ABSTRACT

MOORE, RHIANNON BENNETT. Distribution of Planktonic Foraminifera Along the Northwest Atlantic Margin. (Under the direction of Dr. Catherine V. Davis).

Planktonic foraminifera are single-celled zooplankton that are important contributors to carbonate flux to the deep ocean; their calcium carbonate shells and sensitivity to environmental conditions make them useful proxies for reconstructing past climate. However, changing marine carbonate chemistry threatens to negatively impact foraminifera by inhibiting calcification, while rising sea surface temperatures are likely to shift species ranges. This study documents current foraminifera species abundance and diversity in the western Atlantic using plankton tows from the 2022 NOAA East Coast Ocean Acidification cruise. Samples were collected at 59 stations spanning the entire U.S. east coast from the Gulf of Maine (45.66º N) to Florida (26.98º N). Sea surface temperatures ranged from 12.98 ºC to 30.50 ºC, and pH ranged from 7.81 to 8.14.

Findings indicate a north-south gradient in species composition resulting in two distinct ecological regions. The Gulf of Maine and Scotian Shelf (> 42º N) are characterized by high abundance of *Neogloboquadrina incompta* along with *Turborotalita quinqueloba* and the polar species *Neogloboquadrina pachyderma*. South of Cape Cod, the Mid-Atlantic Bight and South Atlantic Bight are overwhelmingly dominated by the tropical species *Globeriginoides ruber ruber* and *Globeriginoides ruber albus*. No single environmental driver explained the overall assemblage size or diversity, though abundance of multiple species is correlated with sea surface temperature and dissolved inorganic carbon. Compared to previous studies in the region, we note a northward assemblage shift that is potentially related to changes in Gulf Stream dynamics or an increase in SST over the past 5+ decades. These latitudinal changes in assemblage composition suggest a poleward migration, highlighting the way that changes in ocean conditions have impacted and will continue to impact these important calcifying organisms.

Distribution of Planktonic Foraminifera Along the Northwest Atlantic Margin

by
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____

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DEDICATION

For my family: thank you for being my biggest cheerleaders, for being as enthusiastic to hear about my research as I am to talk about it, and for always answering when I asked, “why?”

BIOGRAPHY

Rhiannon was born and raised in California, where she first fell in love with the ocean at the Monterey Bay Aquarium. Her first foray into scientific research was in pre-school, when she was convinced that she had found zooplankton in a puddle in the parking lot. She attended Emory University for undergraduate study, majoring in biology and political science, and took on her first real research project in the environmental science department, where she assessed the potential phytoremediation capability of non-native aquatic plants. As an undergraduate, she worked on projects involving organisms ranging from ticks and clams to zooplankton. She came to North Carolina State University in 2023, joining the Past and Present Climate Lab to continue her passion for zooplankton and to research planktonic foraminifera. In her free time, Rhiannon enjoys reading, writing, and spending time in nature.

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1. INTRODUCTION

Background

The Northwest Atlantic is an ecologically diverse and economically critical region, shaped by large environmental gradients and complex oceanographic influences. Strong contrasts in temperature, salinity, and nutrient availability arise from the interplay of freshwater outflows, the Gulf Stream, and the Labrador Current, creating habitats that support commercially valuable fisheries and complex marine ecosystems. The region is important for the U.S. fisheries economy, bringing in over $2 billion and supporting over 530,000 jobs as of 2022 (*Fisheries Economics of the United States 2022*, 2024). Understanding changes to environmental conditions is therefore critical for protecting this economically vital area. As sea surface temperatures rise and the oceans continue to acidify, it is increasingly important to draw on records from shelf and slope environments, which are central in reconstructing past variability in Gulf Stream dynamics and regional carbon cycling that can put observed changes into context (Chen et al., 2020; Doney et al., 2009; Loder & Wang, 2015; Lynch-Stieglitz et al., 1999; Lynch-Stieglitz et al., 2024; Rasmussen & Thomsen, 2012; Wharton et al., 2024). Marine microfossils and the organisms that form them play a key role in allowing us to understand how this dynamic region has been changing and may continue to change in the future. Among these, planktonic foraminifera have been particularly important as tracers of past water mass movement through oxygen isotope chemistry (Lynch-Stieglitz et al., 1999; Matsumoto & Lynch-Stieglitz, 2003; Wharton et al., 2024). However, modern surveys of planktonic foraminifera along the northwest Atlantic margin are sparse, leaving a gap in our ability to assess both present-day population drivers and long-term environmental change.

Foraminifera are a useful proxy for extending the study of physical and chemical conditions in the upper water column beyond observational records. Their calcium carbonate shells (‘tests’) preserve well in many marine sediments, providing a rich record that can be used to reconstruct past ocean conditions (Katz et al., 2010; Kucera, 2007). Individual species have distinct environmental niches, and both species distribution and test geochemistry can be used to understand ocean ecology and diversity across multiple timescales (Durazzi, 1981; Emiliani, 1954; Ottens & Nederbragt, 1992; Ravelo & Fairbanks, 1992; Tolderlund & Bé, 1971). For example, species of foraminifera with well-constrained niches can be useful proxies for the location of those niches, such as oxygen minimum zones, thermoclines, and the chlorophyll maximum, through time (Davis et al., 2021; Feldmeijer et al., 2015; Ganssen & Kroon, 2000).

Understanding the ecology of modern planktonic foraminifera also has broader implications for ecosystem dynamics and for the marine carbon cycle. Though small, foraminifera are one of the largest sources of carbonate flux to the deep ocean and participate in marine food webs as both consumers and producers (Kucera, 2007; Schiebel & Hemleben, 2017; Spero & Parker, 1985). Their shells sink rapidly (Takahashi & Bé, 1984), contributing to the flux of particulate inorganic carbon to the deep ocean (Fowler & Knauer, 1986; Subhas et al., 2023). Foraminifera account for 32-80% of calcite flux to depth, contributing around 0.71 gigatons per year (Schiebel, 2002; Schiebel et al., 2007). Foraminiferal tests and fragments may further act as ballast for sinking organic material, though it is unclear whether this represents a significant contribution to particulate organic carbon flux (Barker et al., 2003; Klaas & Archer, 2002; Loubere et al., 2007; Subhas et al., 2023; Ziveri et al., 2007).

Modern surveys of planktonic foraminifera are important for assessing how these organisms’ abundance and distribution relate to modern environmental conditions, and how they may already be shifting in the context of anthropogenic climate change. Most surveys of planktonic foraminifera have focused on the open ocean, with less study on the continental shelf and slope, and very little on the western Atlantic margin (Chaabane et al., 2023). Several studies have been conducted in the northwest Atlantic, all focused primarily in the northern and open ocean region: off of Cape Cod in 1941 (Phleger, 1945) and 1981-1982 (Keigwin et al., 2005), open ocean sites north of 32º N in 1955 (Bé, 1959), transects from Bermuda to Cape Cod in 1961 (Cifelli, 1967) and Bermuda to ~500 miles east of Cape Hatteras in 1962 (Bé & Hamlin, 1967), from Newfoundland to the Caribbean in 1968 (Bé et al., 1971), and sites near Bermuda in 1957 (Bé, 1960) and 1975-1977 (Williams et al., 1981). The most recent and comprehensive plankton tow survey of foraminifera in the western Atlantic Ocean occurred between 1959-1963, when Bé and Tolderlund conducted 520 tows at five stations ranging from 56 – 32º N latitude in the open ocean to determine seasonal trends in foraminiferal community composition. The study yielded data about the environmental associations of seventeen species, including their temperature and salinity ranges as well as distribution at the locations surveyed (Tolderlund & Bé, 1971). This study in particular has served as a foundation for understanding extant foraminiferal ecology both in the northwest Atlantic and globally. In the six decades since the work of Bé and Tolderlund (1971), several key environmental shifts and corresponding community shifts in planktonic foraminifera have occurred (Chaabane et al., 2024), while foraminiferal distribution in the marginal Atlantic has remained unexplored.

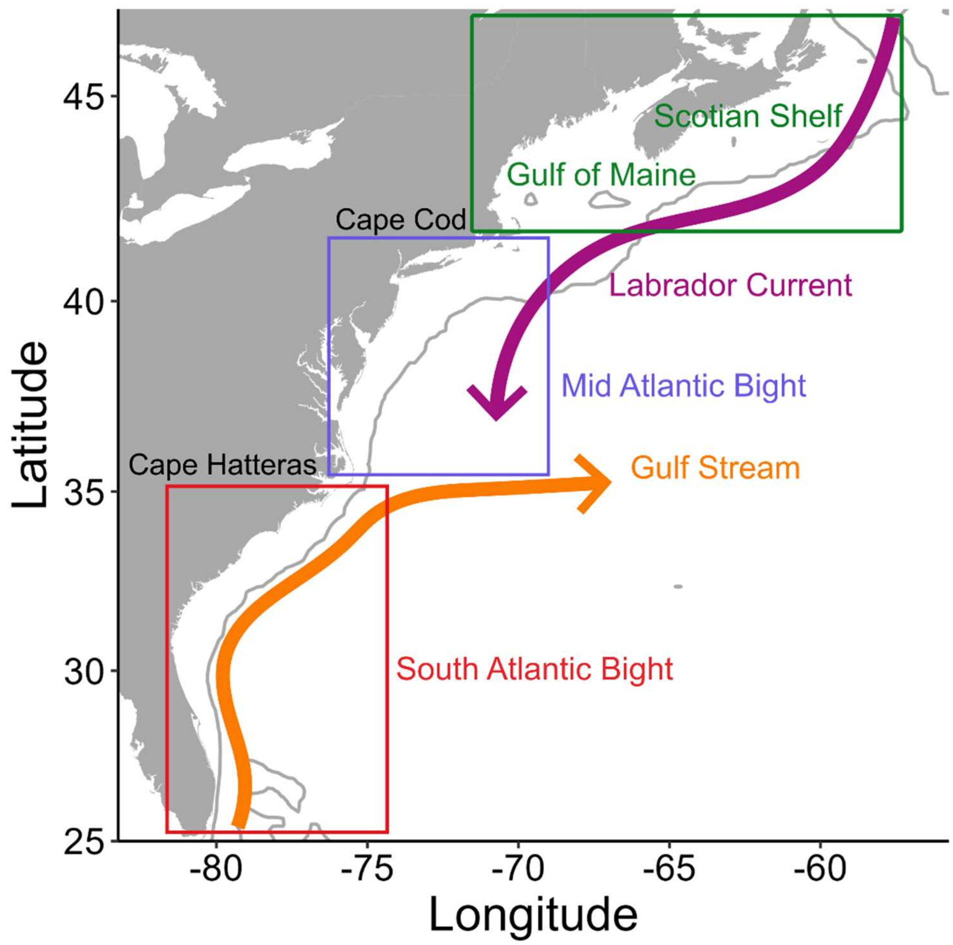

Figure 1. Western North Atlantic subregions and relevant locations. Grey lines off the coast represent the 250m depth contour.

Ocean temperatures have increased since industrialization. Marine species across taxonomic groups, from invertebrates (Hastings et al., 2020) to tiger sharks (Hammerschlag et al., 2022) to bluefin tuna (Crear et al., 2023), have already shifted in latitude and abundance as they adapt or migrate in response to warming. Modeled projections indicate that foraminiferal abundance will shift toward the poles as warm-water species are forced out of their habitats in the tropics (Chaabane et al., 2024; Roy et al., 2015). Thus, while populations of warm-water foraminifera may increase at higher latitudes, cool-water species are likely to suffer concurrent decreases in population as there is a contraction of habitat that has both cool temperatures and a sufficiently high calcite saturation state (Chaabane et al., 2024). In the past decade, foraminifera that were formerly rare at high latitudes have become increasingly common in the Arctic and Antarctic Oceans as sea temperatures rise (Schiebel et al., 2017). Polar waters that were previously inhabited by only three species (*Neogloboquadrina pachyderma, Turborotalita quinqueloba,* and *Globigerina bulloides*) now include the traditionally 'subpolar' species *Orcadia riedeli*, *Globorotalia inflata*, and *Neogloboquadrina incompta* (Schiebel et al., 2017). Understanding these shifts in species distribution is important for comparing modern assemblages to past records, helping to elucidate the similarities and differences between record types and thereby consolidate our understanding of modern and ancient assemblages.

Rising carbon dioxide concentrations in the atmosphere have led to acidification as well as changes in availability of dissolved inorganic carbon (DIC) in the surface ocean (Caldeira & Wickett, 2003; Doney et al., 2009; Feely et al., 2009). In the Mid- and South Atlantic Bights, aragonite saturation states decreased by 2% in a five-year period in the late 2000s (Wanninkhof et al., 2015). Near Nova Scotia and the Gulf of Maine, near-surface waters already experience undersaturation each winter (Gledhill et al., 2015). As the ocean continues to warm and acidify, the fate of planktonic foraminifera is uncertain (Chaabane et al., 2024; De Moel et al., 2009; Jonkers et al., 2019; Moy et al., 2009; Roy et al., 2015; Strack et al., 2022). Negative impacts of ocean acidification have been observed in both culture and in situ studies. For example, decreases in carbonate ion concentration ($[CO_3^{2-}]$) have been associated with decreased test thickness and weight of *Globigerinoides ruber* in both the Arabian Sea and Cariaco Basin (Davis et al., 2019; De Moel et al., 2009; Marshall et al., 2013; Weinkauf et al., 2016). Across multiple species, the tests of modern foraminifera are approximately 30-35% thinner than those living during pre-industrial times (Moy et al., 2009). As ocean pH decreases and calcification is inhibited, foraminifera are likely to continue to struggle to construct their tests, impacting buoyancy and physiological processes (Davis et al., 2017; Manno et al., 2012; Marshall et al., 2013). As foraminifera are major contributors to the carbon cycle via the alkalinity pump, decreases in foraminiferal populations could impact global marine carbon cycling by decreasing flux of calcium carbonate to depth via sinking tests (Davis et al., 2017; Lawton et al., 2003).

