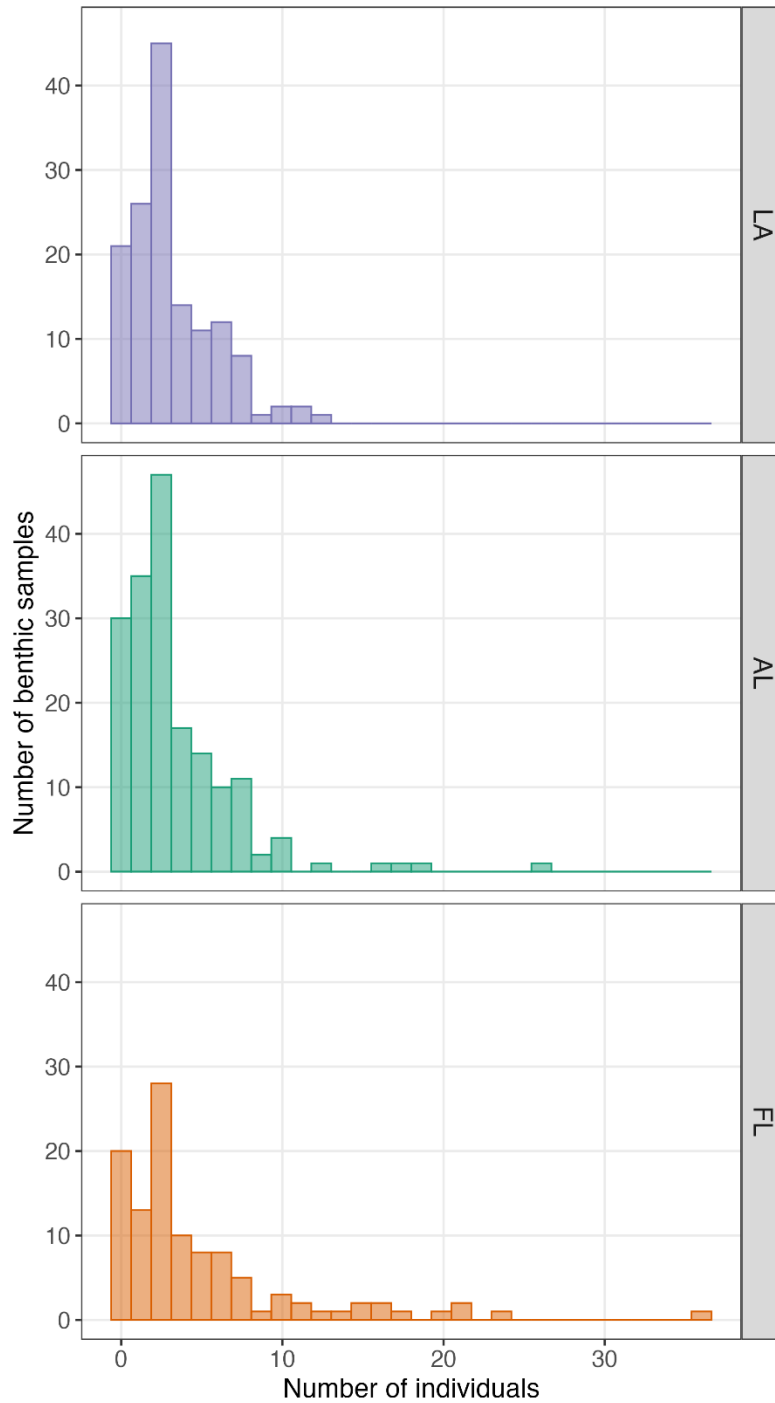


Fig. S1. The number of live individuals collected per benthic sample in each region of the northern Gulf of Mexico. LA, Louisiana, AL, Alabama, and FL, Florida.

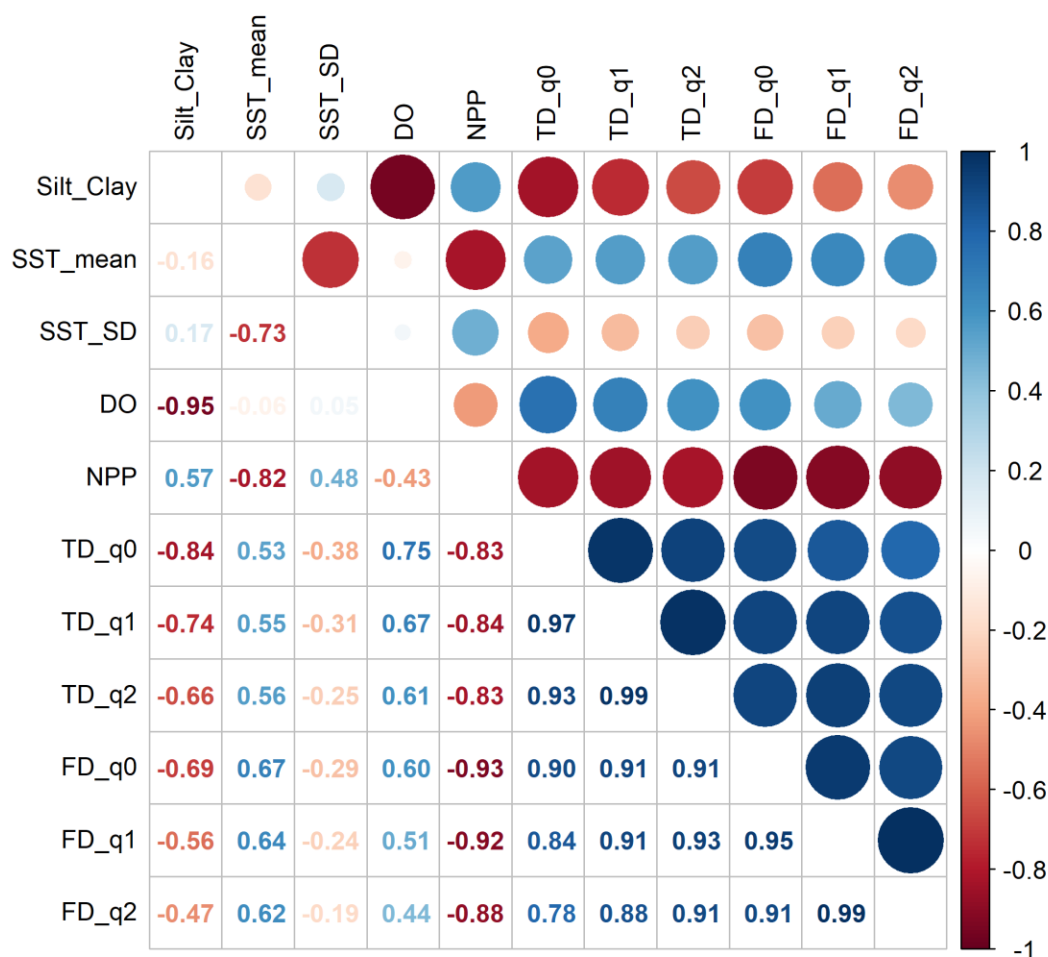


Fig. S2. Correlation matrix between environmental variables and taxonomic (TD) and functional (FD) diversity for different diversity orders at 12 sampling stations in the northern Gulf of Mexico; three stations (LA24, LA25, and AL22) were excluded from these analyses because their data were too sparse to accurately estimate sample coverage (see 3. Results). Correlation coefficients calculated using Pearson correlation. Diversity order $q = 0$ is the effective number of rare species or functional groups; $q = 1$ is the effective number of common species or functional groups; $q = 2$ is the effective number of highly abundant species or functional groups. Negative correlations are in red, positive correlations in blue, and the strength of the correlation given by the coefficient value and by the circle size.