Abundance and distribution of planktonic foraminifera can be driven by various factors, such as latitude and temperature (Bijma, Faber, et al., 1990; Rebotim et al., 2017; Tolderlund & Bé, 1971), carbonate chemistry parameters like pH, DIC, and carbonate ion concentration (Barker & Elderfield, 2002; Chaabane et al., 2024; Henehan et al., 2017), season (Deuser et al., 1981; Tolderlund & Bé, 1971; Weinkauf et al., 2016), salinity (Bijma, Faber, et al., 1990), lunar cycle (Bijma, Erez, et al., 1990), and biological influences such as algal symbionts, food supply, and predation (Bé & Hutson, 1977; Berger, 1969). Given the importance of foraminifera in the modern ocean, this study seeks to address critical gaps in both understanding the spatial distribution of foraminifera along the northwest Atlantic margin and in beginning to assess whether these distributions may have shifted over the past half century.

Oceanographic Setting

The northwest Atlantic is a large and highly variable region that is influenced by multiple currents as well as coastal outflows. Annual mean sea surface temperature (SST) varies from about 7 ºC in the Gulf of Maine to about 27 ºC near Florida (Reagan et al., 2024; Shearman & Lentz, 2010) and is controlled by uneven solar radiation as well as latent and sensible heat flux, particularly over the Gulf Stream (Thompson et al., 1988). The region has warmed in the past several decades due to a combination of natural atmospheric fluctuations and anthropogenic climate change (Chen et al., 2020; Loder & Wang, 2015). The region also undergoes natural oscillations in SST on a decadal time scale as part of the North Atlantic Oscillation (NAO), which influences precipitation, circulation, salinity, and mixed layer depth (Hurrell & Deser, 2010). The study area can be split into three major subregions: the South Atlantic Bight, Mid-Atlantic Bight, and Gulf of Maine, all of which are influenced by different combinations of environmental drivers.

The South Atlantic Bight (SAB) is heavily affected by the warm and saline waters of the Gulf Stream, especially near the coast of Florida and the continental shelf break (Ezer, 2019; Friedland & Hare, 2007). The SAB has experienced weak cooling since 1975, which can be attributed to differences in sensible and latent heat flux (Kavanaugh et al., 2017; Shearman & Lentz, 2010). The region is also influenced by runoff from an extensive coastal river and wetland system (Blanton et al., 2003). Nearshore waters are affected by river discharge, which can cause significant changes in sea level, sediment transport, and levels of nutrients and contaminants in the nearshore ocean (Lee & Maruya, 2006; Piecuch et al., 2018; Windom & Palmer, 2022).

The Mid-Atlantic Bight (MAB) is more characterized by coastal influences than the SAB, as the Gulf Stream moves away from the coast near Cape Hatteras (Chen et al., 2020). Cooler, low salinity coastal waters from the coast and the most southern extent of the Labrador Current interact with warm, high salinity water from the Gulf Stream to create cross-shelf flow (Flagg et al., 2002). Gulf Stream eddies may intrude into shelf waters, disrupting density gradients and causing localized warming (Gawarkiewicz et al., 1996; Gawarkiewicz et al., 2025; Silver et al., 2025). Changes in the Gulf Stream have resulted in warming in the MAB, with benthic temperature increases of 0.3-0.6 ºC/decade since the 1980s (Ezer, 2019; Kavanaugh et al., 2017).

The Gulf of Maine (GOM) is the most variable region of the North Atlantic, with a strong seasonal temperature cycle and SST that can fluctuate by up to 16 ºC (Thompson et al., 1988). The Gulf and nearby Scotian Shelf are characterized by the interplay of two major currents: the Labrador Current, which carries cool water from the Arctic, and weak influence from the Gulf Stream, which carries warm, salty water northward from the Gulf of Mexico (Friedland & Hare, 2007; Seidov et al., 2021). The GOM is the fastest-changing portion of the study region, warming about as rapidly as the Arctic Ocean at a rate of about 1.0 ºC per hundred years (Shearman & Lentz, 2010). This is attributed to a combination of warming of the Labrador Current and a northward shift of the Gulf Stream extension, which is of greater magnitude in the Scotian Shelf (Seidov et al., 2021). Recent studies have suggested that the Gulf Stream may be slowing and producing more warm-core rings, which may also accelerate warming in the north Atlantic (Dong et al., 2019; Gangopadhyay et al., 2019; Seidov et al., 2021; Shearman & Lentz, 2010).

2. METHODS

Sample collection

Samples were collected on the third NOAA East Coast Ocean Acidification (ECOA-3) cruise in August and September of 2022. Sites spanned the eastern margin of the North American continent from Florida to Nova Scotia (26.98 – 45.66° N, 58.17 – 81.11° W). Plankton samples were collected using bongo net tows (153 µm mesh) equipped with a flow meter to measure the total water volume sampled by each tow. Vertically integrated tows were conducted at varying times of day in varying weather conditions with maximum depths ranging from 7 – 202 m. Hydrographic variables, including temperature, salinity, dissolved oxygen, DIC, $\delta^{13}C$, pH, nitrate, phosphate, and silica concentrations, were collected at the same stations using a Sea-Bird SBE-911plus CTD system. All variables are reported from the near surface (1m depth) unless otherwise stated. Samples were preserved onboard the ship in 5% borate-buffered formalin and refrigerated. Further details on sampling region, protocols, and approaches can be found in the ECOA-3 Cruise Report (Shellito & Alpert, 2022).

Sample processing

All tow material was removed from formalin using a 125 µm sieve and then rinsed and diluted with tap water. Some larger samples (> 300 individuals) were split using a Folsom plankton splitter to obtain smaller subsamples (McEwen et al., 1954). The entire (sub)sample was then examined using a light microscope. Major plankton groups (e.g., copepods, amphipods, gastropods, larval stages of crabs and fish) were identified and qualitatively noted to provide an estimate of the composition of each sample. Foraminifera were separated from other sample material using a paint brush and transferred to dry slides, where they were grouped according to the presence or absence of cytoplasm as an indicator of whether they were alive at time of collection. Foraminifera with evidence of cytoplasm in all but two or more chambers were considered “live” at collection. All non-foraminiferal biomass was then returned to formalin for storage.

Species were visually identified using the taxonomy of Brummer and Kučera (2022). Juvenile and unidentified foraminifera were grouped into an “unknown” category. Samples were then dried and cleaned using a paintbrush to remove organic material attached to individuals. Benthic species were grouped into their own category but were not further speciated. All conspecifics in a sample were spaced apart from one another and imaged on a Keyence VHX700 microscope to measure the minimum and maximum diameter and two-dimensional surface area of each individual. Size data was quality-checked, and any measurements less than 53 µm were discarded.

Statistical analyses

Shannon and Simpson’s diversity indices were calculated using the ‘vegan’ package in R for all samples (Oksanen et al., 2022). Carbonate chemistry variables were computed from in situ DIC and pH measurements, corrected to account for in situ temperature, using ‘seacarb’ in R (Gattuso et al., 2024). Lunar illumination was computed based on date using the ‘lunar’ package in R (Lazaridis, 2022). Linear regression was performed to test relationships between various environmental variables and foraminiferal size, abundance, and diversity. Hierarchical clustering of concentration (individuals/L) was performed using the hclust function from the ‘stats’ package in R (R Core Team, 2022) with a Bray-Curtis dissimilarity, which adequately addresses species distributions where rare species do not play a major role (Bray & Curtis, 1957; Ricotta & Podani, 2017). Approximately unbiased (AU) p-values and bootstrap probability (BP) values were calculated using pvclust in R to determine clusters at a significance level of 95%.

Data was Z-standardized to reduce the impact of error, and backward stepwise linear regression was used to estimate the relative influence of variables without oversimplification (i.e., without attributing all influence to a single variable rather than a suite of related variables) (Wang et al., 2016).

3. RESULTS

Oceanographic setting

Study sites ranged from 26.98º – 45.66º N. Sea surface temperatures ranged from 12.98 ºC to 30.50 ºC, DIC ranged from 1897 – 2058 μmol/kg, pH ranged from 7.81 to 8.14, and salinity ranged from 29.80 – 36.32 ‰ (Figure 2).

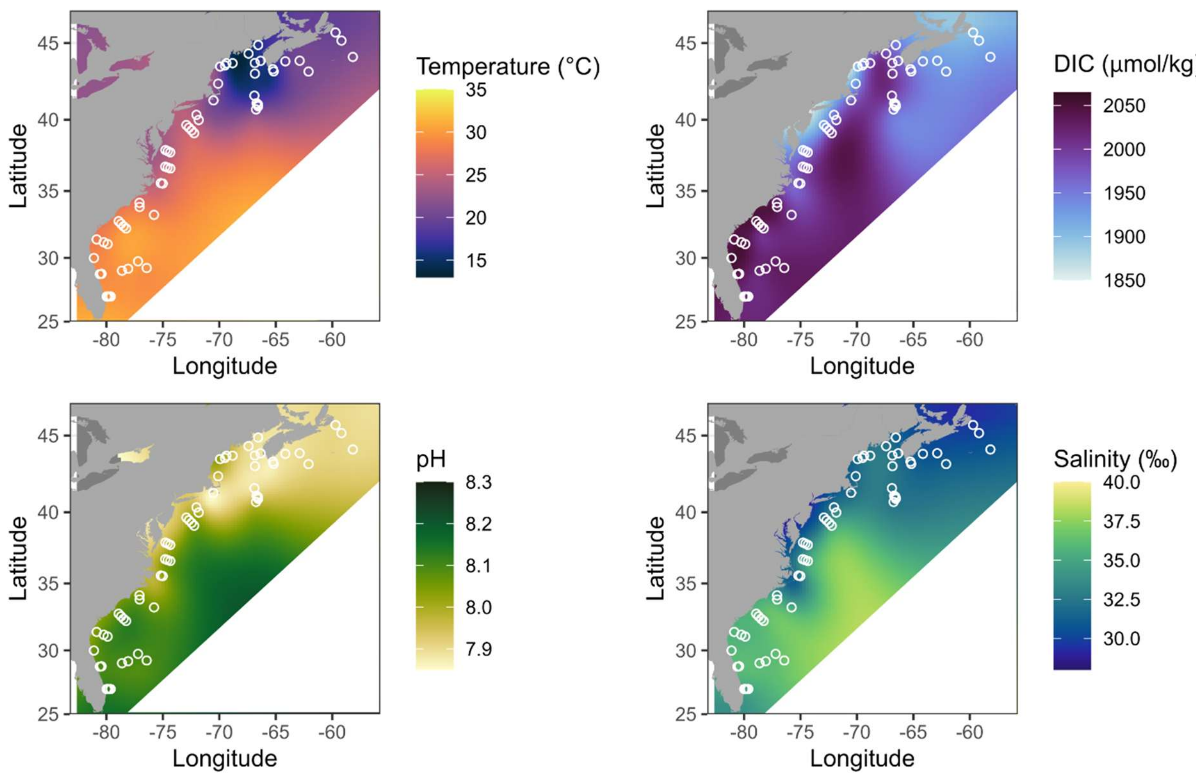

Figure 2. Interpolated sea surface temperature, DIC, pH, and salinity in the study region using generalized additive models.

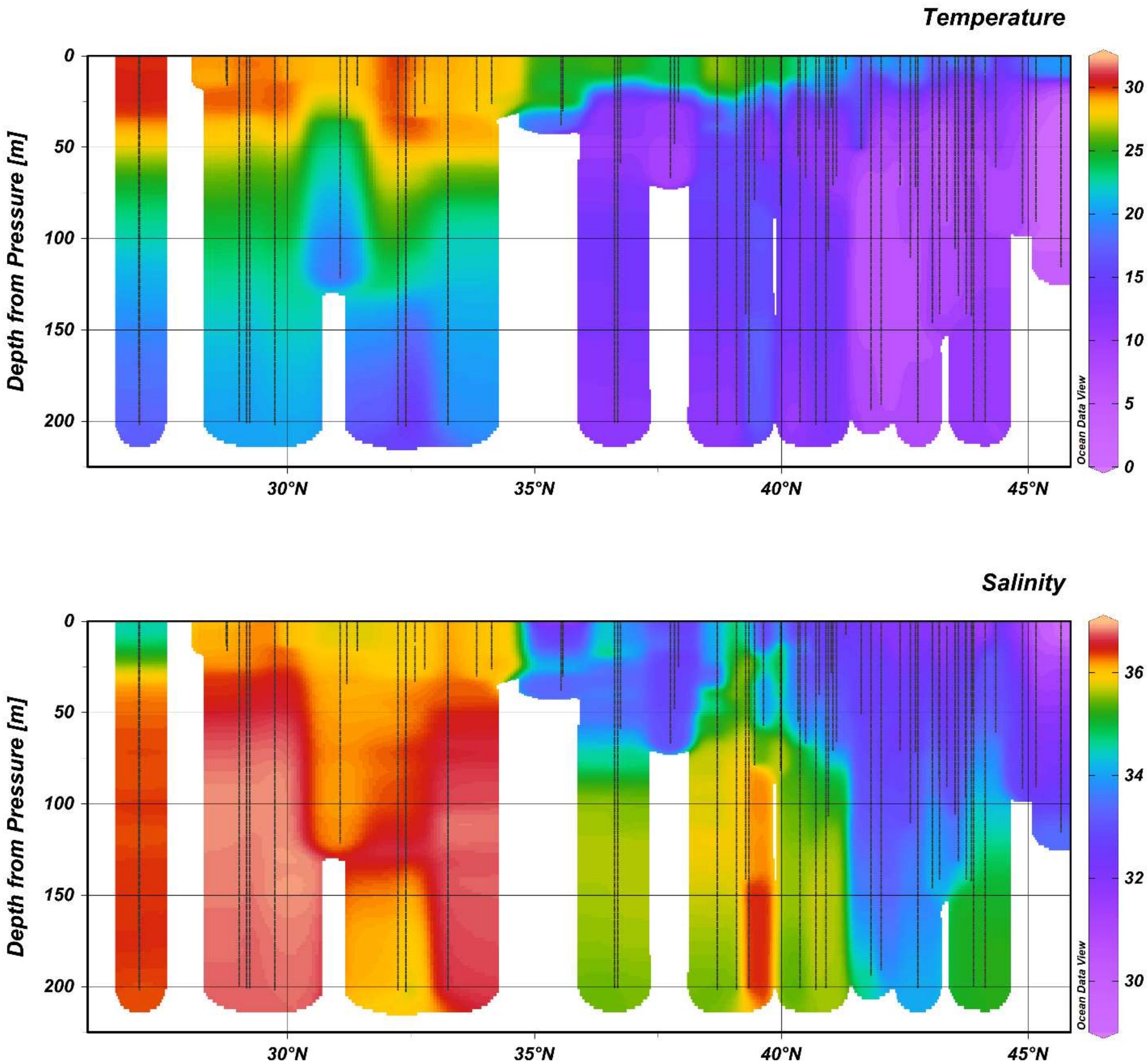

Figure 3. Temperature (top) and salinity (bottom) profiles for the study region.