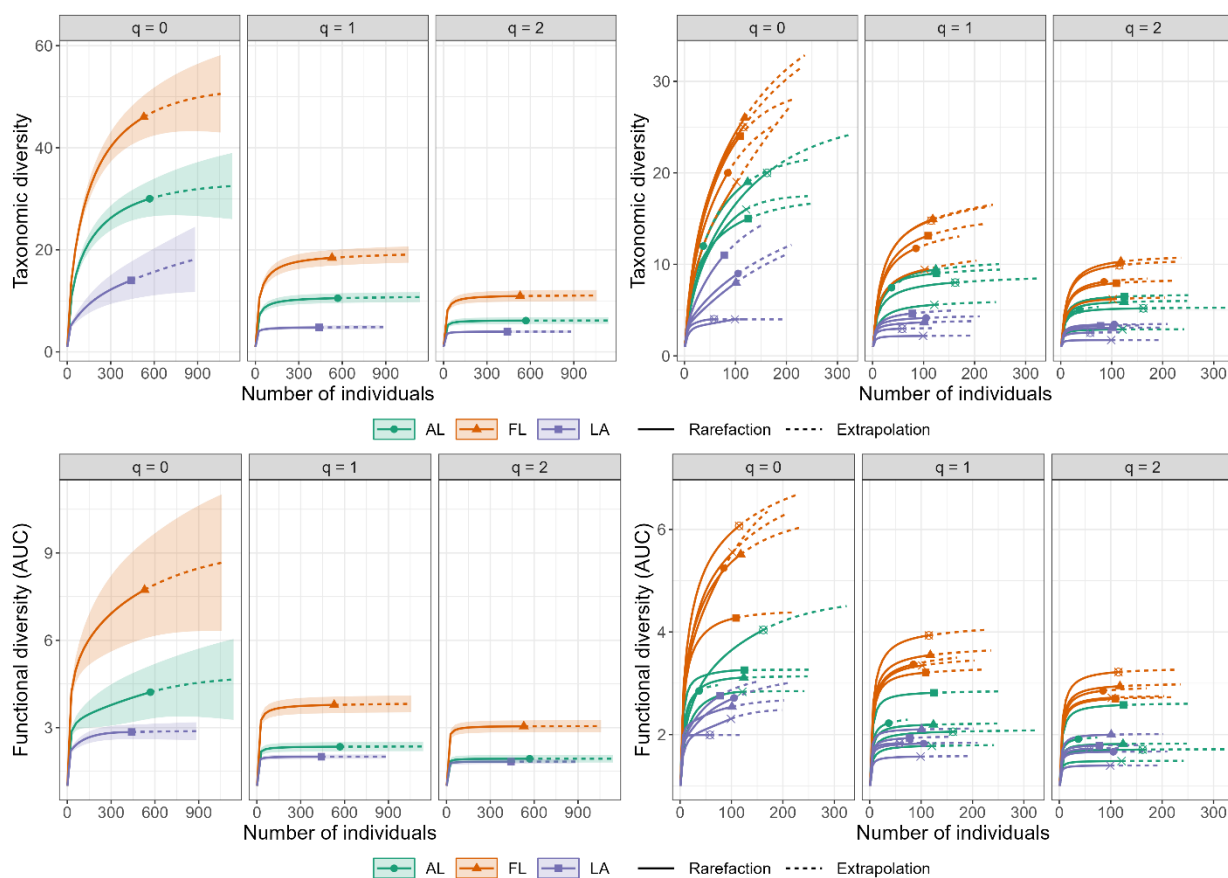


Fig. S3. Size-based (i.e., number of individuals) sampling curves for taxonomic (TD) and functional (FD) diversity for regions (left columns) and stations (right columns) for rare ($q = 0$), common ($q = 1$), and highly abundant ($q = 2$) species (top row) and functional groups (bottom row). Size-based curves indicate that all samples are incomplete due to undetected rare species. Size-based curves were unstable for rare species and functional groups, and stable for common and highly abundant species and functional groups. Consequently, in all analyses we compared taxonomic and functional diversities at a standardized sampling coverage of 90%. LA, Louisiana, AL, Alabama, and FL, Florida.