There is a significant increase in both salinity and temperature just below 35 ºN, near the latitude of Cape Hatteras (Figure 3).

Species distribution

A total of 14,075 individuals (live = 11,050; dead = 3,025) were counted at 41 sites. Species distribution followed latitudinal trends. The most abundant species at sites north of 41.4º N (Cape Cod) were *Neogloboquadrina incompta, Neogloboquadrina pachyderma,* and *Turborotalita quinqueloba* (Figure 4). In the Mid-Atlantic Bight, assemblages were dominated by *Globigerina inflata* and *Orcadia riedeli*, while the most abundant species south of the Chesapeake Bay were *Globigerinoides ruber ruber* and *Globigerinoides ruber albus* (Figure 4). Assemblage size and total surface area of foraminifera in a sample (which we interpret as a proxy for calcite production) did not vary significantly with latitude (Appendix C).

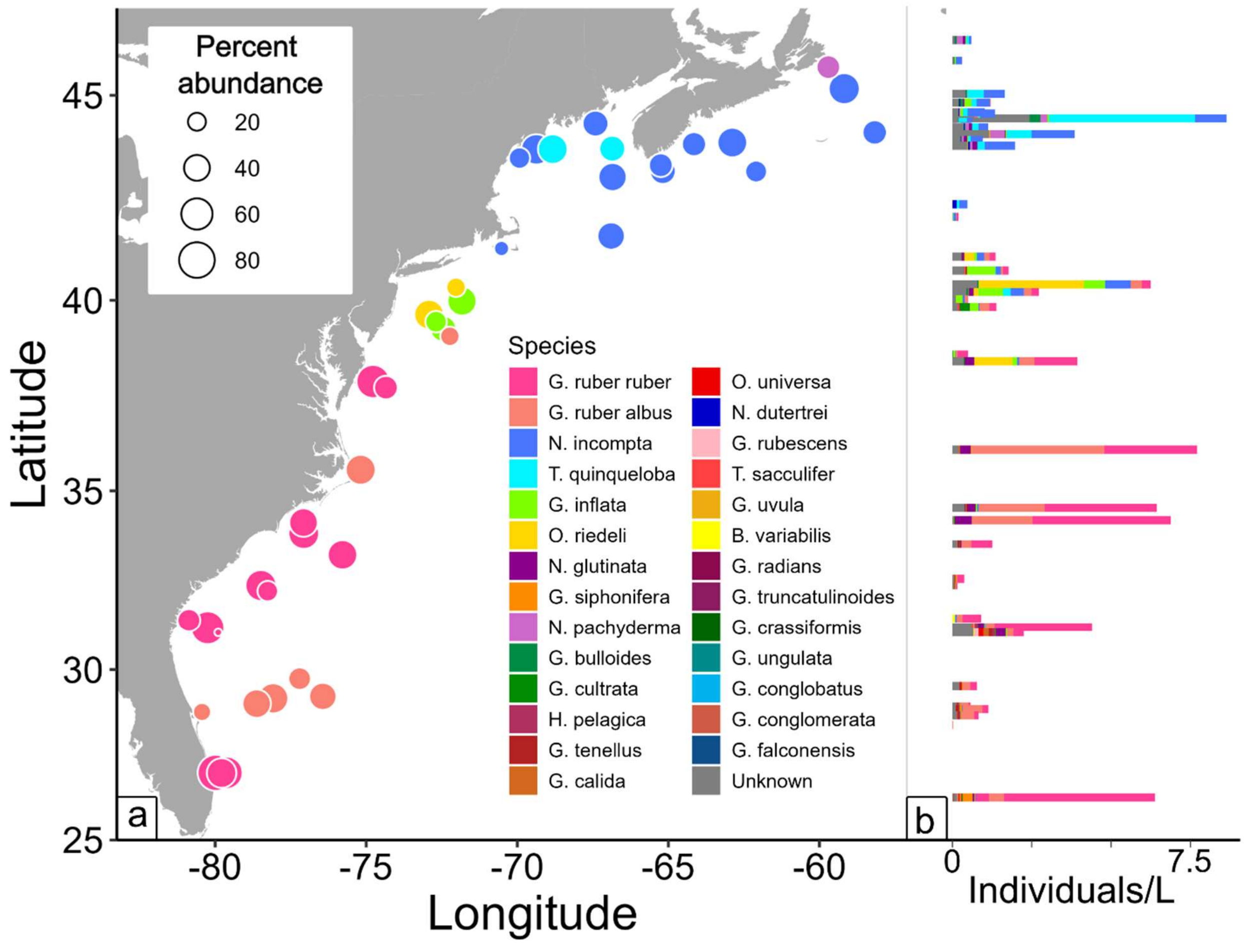

Figure 4. a) ECOA sites colored by the most common species and sized by the percentage of the assemblage made up of that species. **b)** Species composition at each site by latitude. Bar length corresponds to the number of individuals per liter. Species key order corresponds to the order of abundance in the full dataset.

Differences in species composition yielded two distinct regional clusters (Figure 5). Of the ten most abundant species in the dataset, a Mann-Whitney U test demonstrates that eight were significantly ($p < 0.05$) more common in one of the regions than the other (Figure 5). There was a particularly high abundance of *N. incompta* in northern stations and of *G. ruber albus* and *G. ruber ruber* in southern stations.

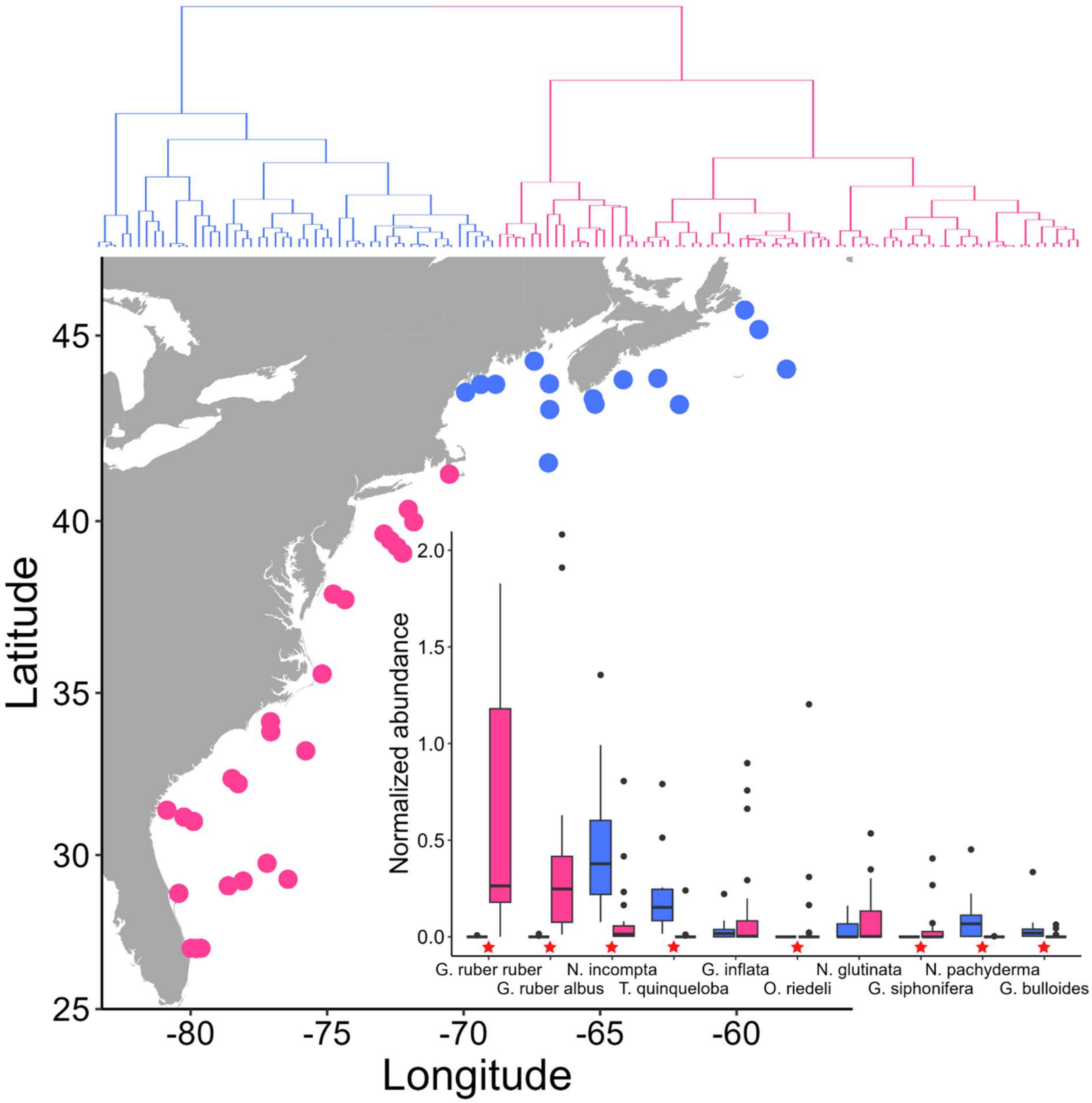

Figure 5. ECOA sites colored according to the results of hierarchical clustering. The ten most abundant species tend to favor either the northern (blue) or southern (pink) region. Species with a significant difference in distribution between the clusters are starred.

Environmental drivers

Backward stepwise linear regression was used to test the relationship between assemblage diversity versus environmental factors (latitude, longitude, SST, pH, alkalinity, DIC, depth, lunar illumination, and salinity). All environmental parameters were assessed at 1m depth. No model explained a meaningful amount of variance (adjusted R^2 of total foraminiferal abundance = 0.165, Shannon diversity index = 0.182, Simpson's diversity index = 0.175, total calcite R^2 = 0.115; Appendix C). Environmental variables were highly correlated with each other (Figure 6) and associated to various degrees with the distribution of certain species (Figure 7).

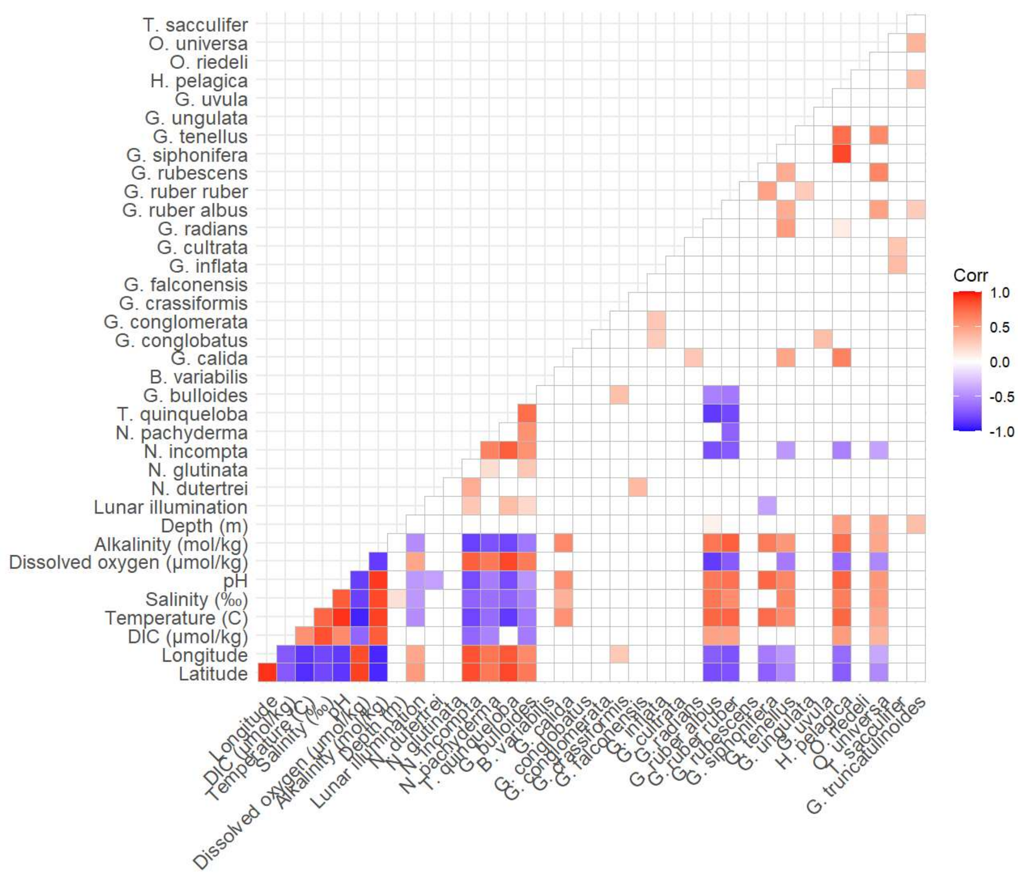

Figure 6. Spearman correlation matrix showing significant relationships between environmental variables and species distribution (non-significant correlations shown in white).