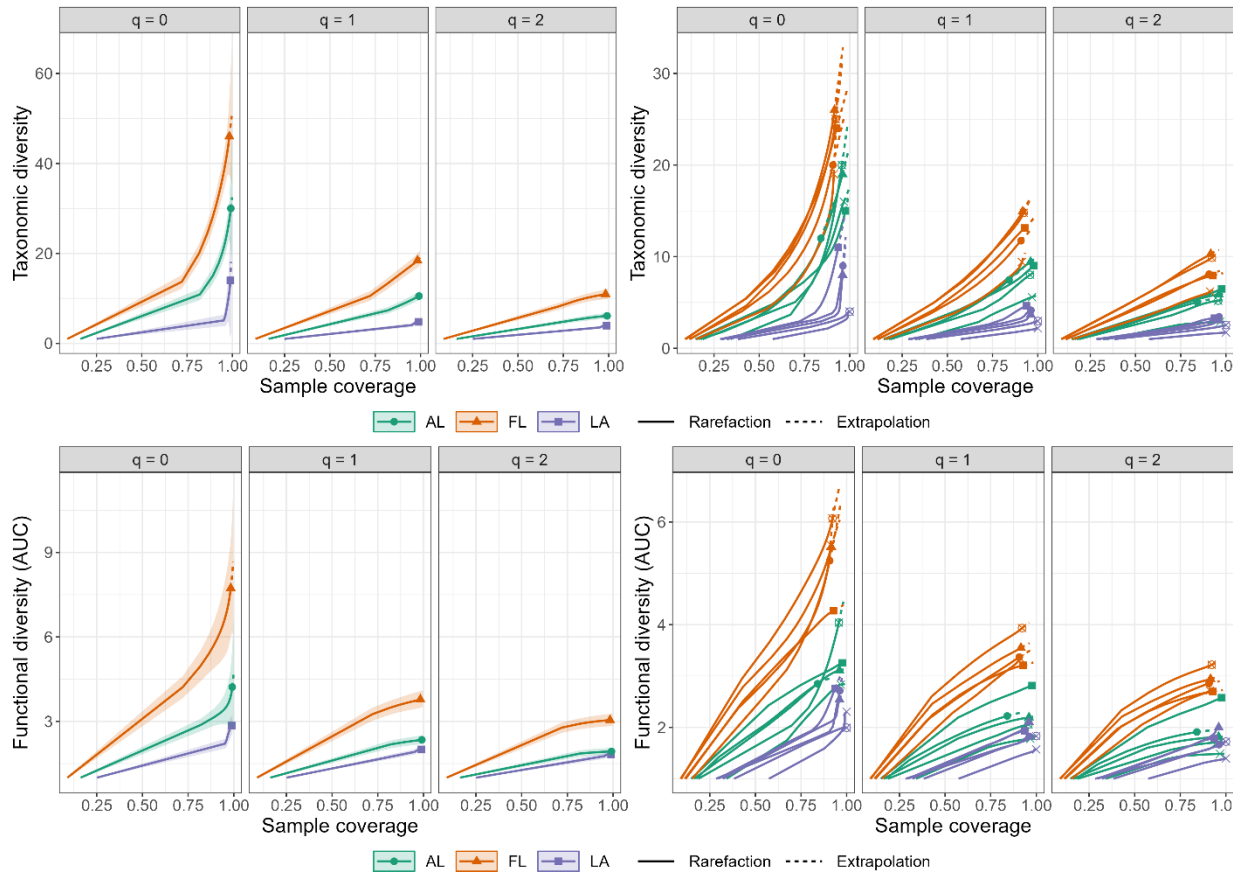


Fig. S4. Coverage-based sampling curves for taxonomic (TD) and functional (FD) diversity for regions (left columns) and stations (right columns) for rare ($q = 0$), common ($q = 1$), and highly abundant ($q = 2$) species (top row) and functional groups (bottom row). In all analyses, we compared station-level taxonomic and functional diversities at a standardized sampling coverage of 90%. LA, Louisiana, AL, Alabama, and FL, Florida.