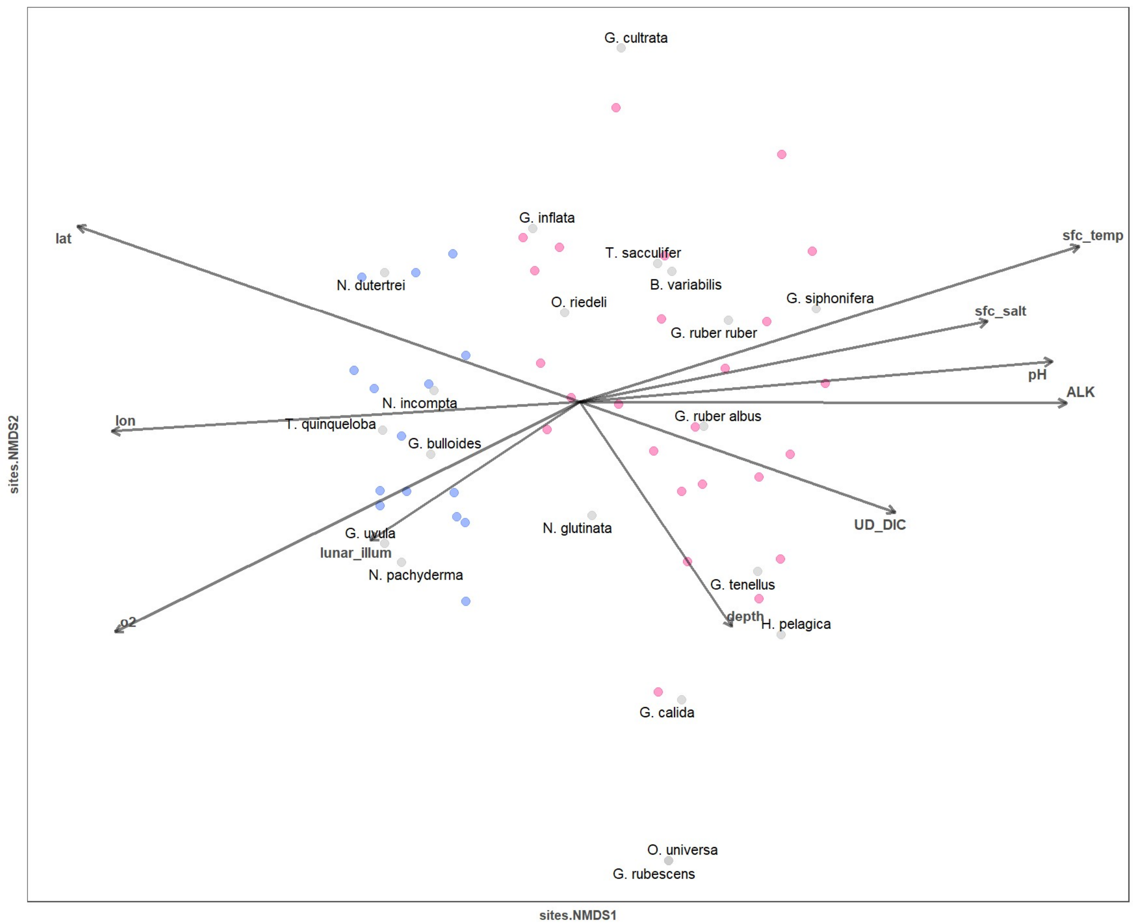

Figure 7. NMDS of study sites (blue and pink dots, colored according to clusters) and species (grey dots).

The same regression approach was applied to the combined abundance of living and dead specimens of nine of the ten most abundant species in the dataset. *O. riedeli* was excluded because it was not present at enough sites (n = 3 sites with dead individuals) for model generation. *G. bulloides* was present at enough sites but showed no relationship between abundance and any variable. No model of abundance explained more than 69% of variance except for *G. siphonifera*, which had no significant parameters and a small sample size, likely indicating model overfit rather than high explanatory power. Most models explained less than 50% of variance (Table 1). DIC was positively correlated with the abundance of five species (*G.*

inflata, G. ruber albus, G. ruber ruber, N. glutinata, T. quinqueloba), and SST was correlated with the abundance of three species (*G. inflata, N. incompta, N. glutinata)* (Table 1). Alkalinity was negatively correlated with the abundance of three species (*G. inflata, N. glutinata, T. quinqueloba*), all of which were positively correlated with DIC (Table 1). Species that were geographically close to one another tended to share similar drivers and to be positively correlated with one another in linear modeling, Spearman correlation, and NMDS (Figure 6, Figure 7).

Species tend to peak in abundance at an apparent optimum temperature, with decreases in abundance as temperature increases or decreases away from the optimum (Figure 8). This dataset likely does not capture the entire temperature range for species that peak at either very low or very high temperatures (e.g., *N. pachyderma, G. siphonifera*).

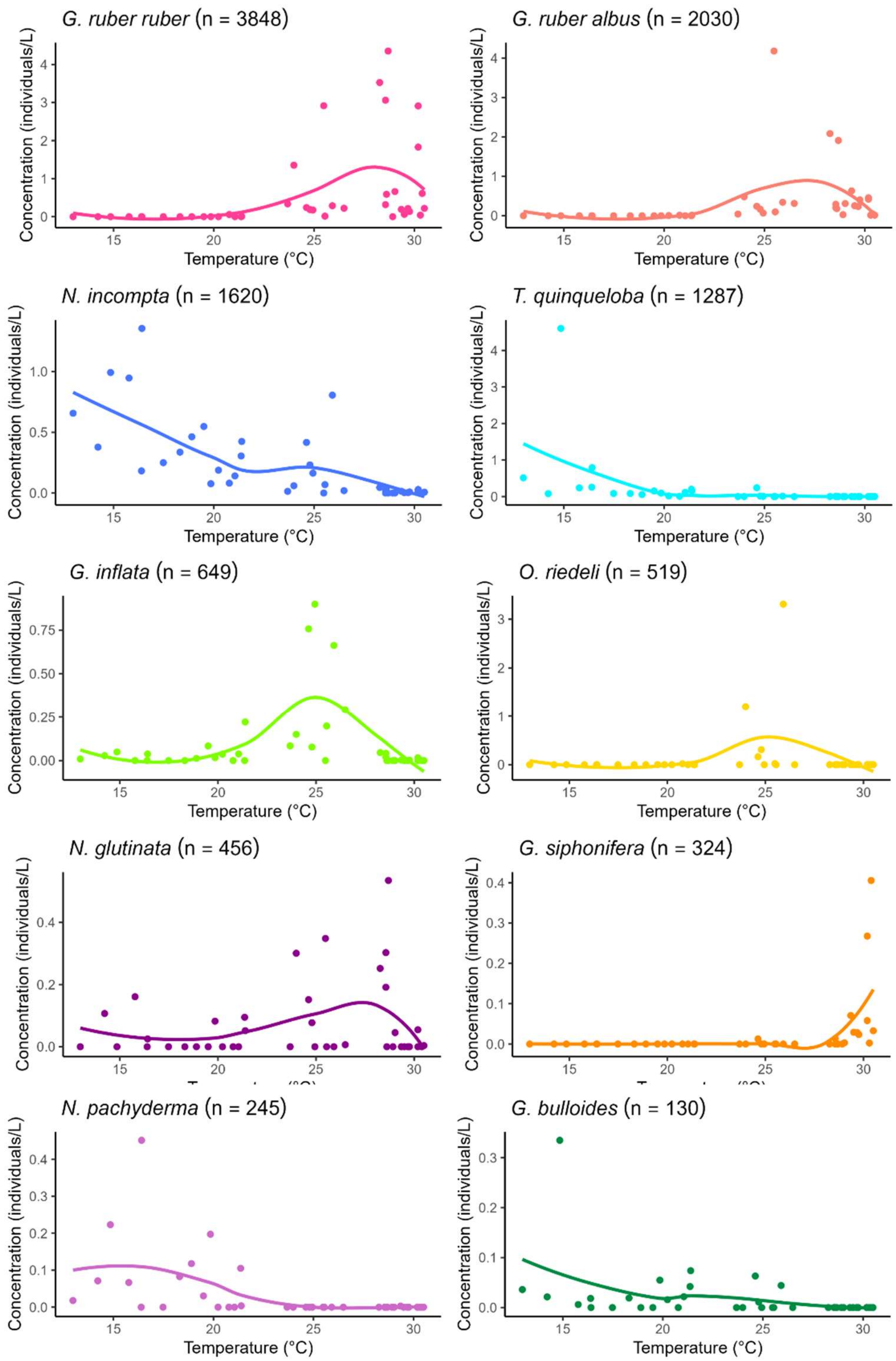

Figure 8. Temperature versus concentration of individuals for the ten most common species in the dataset. LOESS curves are included to visualize peaks in abundance.

Table 1. Stepwise linear regression models of abundance (measured as a concentration of total individuals/L, both live and dead) and average surface area (size) of dead foraminifera versus environmental drivers for nine of the most abundant species. Only dead foraminifera were used in size analysis to prevent variation due to differences in life stage (e.g., to avoid comparing juveniles to adults of reproductive age). All parameters retained in the final model are shown for each. Significant variables ($p < 0.05$) are designated with an asterisk.

Species (n sites)	Concentration (individuals/L)		Average surface area of dead individuals	
G. bulloides (12)	No parameters retained		**R^2**	**0.128**
			Latitude	1.29
			Longitude	-0.95
			DIC	2.22
			SST	1.82
			Salinity	-1.19
G. inflata (23)	**R^2**	**0.251**	**R^2**	**0.436**
	DIC*	2.72	Longitude	0.60
	SST*	2.28	DIC*	2.44
	pH*	3.05	SST*	3.18
	Alkalinity*	-7.24	Alkalinity*	-4.53
			Lunar illumination	-0.34
G. ruber albus (26)	**R^2**	**0.427**	**R^2**	**0.379**
	DIC*	2.39	SST*	1.81
	SST	1.64	Salinity*	0.91
	Salinity	-0.79	pH*	2.05
	pH	1.38	Alkalinity*	-5.64
	Alkalinity	-4.30	Lunar illumination*	-0.43
	Lunar illumination	0.34		
G. ruber ruber (25)	**R^2**	**0.405**	**R^2**	**0.271**
	DIC*	1.17	Latitude	0.69
	Salinity*	-0.86	SST*	1.70
	Lunar illumination	0.26	pH	-0.76
			Depth	0.32

Table 1 (continued).

G. siphonifera (11)	**R^2**	**0.930**	**R^2**	**-0.172**
	Latitude	10.55	Latitude	9.97
	Longitude	3.26	Longitude	3.61
	DIC	26.17	DIC	64.81
	SST	22.48	SST	47.19
	Salinity	5.07	Salinity	17.06
	pH	18.37	pH	51.57
	Alkalinity	-56.53	Alkalinity	152.12
	Depth	-0.48	Lunar illumination	4.61
	Lunar illumination	-6.79		
N. glutinata (18)	**R^2**	**0.571**	**R^2**	**0.194**
	Longitude	0.59	SST	-1.46
	DIC*	4.42	pH*	2.74
	SST*	1.88	Alkalinity	-1.15
	pH	3.89		
	Alkalinity*	-8.27		
	Depth*	-0.44		
	Lunar illumination	0.23		
N. incompta (33)	**R^2**	**0.451**	**R^2**	**0.139**
	SST*	-0.68	Salinity*	1.55
			Alkalinity*	-1.44
N. pachyderma (12)	**R^2**	**0.689**	**R^2**	**0.296**
	Latitude*	-4.94	Latitude	2.96
	Longitude*	5.36	DIC	-1.61
	DIC	-1.28	pH	-1.90
	Salinity	7.26	Alkalinity	5.90
	pH	1.47		
	Alkalinity	-5.33		
	Depth*	-3.15		
	Lunar illumination	0.61		
T. quinqueloba (19)	**R^2**	**0.143**	**R^2**	**0.655**
	DIC*	1.27	Latitude*	2.00
	pH*	1.41	DIC*	6.51
	Alkalinity*	-1.98	SST*	5.51
			Salinity	1.01
			pH	3.54
			Alkalinity*	-9.72
			Depth*	-0.50
			Lunar illumination*	0.70

Size

Size (average 2-dimensional surface area) of non-living foraminifera of each major species was modeled using backwards stepwise linear regression against the same set of environmental drivers as abundance. To reduce variability due to different ontogenic states, only dead individuals were considered. Foraminifera lacking cytoplasm (classified as ‘dead’ here) are assumed to have completed their life cycle and have reached maximum size; when foraminifera reproduce, cytoplasm is converted into gametes, leaving the shell empty. Although other causes of mortality cannot entirely be ruled out, other causes that would leave a shell of adult morphology empty are assumed to be uncommon. Therefore, differences in the size of cytoplasm-barren (‘dead’) foraminifera can be attributed to growth conditions experienced during life rather than differences in life stage. The best model explained 66% of variance (*T. quinqueloba)*, with all other models having adjusted R^2 values less than 0.45 (Table 1). SST and alkalinity were correlated with the size of four species each (SST: *G. inflata, G. ruber albus, G, ruber ruber, T. quinqueloba*; alkalinity: *G. inflata, G. ruber albus, N. incompta, T. quinqueloba*), while no other driver was correlated with more than two species.

Comparison to other datasets

Hierarchical clustering of assemblages from the ECOA, FORCIS (net tow), and ForCenS (core top) datasets yielded two clusters, roughly divided into a northern and southern region (Figure 6). Only data from 26 – 46º N and 57 – 82º W was included to match the study region. FORCIS data was filtered to only include data from August and September for consistency in seasonality with ECOA. ForCenS data is based on recent sediments, and all sites with data in the study region were included. In cases where species were subdivided (for example, into left- and right-coiling varieties of *G. truncatulanoides*), data was combined to yield a single abundance value for each species present.

Table 2. Comparison of datasets.

Dataset	Record type used in analysis	Years surveyed	Months
ECOA-3 (this study)	Plankton tow	2022	August-September
Tolderlund and Bé	Plankton tow	1959 – 1963	Year-round
FORCIS	Plankton tow	1941 – 1958	August-September
ForCenS	Core top	NA	Year-round

The latitudinal divide between the two regions is shifted south relative to the clusters in the ECOA dataset, diverging near the Chesapeake Bay just north of Cape Hatteras rather than near Cape Cod (Figure 5, Figure 9). The species most common in the northern and southern regions are similar to the ECOA clusters, with the north dominated by *N. incompta* and the south dominated by *G. ruber albus*. However, *G. ruber ruber* is less abundant in both the FORCIS and ForCenS datasets and is therefore less dominant overall.