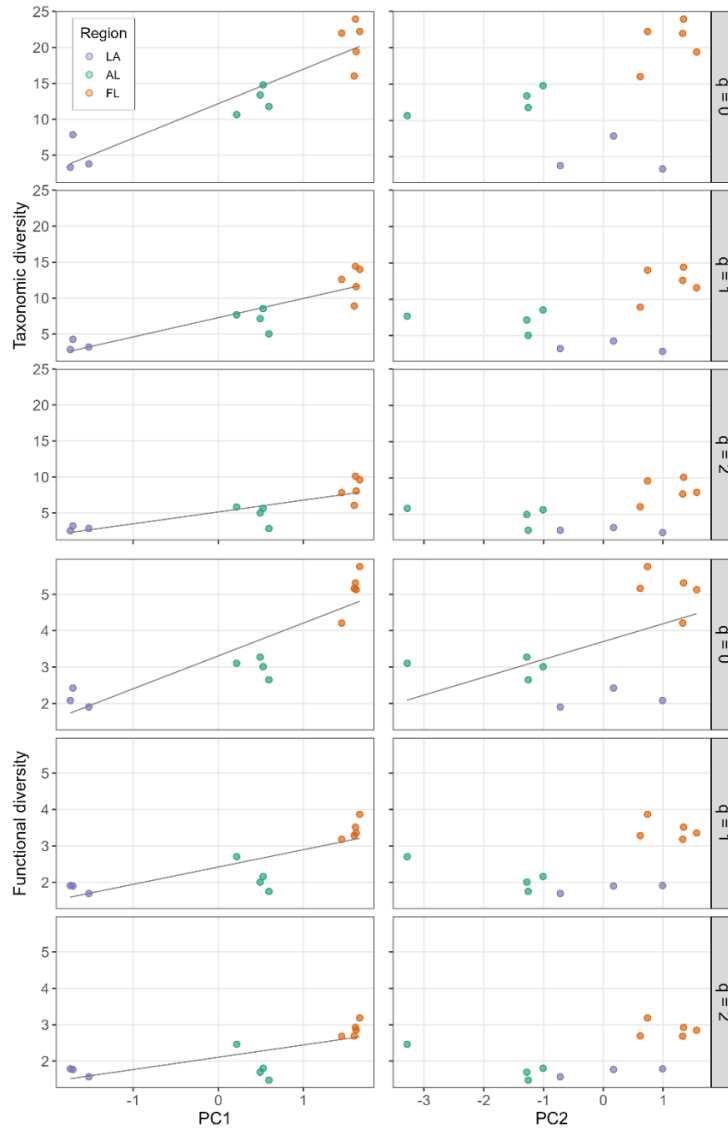


Fig. S5. Relationships between taxonomic (TD) and functional diversity (FD) and regional environmental conditions across the northern Gulf of Mexico. TD and FD were modeled using estimates for the diversity of rare ($q = 0$), common ($q = 1$), and highly abundant ($q = 2$) species and functional groups (Fig 2). Regional environmental conditions were modeled using PCA axis 1 and 2 scores as composite environmental variables (Fig. 1c); dissolved oxygen concentration, net primary productivity, and percent silt-clay contribute to variation along PC1, and sea surface temperature (mean and standard deviation) contribute to variation along PC2. Trendlines are included for statistically significant linear models (Table 2). LA, Louisiana, AL, Alabama, and FL, Florida.

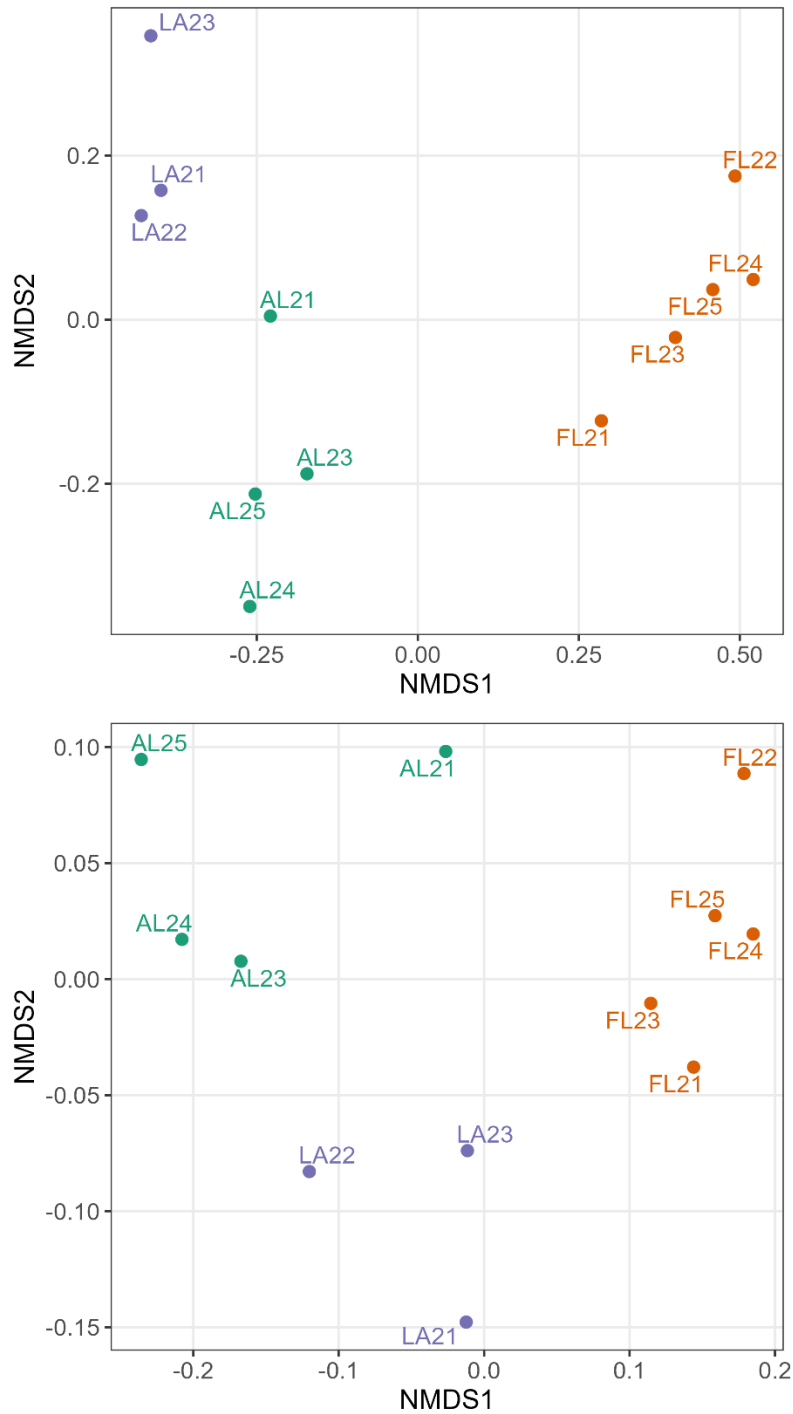


Fig. S6. nMDS ordination of (a) taxonomic and (b) functional composition at stations across the northern Gulf of Mexico, generated using Sørensen-type dissimilarities (diversity order $q = 2$ at a sampling coverage of 90%). LA, Louisiana, AL, Alabama, and FL, Florida.