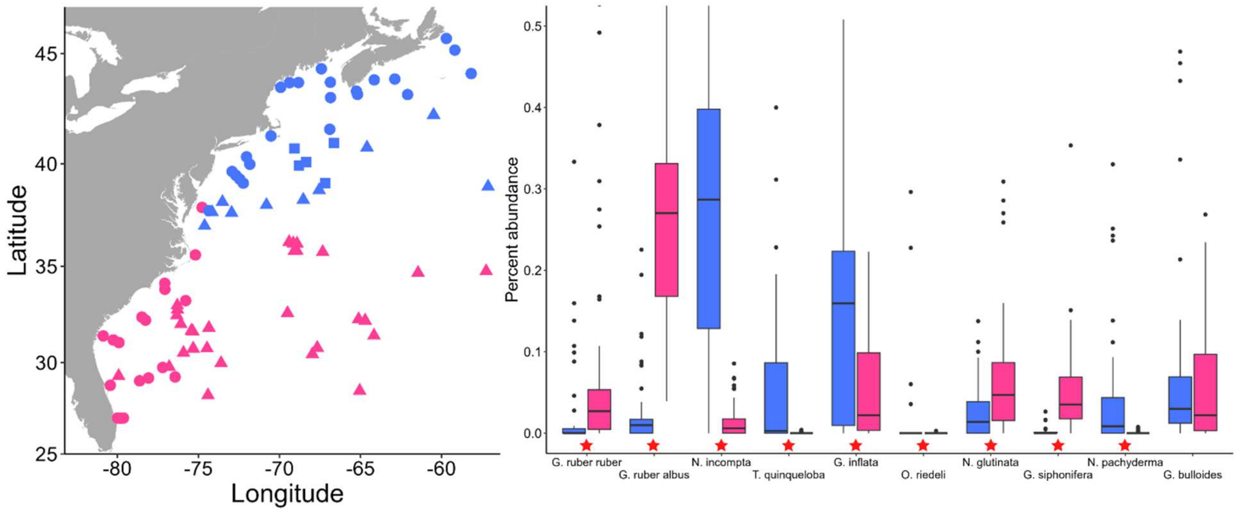

Figure 9. ECOA (circle), FORCIS (square), and ForCenS (triangle) sites colored according to the results of hierarchical clustering. The ten most abundant species from the ECOA dataset tend to favor either the northern (blue) or southern (pink) region. Species with a significant difference in distribution between the clusters are starred.

4. DISCUSSION

Distinct species clusters north and south of Cape Cod

Foraminiferal assemblages vary with latitude, with two distinct species clusters emerging from the ECOA dataset according to both hierarchical clustering and NMDS (Figure 5, Figure 7). The northern species (*G. bulloides, N. incompta, N. pachyderma,* and *T. quinqueloba*) are all traditionally classified as transitional or subpolar to polar species, meaning that their highest abundances are usually found at mid-to-high latitudes (Arnold & Parker, 2003; Berger, 1969; Kennett & Srinivasan, 1983). The southern species (*G. ruber albus, G. ruber ruber, G. siphonifera,* and *O. riedeli*) occur in highest abundance in subtropical to tropical regions (Arnold & Parker, 2003; Bé, 1969; Kennett & Srinivasan, 1983).

Differences in symbiont associations and depth habitat may explain why species are significantly more likely to occur in a particular region. Symbiont type and association are possible drivers of habitat preference (Bijma et al., 1998; Kuroyanagi & Kawahata, 2004; Numberger et al., 2009). Though planktonic foraminifera are heterotrophs, some species form symbiotic relationships with dinoflagellates, haptophytes, and possibly cyanobacteria that allow them to benefit from photosynthesis (Bird et al., 2017; Gast & Caron, 1996; Schiebel & Movellan, 2012; Spero, 1987; Takagi et al., 2019). The most abundant species in the northern group are symbiont-barren and may require more access to food sources in the absence of photosynthesis (Takagi et al., 2019). Primary productivity and zooplankton biomass tend to be higher at mid to high latitudes and in regions with elevated nutrient levels (Berger et al., 1989; Drago et al., 2022; Franz et al., 2013; Westberry et al., 2023). *Neogloboquadrina incompta* and *N. pachyderma* tend to co-occur with *G. bulloides* and *T. quinqueloba* (Figure 4, Figure 5) and to live deeper in the water column than the southern species, especially during the summers when food availability is higher (Kretschmer et al., 2018; Rebotim et al., 2017; Schiebel et al., 2001). Above 42 ºN, consistent with the break between clusters around Cape Cod, oceanographic profiles show a shallower thermocline with much cooler waters at depth that would be preferred by these species (Figure 3). By contrast, three of the four southern species (*G. ruber albus, G. ruber ruber,* and *G. siphonifera*) are symbiont-bearing and live in the mixed layer, where their symbionts can perform photosynthesis (Fairbanks et al., 1982; Kennett & Srinivasan, 1983; Kretschmer et al., 2018; Rebotim et al., 2017; Salmon et al., 2015; Takagi et al., 2019). Little is known about the living depth and presence of symbionts for the usually rare species *O. riedeli*, which was found abundantly in ECOA tows in the Mid-Atlantic Bight and falls within the southern cluster.

Single environmental drivers do not explain species abundance

Species composition changes predictably with latitude and temperature, and SST and DIC were the most common significant drivers in models predicting species abundance, although no single driver or set of drivers explains much variance in total foraminiferal abundance or assemblage diversity. Previous studies have suggested relationships between environmental variables and species distribution (Barker & Elderfield, 2002; Bé & Hutson, 1977; Bijma, Faber, et al., 1990; Chaabane et al., 2024; Henehan et al., 2017; Tolderlund & Bé, 1971). We tested this in our dataset using stepwise linear regression to determine predictors of abundance, rather than occurrence. We found that surface DIC, SST, and alkalinity were the variables most likely to covary with abundance (Table 1), but most models have low R^2 values, indicating that no single variable has much explanatory power. This dataset affirms the limits of any single-variable explanation for planktonic foraminiferal ecology; correlations from stepwise linear regression were small and frequently interdependent, suggesting that assemblage composition and diversity reflect suites of interacting drivers rather than 1:1 relationships with any single driver. The results of stepwise linear regression were affirmed with both NMDS and Spearman correlation, which both showed similar varied responses of species to environmental drivers.

SST has been noted in the literature (alongside latitude) as one of the main predictors of foraminiferal distribution (Bijma, Faber, et al., 1990; Hemleben et al., 1989; Rebotim et al., 2017; Schiebel & Hemleben, 2017; Tolderlund & Bé, 1971). Although our results do not show SST as a predictor of abundance for every species, its presence as a significant variable for multiple species suggests that it cannot be entirely disregarded. As species do not have a linear relationship with SST but a range around a preferred temperature (Tolderlund & Bé, 1971), a stepwise linear model cannot fully capture these relationships because it does not account for zeroes or nonlinear relationships. However, analysis of these drivers via Spearman correlation and NMDS (which do account for zeroes) supports previous conclusions that species prefer distinct temperature ranges (Figure 8). Abundance peaks at an optimum temperature that varies by species; for example, *T. quinqueloba* occurs from 12.98 – 28.56 ºC, while *G. ruber ruber* occurs from 20.77 – 30.50 ºC.

Carbonate chemistry is an important driver of foraminiferal calcification, with increasing acidity correlating with a significant reduction in shell calcification (Barker & Elderfield, 2002; Davis et al., 2017; Henehan et al., 2017; Manno et al., 2012; Marshall et al., 2013). In this dataset, all species for which DIC and alkalinity are significant parameters in the model have a positive correlation with DIC and a negative correlation with alkalinity. Similarly, total assemblage surface area (interpreted as a proxy for calcite production) is significantly positively correlated with DIC and pH; however, variance explained is low ($R^2 = 0.115$), making it difficult to support the idea that foraminifera are producing more calcium carbonate because of high DIC and pH.

It is possible that within a species' range, certain species (*G. inflata, G. ruber albus, G. ruber ruber, N. glutinata, T. quinqueloba*) prefer areas with higher DIC or thrive in more oligotrophic conditions. We investigated whether correlation with DIC may be a function of productivity; DIC is negatively correlated with dissolved oxygen ($R^2 = 0.28$, $p < 0.001$; Appendix C), suggesting that preferences for high DIC may suggest a preference for lower productivity environments. However, given the low R^2, these trends may instead be the result of strong covariance between latitude, SST, and DIC (Figure 5). Ocean acidification has been hypothesized as an important driver of ongoing and future range shifts in planktonic foraminifera (Chaabane et al., 2024; Roy et al., 2015), but this study does not find that it is overwhelmingly responsible for any trends in species distribution on a snapshot regional scale. Although changing ocean carbonate chemistry remains a long-term concern for foraminifera, current species distribution patterns are likely governed more by coupled temperature and productivity gradients than by carbonate chemistry alone.

Calcite production of individuals and assemblages is not highly linked to carbonate chemistry

The optimum-size hypothesis posits that species size is maximized under ideal conditions, exemplified by a correlation between maximum abundance and maximum size (Hecht, 1976; Kahn, 1981; Malmgren & Kennett, 1976; Moller et al., 2013). The lack of significant relationship between abundance and the size of dead individuals for all species in the dataset (Appendix B) challenges this hypothesis, adding another line of evidence that foraminiferal size is only weakly related to environmental variables specific to each species.

Some studies have found relationships between SST, productivity, and relative abundance versus the size of particular species, though similarly to this study, overall variance explained was low (Adebayo et al., 2023; Rillo et al., 2020). Weinkauf's 2016 observations of *G. bulloides, G. ruber albus,* and *G. elongatus* likewise did not support the optimum-size hypothesis, concluding that optimum growth conditions are not uniformly correlated with maximum test size, SST, or chlorophyll *a* (Weinkauf et al., 2016). These three studies all use sediment samples compared against environmental data sourced from oceanographic databases; this study provides a complement, showing similar results in a snapshot of foraminiferal community composition alongside in situ environmental measurements.

Additionally, we find only weak relationships between SST and larger size in four species (*G. inflata, G. ruber albus, G. ruber ruber,* and *T. quinqueloba*). Of these species, only the size of *G. inflata* was also observed to increase significantly with SST by Adebayo et al. (2023). These weak relationships may point to a limitation in survey methods; this dataset represents only a snapshot rather than a comprehensive knowledge of the conditions under which individuals grew. Fluctuations away from preferred environmental conditions during an individual's life likely have more impact than SST at time of collection.

Previous studies have shown a relationship between oceanic carbonate chemistry and foraminiferal test thickness, calcification, and size/weight (Bijma et al., 2002; Davis et al., 2019; De Moel et al., 2009; Henehan et al., 2017; Lombard et al., 2010; Marshall et al., 2013; Weinkauf et al., 2016). We initially hypothesized that assemblages would produce less calcite in more 'acidic' conditions (characterized by higher DIC and lower pH and alkalinity). We use the sum of the 2-dimensional surface areas of all individuals in a sample as a proxy for total calcite production and find that it does not vary considerably even when the species composition of an assemblage varies; there is no correlation between latitude and total calcite production (Appendix C). There is also no significant difference between the northern and southern clusters, $t(32.4) = -1.66$, $p = 0.11$. While total calcite production is significantly positively correlated with pH and DIC, the variance explained is so low ($R^2 = 0.115$) that the model is effectively meaningless; variation in total 2-dimensional surface area of foraminifera in an assemblage cannot adequately be predicted by any of the environmental variables measured. Ultimately, there is no correlation between the amount of $CaCO_3$ produced by foraminifera, the size of individuals, and the species present in a region; the only strong predictor of calcite production is the number of individuals in an assemblage. This suggests that calcite production is governed more by population composition and size than by changes in carbonate chemistry.

This study does not support the idea that there is a meaningful relationship between DIC, alkalinity, or pH and the average surface area (size) of dead foraminifera except in *T. quinqueloba*. At the stations where this species occurs, DIC increases significantly with latitude ($R^2 = 0.32$, $p < 0.01$). It is possible that we are capturing the lower range extent of this species and that size increases as DIC and latitude increase.

The lack of a strong relationship between size and carbonate chemistry variables for most species implies that changes to carbonate chemistry may not have a straightforward effect on foraminiferal calcification as the oceans continue to acidify. Since the 1970s, assemblages have shifted to favor smaller species (Chaabane et al., 2025), possibly because smaller individuals may experience less reduced calcification rates than larger individuals under more acidic conditions (Henehan et al., 2017). However, even in the absence of large gradients in carbonate chemistry, foraminiferal test sizes vary in response to other environmental factors, and these relationships are species-dependent (Weinkauf et al., 2016). Our results further the idea that carbonate chemistry variables are not the exclusive drivers of calcification. Depth habitat and corresponding density of seawater have also been suggested as an explanation for interspecies differences in test thickness (Zarkogiannis et al., 2022), and it may be worth investigating if there is a similar relationship with body size.

Lunar illumination does not predict size

Species including *G. ruber albus, G. ruber ruber, G. siphonifera,* and *T. quinqueloba* have been shown to reproduce following a lunar or semi-lunar cycle in which individuals reach maximum size, reproduce, and then die (Bijma, Erez, et al., 1990; Jonkers et al., 2015; Lončarić et al., 2005; Spindler et al., 1979; Venancio et al., 2016). Empty tests were considered here as any empty shells observed are likely to be very recently dead given the rapid sinking rate of foraminiferal tests (Takahashi & Bé, 1984). A high abundance of empty shells could thus indicate a reproductive event synchronized across many individuals and perhaps timed to the lunar cycle. However, no significant correlation between lunar illumination and abundance of dead foraminifera were found for any species. Lunar illumination is also not likely to be a major driver of size. Average surface area of *G. ruber albus* was negatively correlated with lunar illumination, while size of *T. quinqueloba* was positively correlated (Table 1). The model for *T. quinqueloba* explains a relatively large amount of variance (R^2 = 0.655), but lunar illumination is unlikely to be the main driver. The coefficients for SST, DIC, and alkalinity are all greater in magnitude by more than seven times, suggesting that these three variables are far more important than lunar illumination as a predictor of size.

The semi-lunar periodicity of reproduction for both species means that using a linear coefficient for lunar illumination is perhaps not the most useful metric for analyzing this relationship, as abundance and size would not increase/decrease uniformly. Though this does not negate the possibility of lunar reproductive cycles, these results indicate that lunar phase is not necessarily useful as a predictor of dead test size for some species in plankton tow samples, although this method would work for species with a cycle centered on either the full or new moon. It is also possible that terminal size is not consistent and is possibly correlated with the environment in which a particular individual grew.

Shifts in species distribution

The apparent temperature preferences of individual species have remained relatively consistent since the 1960s, with species occurring within to slightly above the ranges reported by Bé and Tolderlund (1971). However, there appears to have been an overall shift in the latitudinal range of assemblages, driven primarily by northward shifts in the ranges of both *G. ruber* and *N. incompta*.

There are a few notable limitations in comparing ECOA data with that from FORCIS, ForCenS, and Bé and Tolderlund (1971). ForCenS is a database of recent sediment records, which integrates foraminiferal shells from the entire water column over a long period (decades to centuries) rather than a snapshot of the upper water column. Although FORCIS and the Bé and Tolderlund dataset are both net tow data, the differences in method (e.g., mesh size, tow depth, station location) mean that comparisons must remain relatively general. Since foraminiferal species have distinct depth habitats, the shallow nature of the ECOA tows (< 202 m, versus Bé and Tolderlund's 300 m tows) may mean that species like *G. truncatulinoides* may have been excluded (Kretschmer et al., 2018; Rebotim et al., 2017). Likewise, the finer mesh size used in the ECOA tows (153 μm versus 200 μm) means that more small or juvenile foraminifera may have been captured than in the past dataset. Furthermore, the stations from all three previous datasets tend to be much further offshore (past the continental shelf break) than ECOA stations and are therefore influenced by different current dynamics. While nearshore stations are likely to be influenced by combinations of the Gulf Stream and Labrador Current in degrees based on latitude, stations in the western North Atlantic Gyre are influenced by cold rings from the Gulf Stream and by less large-scale water movement due to their locations within the gyre (Parker, 1971). However, broad comparisons based on latitude and similar oceanographic zones are still useful. Bé and Tolderlund designate three major regions: “tropical,” south of Cape Hatteras; “transitional,” which includes the region from Cape Hatteras to just above Cape Cod; and “subarctic,” which encompasses the coastal waters north of Cape Cod, including the Gulf of Maine.

One of the most notable differences between ECOA and earlier data is the rarity of *G. bulloides*. This species was by far the most prolific species in Bé and Tolderlund’s tows in both “subpolar” and “transitional” waters and is described as the dominant northern species. *Globigerina bulloides* is a spinose, symbiont-barren species that lives above the thermocline (Hemleben et al., 1989; Rebotim et al., 2017; Takagi et al., 2019). It is an opportunistic species; its abundance in the water column is likely driven by the presence of food sources (usually though not exclusively algae), and it is often associated with high primary productivity and upwelling (Auras-Schudnagies et al., 1989; Darling et al., 2017; Schiebel et al., 1997; Schiebel et al., 2017). In contrast with the 1960s, when it was abundant as far south as Bermuda, *G. bulloides* is largely absent below Cape Cod in ECOA assemblages and is not the most abundant species at any station. This discrepancy cannot be explained by seasonality, as ECOA tows fall within the July-September range of peak abundance for the species (Tolderlund & Bé, 1971). In the ECOA data, *G. bulloides* has been replaced as the dominant northern species by the cool-water species *N. incompta,* which is more than twelve times as abundant as *G. bulloides*. Bé and

Tolderlund's suggestion of using the ratio of *G. bulloides* to *G. ruber* as a proxy for palaeoceanographic temperature gradients, therefore, may no longer be possible given modern planktonic foraminiferal assemblages in this region. Instead, a ratio of *N. incompta* to *G. ruber* may now provide a more accurate assessment of the temperature of a sample.

The north-south succession of species observed by Bé and Tolderlund remains largely consistent. Cool-water species such as *N. pachyderma* and *N. incompta* (reported in Bé and Tolderlund as left- and right-coiling morphotypes of *N. pachyderma*) as well as *T. quinqueloba* were dominant in ECOA assemblages at sites within the Gulf of Maine. Similar to the 1960s, *G. inflata* was most common in the transitional sites between northern (heavily *N. incompta*) and southern (heavily *G. ruber*) sites. However, the species shows a northward expansion. Whereas *G. inflata* was near-absent in subpolar waters in the 1960s, it is present at nearly all ECOA sites in the subpolar waters of the Gulf of Maine. It is also nearly five times more abundant than *G. bulloides* in ECOA tows despite being a species whose abundance has been shown to peak in late winter/early spring rather than summer at similar latitudes (Tolderlund & Bé, 1971). Consistent with 1960s data, the most common warm-water species are *G. ruber albus* and *G. ruber ruber*. However, ECOA assemblages have much higher relative abundances of these two species. Whereas *G. ruber* (both white and pink) makes up about 25% of Bé and Tolderlund's warm-water assemblages, it makes up more than 80% of individuals at some ECOA sites and at least 50% of every assemblage south of Cape Hatteras.

When compared to FORCIS and ForCenS, hierarchical clustering revealed notable shifts in assemblage regionality. Several ECOA stations that were grouped with southern assemblages (likely due to higher abundances of *G. inflata* and *O. riedeli* as well as the presence of *G. ruber ruber* and *G. ruber albus*) cluster instead with the northern group when all three datasets are considered. Chaabane et al. (2024) suggests that changes in temperature and ocean carbonate chemistry may make low-latitudes inhospitable for tropical species, causing a northward migration of tropical species and a corresponding range contraction for cool-water species. This difference in clustering is consistent with such a potential range shift and includes a northward expansion of both *G. ruber* species and a contraction of *N. incompta* towards higher latitudes.

Neogloboquadrina incompta is a subpolar to temperate species. However, it is increasingly being found in polar waters, suggesting northward expansion (Chaabane et al., 2025; Meilland et al., 2020; Schiebel et al., 2017). Net tows in the Barents Sea found that the species made up 15% of assemblages (Meilland et al., 2020). Although *N. incompta* is found throughout the ECOA dataset, its abundances are low in the MAB and SAB, contrasting with stations between 35 – 40º N in the ForCenS database.

G. ruber albus and *G. ruber ruber* are tropical to subtropical species abundant in the Atlantic Ocean (Hemleben et al., 1989; Tolderlund & Bé, 1971). They are shallow-dwelling and have obligate symbionts, the dinoflagellate *Pelagodinium béii* (Hemleben et al., 1989; Rebotim et al., 2017; Takagi et al., 2019). The range of this species has been observed to increase in abundance and expand north in response to past increases in SST during the mid-Piacenzian warm period (Lam & Leckie, 2020; Lutz, 2011) and over the past 74.7 ka, in the transition from a glacial to an interglacial period (Bonfardeci et al., 2018). In addition, both *G. ruber* varieties have increased in abundance at low latitudes in recent decades (Chaabane et al., 2024), although a northward expansion in the modern Atlantic Ocean since Bé and Tolderlund (1971) has not been documented until this study.

The zone of transition between northern and southern assemblages has shifted north from Cape Hatteras, which is typically considered an oceanographic feature of ecological relevance.

Narrowing of the continental shelf near Cape Hatteras influences cross-shelf water flow between the coast and open ocean, creating a unique environment in which warm and saline Gulf Stream waters mix with coastal freshwater outflow from the Chesapeake Bay and cold water from the southern reach of the Labrador Current (Townsend et al., 2006). These conditions result in a separation between the South and Mid-Atlantic Bights that drives a divide in the genetics and distribution of species either exclusively above or below Cape Hatteras (Engle & Summers, 1999; McCartney et al., 2013; Pappalardo et al., 2015; Roy et al., 2012; Rulifson et al., 2020). However, species range shifts as a result of warming waters may now be occurring around Cape Hatteras due to changes in habitat related to increasing temperatures (Friedland et al., 2020). Invertebrate and fish species from lower latitudes have established populations in the Mid-Atlantic Bight and Gulf of Maine (Friedland et al., 2020), and the distribution of 18 abundant benthic invertebrates, including polychaetes, gastropods, and bivalves, shifted north along the coast from 1990-2010, sometimes across the Cape Hatteras boundary (Hale et al., 2017). Additionally, five species from the Gulf of Mexico and Caribbean were found north of Cape Hatteras where they had never been recorded before, suggesting that warming may be enough to drive poleward range shifts despite traditionally recognized zoogeographical boundaries (Hale et al., 2017). These trends have also been recorded in larger pelagic organisms, and important fisheries species such as American shad, alewife, silver and red hake, and yellowtail flounder have shifted northward along the Atlantic coast since the 1970s (Nye et al., 2009). Shifts were more pronounced for populations in the Mid-Atlantic Bight than those the Gulf of Maine (Nye et al., 2009), suggesting that the MAB in particular may be shifting toward conditions that are more similar to more southern regions (Friedland et al., 2020).

A shift in the boundary between foraminiferal assemblage types from Cape Hatteras north to Cape Cod is the first example of this shift occurring in a holoplanktonic group. Additionally, the Gulf Stream has shifted both northward and laterally toward the coast since 2001 (Todd & Ren, 2023), which could also provide a mechanism for species dispersal farther north than previously recorded. As the Arctic source waters of the Labrador Current warm and incursions from the Gulf Stream brings warm southern water farther north (Seidov et al., 2021; Shearman & Lentz, 2010), these northern habitats are becoming more hospitable to the warm-water species that were not previously found there. A combination of these dynamics is likely responsible for the breakdown in the strong biogeographic boundary near Cape Hatteras.

5. CONCLUSIONS

This study provides a snapshot of modern planktonic foraminiferal assemblages along the Northwest Atlantic margin. We find that species distribution shifts with latitude, with a distinct transition in assemblage around Cape Cod. No single environmental variable measured at the time of sampling provides high explanatory power for foraminiferal abundance or size, underscoring that the interplay between temperature, carbonate chemistry, and numerous other variables is key in shaping foraminiferal ecology. Comparison of this data with historical datasets reveals a northward shift in the divide between northern and southern species assemblages, from Cape Hatteras to Cape Cod. This displacement of biogeographic boundaries since the 1960s underscores how migration and range shifts of individual species are dramatically reshaping community composition. Rather than adapting to new environmental conditions in their historical ranges, foraminiferal species appear bound to particular environmental conditions and must therefore shift in range. Changes in species distributions and decreases in formerly abundant species such as *G. bulloides* alter the baseline relationships between assemblage composition and environmental conditions as they have been traditionally understood, complicating the ability to compare present and future foraminiferal ecology with fossil records.

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APPENDICES

Appendix A: Study data

Table A1. Environmental data from all ECOA tow stations.

Station	Latitude	Longitude	Date	Depth (m)	Surface temperature (°C)	Surface salinity (‰)	pH	DIC (µmol/kg)	Oxygen (µmol/kg)	Volume (L)
1	43.51	-69.93	2022-08-08	115	21.36	31.57	7.99	1896.70	267.3	190.02
2	43.58	-69.50	2022-08-09	140	20.74	32.09	8.06	1897.90	278	200.63
3	43.72	-69.37	2022-08-09	87	18.31	31.99	7.98	1933.30	288	157.49
4	43.73	-68.83	2022-08-09	105	14.85	32.50	7.95	1975.20	304	161.24
6	44.34	-67.41	2022-08-09	70	12.98	32.82	7.88	2022.20	293.9	111.16
9	44.88	-66.56	2022-08-10	100	16.24	31.83	7.92	1954.40	269.5	236.59
13	43.88	-66.34	2022-08-11	60	14.38	32.50	7.81	2029.70	278.1	102.31
16	43.74	-66.86	2022-08-11	150	16.39	32.56	7.93	1983.90	281.2	219.29
23	43.34	-65.25	2022-08-12	100	16.41	31.74	7.89	1956.60	276.1	159.40
24	43.85	-64.15	2022-08-12	145	18.90	31.02	7.88	1945.60	244.6	237.47
27	43.88	-62.89	2022-08-13	268	19.50	30.88	7.90	1933.10	246.1	131.41
29	43.19	-62.10	2022-08-13	95	21.05	31.44				184.20
32	44.13	-58.17	2022-08-14	730	21.39	31.06	7.91	1932.80	234.8	270.96

Table A1 (continued).

35	45.16	-59.18	NA	100	20.23	30.37	7.89	1923.90	237.9	191.38
37	45.66	-59.71	2022-08-15	125	19.85	29.80	7.92	1900.30	247.9	182.37
39	43.20	-65.19	2022-08-16	150	14.22	31.67	7.86	1983.80	287.8	140.27
54	43.06	-66.85	2022-08-18	155	15.77	32.49	7.91	1994.30	263.7	329.49
59	41.61	-66.90	2022-08-18	60	17.48	32.72	7.87	2014.40	242.4	72.01
60	41.11	-66.70	2022-08-19	80	20.29	32.50	7.98	1959.20	239.2	116.74
61	41.04	-66.58	2022-08-19	80	20.97	32.63	7.99	1960.20	235.6	133.01
62	40.95	-66.56	2022-08-19	115	21.47	32.63	7.99	1959.10	232.7	189.47
63	40.90	-66.56	2022-08-19	310	21.84	32.61	7.99	1957.90	229.4	310.03
67	40.69	-66.75	2022-08-20	630	22.19	32.60	7.99	1956.30	230.7	316.02
96	41.30	-70.52	2022-08-25	12	20.77	32.18	7.85	1979.30	234.9	159.72
113	40.33	-72.03	2022-08-27	63	24.79	32.86	8.00	1945.80	215.9	90.51
115	39.98	-71.83	2022-08-27	90	24.94	34.17	8.04	1991.60	212.9	176.95
123	39.64	-72.92	2022-08-28	65	25.91	32.31	7.97	1942.00	218.7	90.59
124	39.46	-72.69	2022-09-07	84	24.62	32.79	8.02	1943.10	215.2	158.45

Table A1 (continued).

126	39.27	-72.45	2022-08-28	150	25.54	33.88	8.04	1980.20	210.6	216.90
127	39.08	-72.23	2022-09-07	1515	26.49	35.04	8.05	1987.80	211.8	307.32
150	37.91	-74.77	2022-09-10	31	23.68	32.21	7.95	1955.30	217.1	142.50
151	37.84	-74.57	2022-09-10	53	23.63	33.17	8.00	1975.20	217.6	131.49
152	37.75	-74.35	2022-09-10	71	23.99	33.17	8.00	1970.80	216.3	133.01
157	36.74	-74.79	2022-09-11	63	24.77	33.13	8.03	1952.60	216.2	144.57
158	36.68	-74.58	2022-09-11	1260	24.89	33.17	8.03	1951.90	214.4	336.75
159	36.61	-74.34	2022-09-11	1900	26.44	35.95	8.07	2050.50	202.3	352.54
164	35.53	-75.01	2022-09-12	42	25.32	32.34	7.99	1958.70	212.6	90.75
165	35.57	-75.18	2022-09-12	34	25.48	30.25	7.98	1973.40	212.2	91.86
169	34.13	-77.08	2022-09-13	30	28.27	35.98	8.08	2043.20	198.7	87.32
170	33.83	-77.07	2022-09-13	34	28.69	36.01	8.09	2043.60	196.1	104.70
175	33.25	-75.79	2022-09-14	3032	29.03	36.23	5.48	0.00	0	329.89
178	32.23	-78.26	2022-09-15	374	30.30	35.95	8.11	2011.10	194.7	401.82
179	32.39	-78.48	2022-09-15	264	30.50	35.51	8.13	2009.90	196.9	274.23

Table A1 (continued).