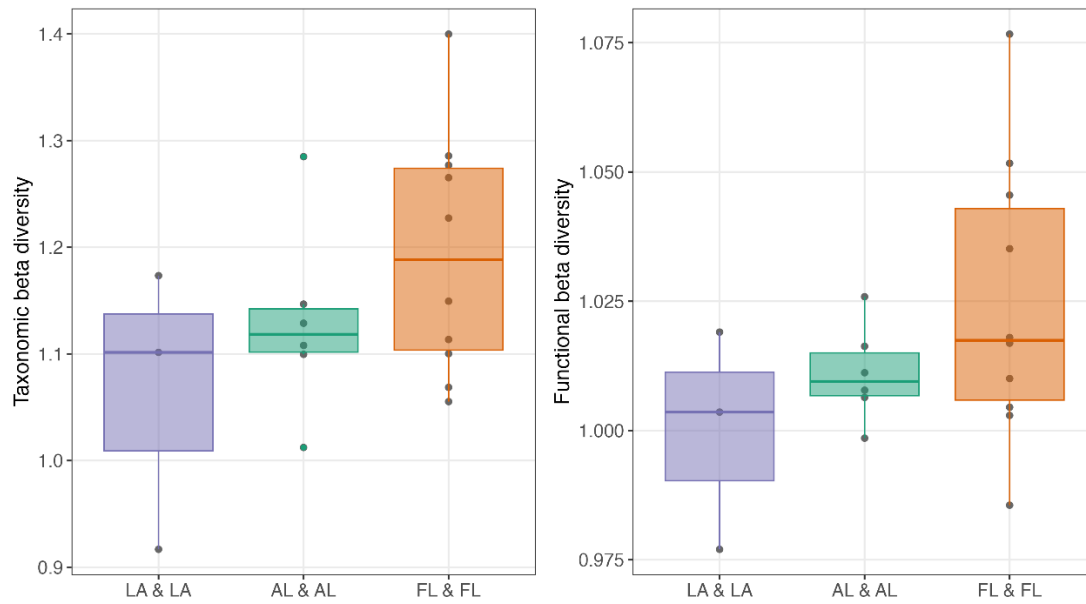


Fig. S7. Taxonomic and functional dissimilarities between sampling stations located within each region of the northern gulf. LA, Louisiana, AL, Alabama, and FL, Florida.

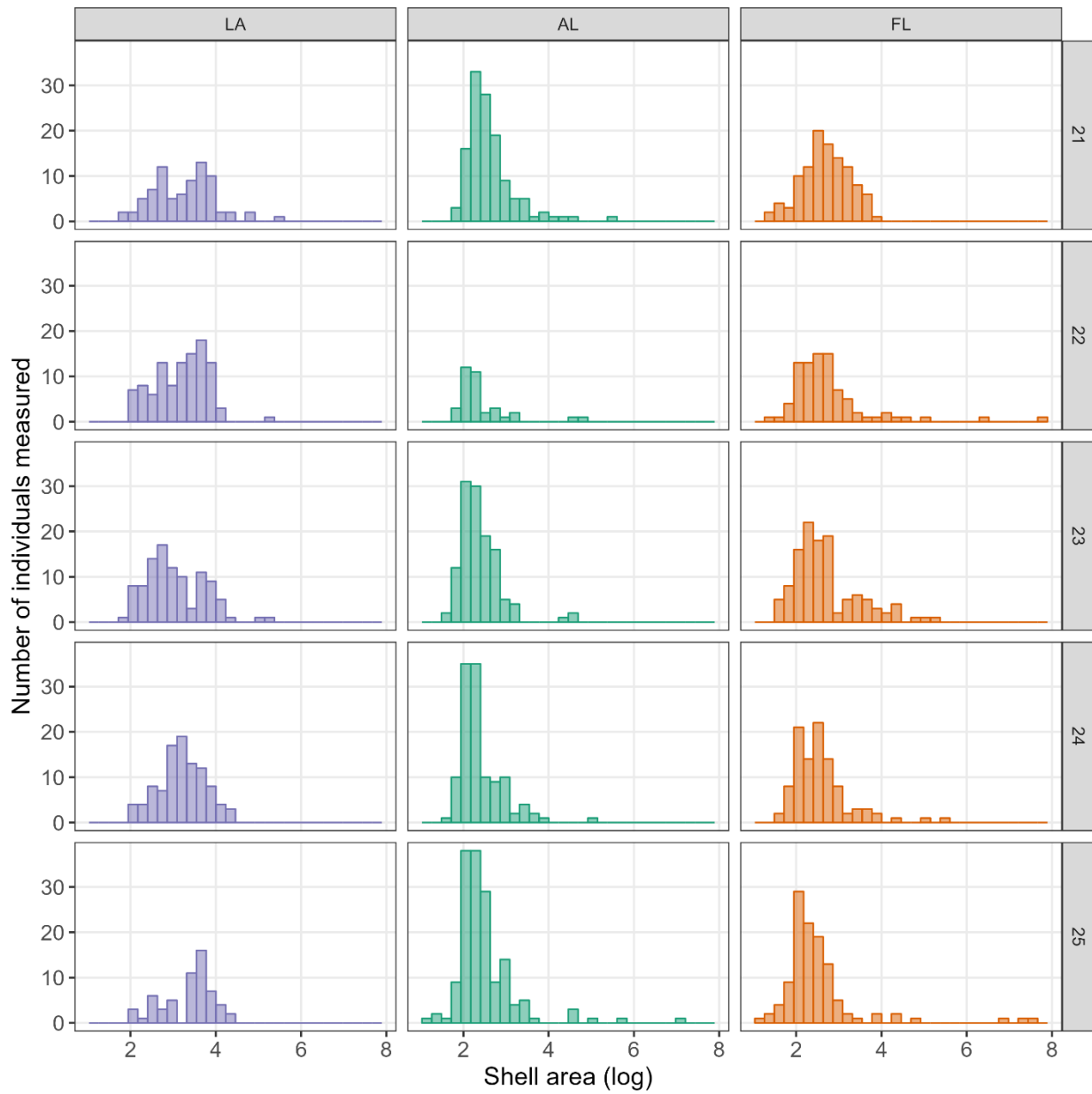


Fig. S8. Variation in bivalve body size by region (columns) and station (rows) across the northern Gulf of Mexico. Stations in each region are numbered from west to east, 21 through 25. LA, Louisiana, AL, Alabama, and FL, Florida.

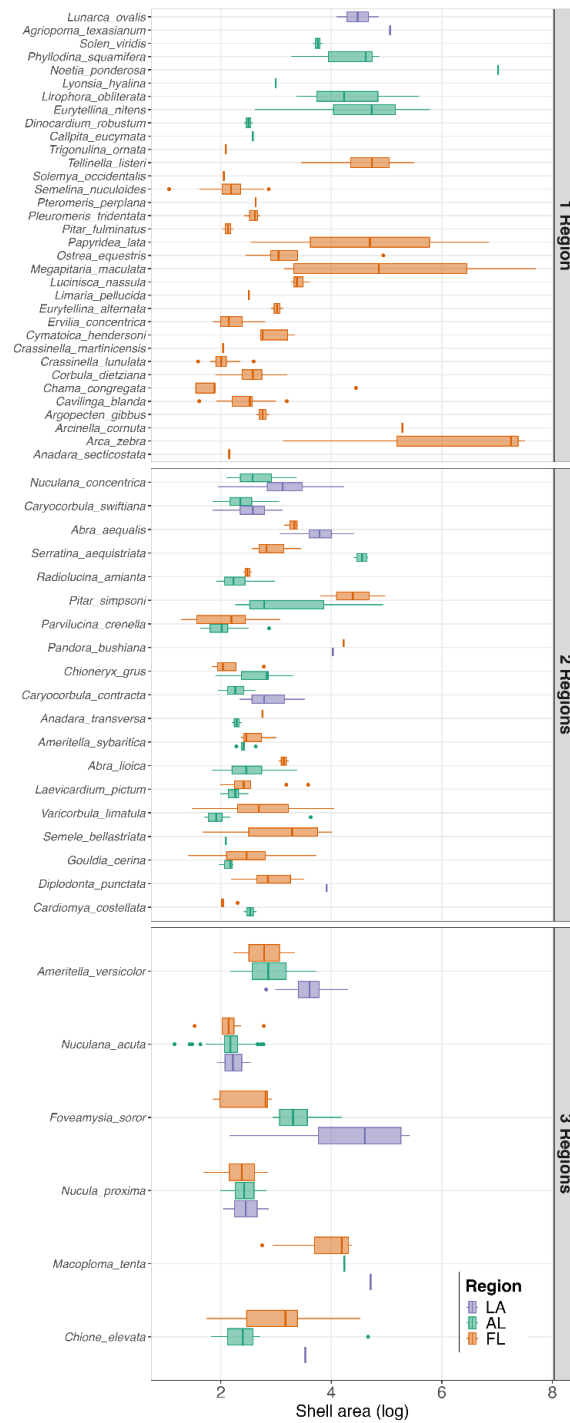


Fig. S9. Variation in individual body size for species that were sampled in one, two, or three regions of the northern gulf. LA, Louisiana, AL, Alabama, and FL, Florida.