180	32.58	-78.71	2022-09-15	43	29.58	35.99	8.10	2025.80	195.4	116.50
181	32.78	-78.92	2022-09-15	31	27.80	36.08	8.08	2052.50	198.8	132.93
186	31.41	-80.87	2022-09-16	21	28.61	35.59	8.04	2036.60	191.6	88.35
190	31.20	-80.25	2022-09-17	38	28.56	36.13	8.08	2058.40	198.4	151.51
191	31.06	-79.90	2022-09-18	125	28.56	35.59	8.10	2047.00	199.6	290.58
197	29.74	-77.20	2022-09-18	919	29.68	36.32	8.10	2028.60	193.3	284.60
199	29.23	-76.44	2022-09-19	5000	29.50	36.32	8.09	2026.00	193.9	310.19
201	29.17	-78.08	2022-09-20	892	29.35	36.10	8.09	2018.50	193.6	339.70
202	29.02	-78.62	2022-09-20	866	29.76	36.08	8.10	2012.60	192.3	339.78
208	28.78	-80.43	2022-09-21	22	28.92	35.87	8.07	2048.60	194.1	75.75
209	28.75	-80.58	2022-09-21	18	29.23	36.15	8.11	2028.30	221.1	60.92
210	27.00	-79.98	2022-09-22	76	30.19	34.26	8.14	2015.90	196.9	138.03
211	26.98	-79.92	2022-09-22	175	30.15	34.16	8.14	2012.00	200	277.50
212	27.00	-79.86	2022-09-23	279	30.10	34.17	8.14	2014.60	197.2	365.77
213	26.99	-79.79	2022-09-23	386	30.39	34.55	8.13	2022.30	197.1	374.86

Table A1 (continued).

214	27.00	-79.62	2022- 09-23	633	30.19	35.33	8.11	2026.20	195. 1	366.33
222	29.99	-81.11	2022- 09-22	17	28.65	35.90	8.06	2059.10	197. 1	52.15
8888	42.40	-70.10	2022- 08-07	80	19.15	31.88	NA	NA	NA	82.05

Table A2. Total concentration of all foraminifera in the study (individuals/L).

Station	N. dutertrei	N. glutinata	N. incompta	N. pachyderma	T. quinqueloba	G. bulloides	B. variabilis	G. calida	G. conglobatus	G. conglomerata	G. crassiformis	G. falconensis	G. inflata	G. cultrata	G. radians	G. ruber albus	G. ruber ruber	G. rubescens	G. siphonifera	G. tenellus	G. ungulata	G. uvula	H. pelagica	O. riedeli	O. universa	T. sacculifer	G. truncatulinoides	Unknown
1.00	0.02	0.09	0.31	0.11	0.20	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.36
3.00	0.00	0.00	0.34	0.08	0.08	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08
4.00	0.00	0.00	0.99	0.22	4.60	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.43
6.00	0.00	0.00	0.66	0.02	0.51	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.41
16.00	0.00	0.00	0.18	0.00	0.26	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.18
23.00	0.00	0.03	1.36	0.45	0.79	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	1.16
24.00	0.00	0.00	0.46	0.12	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.69
27.00	0.02	0.00	0.55	0.03	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20
29.00	0.06	0.00	0.14	0.00	0.11	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11
32.00	0.03	0.05	0.42	0.00	0.16	0.07	0.00	0.00	0.00	0.00	0.01	0.00	0.22	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20
35.00	0.01	0.00	0.19	0.00	0.02	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05
37.00	0.01	0.08	0.08	0.20	0.09	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07
39.00	0.01	0.11	0.38	0.07	0.08	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.26
54.00	0.06	0.16	0.95	0.07	0.24	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.47
59.00	0.12	0.00	0.25	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
96.00	0.00	0.00	0.08	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.01
113.00	0.00	0.08	0.23	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.17	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.31	0.00	0.01	0.00	0.28
115.00	0.00	0.00	0.16	0.00	0.01	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.90	0.01	0.01	0.07	0.18	0.01	0.00	0.02	0.00	0.00	0.00	0.00	0.02	0.02	0.00	0.37
123.00	0.00	0.00	0.81	0.00	0.01	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.66	0.00	0.00	0.34	0.29	0.00	0.00	0.00	0.00	0.00	0.00	3.31	0.00	0.00	0.00	0.78
124.00	0.00	0.15	0.42	0.00	0.24	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.76	0.00	0.00	0.24	0.24	0.00	0.01	0.00	0.00	0.00	0.00	0.16	0.00	0.00	0.00	0.44
126.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00	0.10	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11
127.00	0.01	0.01	0.02	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.29	0.29	0.00	0.31	0.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.17
150.00	0.01	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.04	0.34	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
152.00	0.00	0.30	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.03	0.00	0.48	1.35	0.00	0.00	0.00	0.00	0.00	0.00	1.20	0.00	0.00	0.00	0.36
165.00	0.00	0.35	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.18	2.92	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.20
169.00	0.00	0.25	0.05	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.05	0.00	0.02	2.08	3.53	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.39
170.00	0.00	0.53	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	1.91	4.36	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.04
175.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.31	0.66	0.01	0.00	0.04	0.00	0.00	0.02	0.00	0.01	0.00	0.00	0.15
178.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.04	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.04
179.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.22	0.00	0.03	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.04
186.00	0.00	0.00	0.05	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.18	0.59	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
190.00	0.00	0.19	0.01	0.00	0.01	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.02	0.01	0.00	0.29	3.06	0.03	0.00	0.00	0.01	0.01	0.11	0.00	0.00	0.05	0.00	0.58
191.00	0.00	0.30	0.00	0.00	0.00	0.00	0.03	0.17	0.00	0.00	0.00	0.00	0.04	0.03	0.00	0.21	0.32	0.14	0.01	0.12	0.00	0.00	0.07	0.00	0.15	0.00	0.00	0.66
197.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.24	0.21	0.00	0.03	0.03	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.23
199.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.25	0.06	0.00	0.03	0.00	0.00	0.00	0.04	0.00	0.02	0.00	0.00	0.14
201.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.63	0.19	0.00	0.07	0.06	0.00	0.00	0.02	0.00	0.02	0.00	0.00	0.11
202.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.40	0.14	0.01	0.02	0.04	0.00	0.00	0.05	0.00	0.01	0.00	0.00	0.13
208.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
210.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.42	2.91	0.00	0.06	0.00	0.00	0.00	0.03	0.00	0.03	0.00	0.00	0.06
213.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.61	0.00	0.41	0.01	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.03
214.00	0.01	0.05	0.01	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.02	0.02	0.00	0.46	1.83	0.02	0.27	0.00	0.00	0.00	0.02	0.00	0.02	0.00	0.01	0.08

Table A3. Keyence counts and average measurements—live foraminifera

Haul	Species	Count	Average surface area (µm²)	Max diameter (µm)	Total surface area of species (µm²)	Total surface area of sample (µm²)
5	*T. quinqueloba*	488.00	23183.53	205.65	11633956.37	34575150.13
11	*Unknown*	44.00	28168.89	213.26	1239431.19	2784140.73
42	*Unknown*	60.00	33245.43	232.00	1994725.81	15385440.70
56	*G. siphonifera*	0.00	0.00	0.00	0.00	0.00
61	*Unknown*	144.00	104171.08	515.56	7740547.11	29743578.16
72	*G. siphonifera*	99.00	273549.83	789.45	25326480.47	36415884.95
2	*N. dutertrei*	2.00	31743.24	230.40	63486.47	5470834.47
2	*N. glutinata*	14.00	40668.94	264.59	569365.19	5470834.47
2	*N. incompta*	38.00	32205.80	232.72	1223820.35	5470834.47
2	*N. pachyderma*	18.00	54389.31	297.97	979007.64	5470834.47
2	*T. quinqueloba*	16.00	23377.62	196.13	374041.93	5470834.47
2	*Unknown*	54.00	29304.57	223.27	1582446.65	5470834.47
42	*N. incompta*	60.00	31928.66	229.90	1915719.31	15385440.70
42	*T. quinqueloba*	0.00	0.00	0.00	0.00	15385440.70
42	*G. ruber albus*	34.00	57521.91	302.08	1955745.06	15385440.70
43	*G. cultrata*	82.00	359047.12	853.18	28172853.10	43704909.05
43	*N. glutinata*	0.00	0.00	0.00	0.00	43704909.05
43	*N. incompta*	0.00	0.00	0.00	0.00	43704909.05
43	*G. ruber albus*	66.00	47682.05	266.72	3147015.33	43704909.05
43	*G. ruber ruber*	56.00	43942.31	248.42	2460769.39	43704909.05
43	*Unknown*	46.00	41027.42	244.26	1887261.41	43704909.05
44	*N. dutertrei*	0.00	0.00	0.00	0.00	3503674.64
44	*G. inflata*	8.00	46395.97	271.74	371167.73	3503674.64
44	*G. ruber albus*	4.00	45244.65	296.11	180978.60	3503674.64

Table A3 (continued).

44	*G. ruber ruber*	44.00	65362.46	328.19	2875948.43	3503674.64
46	*Benthic*	12.00	25339.11	191.82	304069.31	12201607.51
46	*N. glutinata*	36.00	24809.86	195.60	893155.01	12201607.51
46	*N. incompta*	0.00	0.00	0.00	0.00	12201607.51
46	*G. inflata*	12.00	59467.52	316.21	713610.24	12201607.51
46	*O. riedeli*	100.00	18552.80	174.72	1855279.70	12201607.51
46	*G. ruber ruber*	160.00	29351.00	223.64	4696160.03	12201607.51
46	*Unknown*	40.00	18351.82	169.62	734072.71	12201607.51
5	*N. incompta*	136.00	38253.12	248.83	5202423.77	34575150.13
5	*Unknown*	362.00	28490.49	229.93	10663617.53	34575150.13
51	*O. riedeli*	0.00	0.00	0.00	0.00	56405927.08
51	*G. ruber albus*	382.00	86067.69	414.69	32090200.04	56405927.08
51	*G. ruber ruber*	258.00	90992.92	446.92	22016543.08	56405927.08
51	*Unknown*	16.00	60877.05	319.13	974032.78	56405927.08
52	*Benthic*	52.00	128851.75	447.18	6700290.79	29812839.47
52	*N. glutinata*	20.00	24116.30	194.68	482326.06	29812839.47
52	*G. ruber albus*	180.00	45124.51	281.48	8306326.97	29812839.47
52	*G. ruber ruber*	288.00	53758.26	369.89	13088030.80	29812839.47
52	*G. tenellus*	2.00	55396.90	290.08	110793.80	29812839.47
52	*Unknown*	28.00	17498.46	163.96	489956.96	29812839.47
53	*Benthic*	8.00	73146.63	315.87	585173.04	29630670.07
53	*N. glutinata*	52.00	23674.10	194.86	1231053.00	29630670.07
53	*G. ruber ruber*	450.00	43906.51	280.73	19689849.02	29630670.07
59	*Benthic*	32.00	25695.04	204.57	822241.14	2956996.31
59	*N. incompta*	0.00	0.00	0.00	0.00	2956996.31
59	*G. ruber albus*	12.00	51775.87	274.24	621310.43	2956996.31
61	*Benthic*	68.00	38013.67	241.62	2584929.40	29743578.16
61	*G. calida*	8.00	45736.77	285.85	365894.15	29743578.16
61	*N. glutinata*	36.00	31267.50	232.02	1125629.99	29743578.16

Table A3 (continued).

61	*G. inflata*	8.00	21379.87	182.14	171038.99	29743578.16
61	*G. ruber albus*	0.00	0.00	0.00	0.00	29743578.16
61	*G. ruber ruber*	0.00	0.00	0.00	0.00	29743578.16
61	*G. rubescens*	4.00	49114.78	274.59	196459.11	29743578.16
61	*G. siphonifera*	0.00	0.00	0.00	0.00	29743578.16
67	*Benthic*	0.00	0.00	0.00	0.00	104086.39
69	*H. pelagica*	0.00	0.00	0.00	0.00	15859601.21
69	*G. ruber albus*	56.00	37335.58	234.31	2090792.46	15859601.21
69	*G. ruber ruber*	382.00	32295.34	245.90	11853891.42	15859601.21
69	*Unknown*	6.00	12730.31	141.61	76381.86	15859601.21
74	*Benthic*	0.00	0.00	0.00	0.00	62908895.23
74	*G. calida*	0.00	0.00	0.00	0.00	62908895.23
74	*N. glutinata*	16.00	18901.38	166.66	302422.06	62908895.23
74	*N. incompta*	2.00	59053.36	311.18	118106.73	62908895.23
74	*H. pelagica*	6.00	156120.47	530.87	936722.80	62908895.23
74	*G. ruber albus*	141.00	44151.31	288.08	5961442.70	62908895.23
74	*G. ruber ruber*	642.00	36378.47	277.44	24768720.33	62908895.23
74	*G. rubescens*	2.00	13696.54	154.55	27393.08	62908895.23
74	*Unknown*	22.00	90375.52	338.38	1988261.42	62908895.23
9	*G. bulloides*	0.00	0.00	0.00	0.00	1461580.51
9	*N. incompta*	12.00	27271.22	203.44	327254.60	1461580.51
9	*T. quinqueloba*	20.00	20318.64	185.28	406372.88	1461580.51
9	*Unknown*	28.00	25998.32	205.52	727953.02	1461580.51
10	*Benthic*	21.00	42341.84	257.18	889178.56	12772341.99
10	*N. incompta*	170.00	34198.63	232.45	5813767.26	12772341.99
10	*N. pachyderma*	36.00	35744.76	237.46	1286811.40	12772341.99
10	*T. quinqueloba*	14.00	22418.79	183.50	313863.11	12772341.99
10	*Unknown*	137.00	28525.99	213.68	3908060.46	12772341.99
10	*G. uvula*	4.00	41392.75	255.59	165570.99	12772341.99

Table A3 (continued).

11	*N. incompta*	37.00	32357.99	225.91	1197245.58	2784140.73
11	*G. inflata*	1.00	44482.17	256.42	44482.17	2784140.73
11	*N. pachyderma*	4.00	30381.57	217.70	121526.26	2784140.73
11	*T. quinqueloba*	7.00	25922.22	200.71	181455.53	2784140.73
12	*N. dutertrei*	0.00	0.00	0.00	0.00	1072845.58
12	*N. incompta*	13.00	31107.77	224.10	404401.01	1072845.58
12	*G. inflata*	9.00	40800.72	249.65	367206.47	1072845.58
12	*N. pachyderma*	1.00	82919.16	360.73	82919.16	1072845.58
12	*T. quinqueloba*	9.00	17897.23	169.11	161075.08	1072845.58
12	*Unknown*	3.00	19081.29	179.31	57243.87	1072845.58
13	*G. bulloides*	3.00	53963.07	301.35	161889.21	2244649.80
13	*N. dutertrei*	8.00	58490.87	301.50	467927.00	2244649.80
13	*N. incompta*	20.00	32190.11	228.63	643802.13	2244649.80
13	*T. quinqueloba*	18.00	20045.28	177.63	360814.99	2244649.80
13	*Unknown*	11.00	20856.82	184.00	229425.06	2244649.80
14	*G. bulloides*	18.00	49463.11	283.47	890335.95	10410850.19
14	*N. dutertrei*	5.00	59464.48	305.55	297322.41	10410850.19
14	*N. incompta*	109.00	33869.23	233.52	3691746.44	10410850.19
14	*G. inflata*	57.00	39184.92	245.08	2233540.64	10410850.19
14	*N. pachyderma*	0.00	0.00	0.00	0.00	10410850.19
14	*T. quinqueloba*	39.00	21259.30	182.91	829112.59	10410850.19
15	*N. incompta*	26.00	29918.83	220.81	777889.60	1500528.11
15	*Unknown*	8.00	23349.87	199.79	186798.98	1500528.11
16	*G. bulloides*	7.00	65471.90	324.97	458303.32	2167636.06
16	*N. dutertrei*	0.00	0.00	0.00	0.00	2167636.06
16	*N. glutinata*	8.00	34592.68	236.75	276741.47	2167636.06
16	*N. pachyderma*	20.00	28202.11	205.94	564042.26	2167636.06
16	*T. quinqueloba*	10.00	21531.76	188.26	215317.62	2167636.06
16	*Unknown*	6.00	25768.45	208.30	154610.69	2167636.06

Table A3 (continued).

17	*G. bulloides*	2.00	42820.50	261.79	85641.01	3512016.38
17	*N. pachyderma*	6.00	30402.07	213.98	182412.43	3512016.38
17	*Unknown*	24.00	21558.60	185.78	517406.31	3512016.38
18	*G. bulloides*	0.00	0.00	0.00	0.00	20183858.37
18	*N. dutertrei*	0.00	0.00	0.00	0.00	20183858.37
18	*N. glutinata*	49.00	48661.28	281.46	2384402.71	20183858.37
18	*N. incompta*	272.00	42439.31	260.63	11555302.25	20183858.37
18	*N. pachyderma*	14.00	49129.97	279.06	687819.52	20183858.37
18	*T. quinqueloba*	47.00	25689.70	201.93	1207416.06	20183858.37
18	*Unknown*	137.00	29900.57	218.80	4096378.32	20183858.37
18	*G. uvula*	5.00	50507.90	281.97	252539.51	20183858.37
19	*Benthic*	0.00	0.00	0.00	0.00	62335.18
19	*N. dutertrei*	0.00	0.00	0.00	0.00	62335.18
19	*N. incompta*	0.00	0.00	0.00	0.00	62335.18
19	*T. quinqueloba*	0.00	0.00	0.00	0.00	62335.18
37	*Benthic*	5.00	57271.82	310.72	286359.08	1006576.48
37	*N. incompta*	6.00	35988.54	242.81	215931.26	1006576.48
37	*T. quinqueloba*	0.00	0.00	0.00	0.00	1006576.48
37	*Unknown*	0.00	0.00	0.00	0.00	1006576.48
38	*N. glutinata*	5.00	34016.42	230.22	170082.09	3502608.38
38	*N. incompta*	15.00	42203.83	263.73	633057.51	3502608.38
38	*G. inflata*	5.00	31697.99	223.41	158489.93	3502608.38
38	*T. quinqueloba*	0.00	0.00	0.00	0.00	3502608.38
38	*O. riedeli*	11.00	21611.02	184.39	237721.23	3502608.38
38	*G. ruber albus*	14.00	66311.20	324.02	928356.76	3502608.38
38	*Unknown*	15.00	23158.80	188.48	347381.94	3502608.38
39	*G. conglomerata*	0.00	0.00	0.00	0.00	10698794.99
39	*N. incompta*	14.00	36614.11	238.97	512597.51	10698794.99
39	*G. inflata*	120.00	50671.71	275.08	6080605.58	10698794.99

Table A3 (continued).

39	*T. quinqueloba*	0.00	0.00	0.00	0.00	10698794.99
39	*G. ruber albus*	3.00	59200.20	307.30	177600.59	10698794.99
39	*G. ruber ruber*	24.00	35527.18	226.06	852652.33	10698794.99
39	*G. tenellus*	3.00	36763.18	238.09	110289.53	10698794.99
39	*Unknown*	32.00	34110.06	232.34	1091521.84	10698794.99
4	*G. bulloides*	0.00	0.00	0.00	0.00	1743987.70
4	*N. incompta*	29.00	35116.70	235.73	1018384.32	1743987.70
4	*N. pachyderma*	6.00	59896.86	322.62	359381.16	1743987.70
4	*T. quinqueloba*	8.00	23916.42	201.05	191331.34	1743987.70
4	*Unknown*	4.00	43722.72	263.44	174890.89	1743987.70
40	*G. bulloides*	0.00	0.00	0.00	0.00	13083595.65
40	*N. incompta*	59.00	30977.50	225.93	1827672.38	13083595.65
40	*G. inflata*	59.00	34642.87	246.14	2174477.14	13083595.65
40	*T. quinqueloba*	0.00	0.00	0.00	0.00	13083595.65
40	*G. ruber albus*	20.00	50672.55	287.23	1013450.97	13083595.65
40	*G. ruber ruber*	22.00	63228.84	314.57	1391034.48	13083595.65
40	*Unknown*	45.00	29188.58	222.29	1313486.12	13083595.65
41	*N. incompta*	8.00	36570.66	244.86	292565.25	2961913.02
41	*G. inflata*	34.00	46684.64	263.04	1587277.91	2961913.02
41	*G. ruber albus*	6.00	22578.78	156.01	135472.70	2961913.02
41	*G. ruber ruber*	2.00	19978.85	178.22	39957.70	2961913.02
41	*Unknown*	8.00	64337.84	316.34	514702.69	2961913.02
54	*G. cultrata*	2.00	251992.71	651.01	503985.41	12567088.52
54	*O. universa*	1.00	61557.51	284.24	61557.51	12567088.52
54	*H. pelagica*	3.00	81746.58	381.57	245239.73	12567088.52
54	*G. ruber albus*	85.00	31528.16	214.80	2679893.34	12567088.52
54	*G. ruber ruber*	204.00	37182.60	244.40	7712010.23	12567088.52
54	*G. siphonifera*	0.00	0.00	0.00	0.00	12567088.52
54	*G. tenellus*	4.00	30149.94	213.75	120599.74	12567088.52

Table A3 (continued).

54	*Unknown*	39.00	20165.00	169.00	786434.87	12567088.52
55	*G. calida*	5.00	38483.69	276.61	192418.47	484782.21
55	*G. cultrata*	0.00	0.00	0.00	0.00	484782.21
55	*N. glutinata*	0.00	0.00	0.00	0.00	484782.21
55	*N. incompta*	0.00	0.00	0.00	0.00	484782.21
55	*H. pelagica*	0.00	0.00	0.00	0.00	484782.21
55	*G. radians*	0.00	0.00	0.00	0.00	484782.21
55	*G. ruber ruber*	0.00	0.00	0.00	0.00	484782.21
55	*G. siphonifera*	0.00	0.00	0.00	0.00	484782.21
55	*G. tenellus*	0.00	0.00	0.00	0.00	484782.21
55	*Unknown*	0.00	0.00	0.00	0.00	484782.21
56	*G. calida*	0.00	0.00	0.00	0.00	0.00
56	*G. cultrata*	0.00	0.00	0.00	0.00	0.00
56	*N. glutinata*	0.00	0.00	0.00	0.00	0.00
56	*N. incompta*	0.00	0.00	0.00	0.00	0.00
56	*H. pelagica*	0.00	0.00	0.00	0.00	0.00
56	*G. ruber albus*	0.00	0.00	0.00	0.00	0.00
56	*G. ruber ruber*	0.00	0.00	0.00	0.00	0.00
56	*G. tenellus*	0.00	0.00	0.00	0.00	0.00
56	*Unknown*	0.00	0.00	0.00	0.00	0.00
56	*G. uvula*	0.00	0.00	0.00	0.00	0.00
6	*G. bulloides*	1.00	90872.53	412.80	90872.53	3565311.64
6	*N. incompta*	47.00	36093.96	241.14	1696416.12	3565311.64
6	*N. pachyderma*	0.00	0.00	0.00	0.00	3565311.64
6	*T. quinqueloba*	37.00	25373.16	212.87	938806.75	3565311.64
6	*Unknown*	21.00	38196.14	250.78	802118.91	3565311.64
60	*Benthic*	2.00	51961.08	326.92	103922.16	20366151.18
60	*G. calida*	0.00	0.00	0.00	0.00	20366151.18
60	*G. cultrata*	0.00	0.00	0.00	0.00	20366151.18

Table A3 (continued).

60	*N. incompta*	1.00	33710.21	247.97	33710.21	20366151.18
60	*G. inflata*	0.00	0.00	0.00	0.00	20366151.18
60	*G. ruber ruber*	454.00	32545.92	232.50	14382530.81	20366151.18
60	*Unknown*	82.00	20633.69	179.98	1691962.74	20366151.18
62	*N. incompta*	0.00	0.00	0.00	0.00	7603619.32
62	*H. pelagica*	0.00	0.00	0.00	0.00	7603619.32
62	*G. ruber albus*	63.00	35324.57	231.62	2225448.00	7603619.32
62	*G. ruber ruber*	58.00	42919.07	254.84	2489306.26	7603619.32
62	*G. siphonifera*	4.00	64750.21	335.11	259000.86	7603619.32
62	*G. tenellus*	7.00	38686.09	239.06	270802.62	7603619.32
62	*Unknown*	57.00	23945.04	191.52	1364867.08	7603619.32
63	*G. calida*	0.00	0.00	0.00	0.00	5109042.51
63	*N. incompta*	0.00	0.00	0.00	0.00	5109042.51
63	*O. universa*	4.00	227663.15	549.72	910652.60	5109042.51
63	*H. pelagica*	6.00	28127.79	234.73	168766.73	5109042.51
63	*G. ruber albus*	70.00	28529.41	207.97	1997058.82	5109042.51
63	*G. ruber ruber*	16.00	41909.17	258.67	670546.72	5109042.51
63	*G. siphonifera*	6.00	68327.70	360.00	409966.22	5109042.51
63	*Unknown*	32.00	14922.32	153.34	477514.22	5109042.51
64	*G. cultrata*	1.00	263885.60	677.56	263885.60	9877355.82
64	*N. incompta*	0.00	0.00	0.00	0.00	9877355.82
64	*O. universa*	3.00	120397.22	412.68	361191.67	9877355.82
64	*N. pachyderma*	0.00	0.00	0.00	0.00	9877355.82
64	*H. pelagica*	5.00	59358.16	321.73	296790.80	9877355.82
64	*G. ruber albus*	159.00	27308.19	206.99	4375638.11	9877355.82
64	*G. ruber ruber*	59.00	41310.88	248.64	2437342.05	9877355.82
64	*G. siphonifera*	12.00	72517.81	350.15	870213.72	9877355.82
64	*G. tenellus*	8.00	37679.07	232.60	301432.52	9877355.82
64	*Unknown*	27.00	20992.61	184.27	566800.56	9877355.82

Table A3 (continued).

64	*G. uvula*	0.00	0.00	0.00	0.00	9877355.82
65	*N. incompta*	2.00	40493.57	256.31	80987.13	5797050.37
65	*G. inflata*	0.00	0.00	0.00	0.00	5797050.37
65	*H. pelagica*	12.00	41047.45	269.84	492569.44	5797050.37
65	*G. ruber albus*	81.00	27102.52	205.24	2195304.14	5797050.37
65	*G. ruber ruber*	39.00	38270.69	245.25	1492556.99	5797050.37
65	*G. rubescens*	0.00	0.00	0.00	0.00	5797050.37
65	*G. siphonifera*	3.00	130664.91	476.16	391994.73	5797050.37
65	*G. tenellus*	2.00	27261.01	193.36	54522.02	5797050.37
65	*Unknown*	30.00	16366.73	164.91	491001.95	5797050.37
65	*G. uvula*	0.00	0.00	0.00	0.00	5797050.37
72	*G. calida*	0.00	0.00	0.00	0.00	36415884.95
72	*G. ruber albus*	8.00	44539.88	262.46	356319.08	36415884.95
72	*G. ruber ruber*	227.00	37035.33	261.92	8257576.73	36415884.95
72	*G. tenellus*	0.00	0.00	0.00	0.00	36415884.95
72	*Unknown*	6.00	184964.16	595.59	1109784.95	36415884.95
14	*Unknown*	55.00	30055.99	244.04	1545997.56	10410850.19
40	*O. riedeli*	300.00	17969.98	182.64	5363474.55	13083595.65
53	*G. ruber albus*	200.00	39732.15	259.12	7627104.37	29630670.07
74	*G. siphonifera*	98.00	251111.24	652.92	24600470.02	62908895.23
2	*G. bulloides*	8.00	84833.28	380.78	678666.22	5470834.47
42	*G. bulloides*	10.00	103213.94	400.46	1032139.37	15385440.70
42	*N. glutinata*	24.00	40820.63	266.73	979695.19	15385440.70
42	*G. inflata*	120.00	33646.62	225.81	4037594.30	15385440.70
42	*O. riedeli*	26.00	24672.36	198.39	641481.27	15385440.70
42	*G. ruber ruber*	38.00	71536.77	328.27	2718397.17	15385440.70
42	*G. siphonifera*	2.00	54971.61	313.07	109943.22	15385440.70
43	*G. calida*	4.00	42583.56	278.39	170334.23	43704909.05
43	*N. dutertrei*	2.00	208427.95	566.82	416855.89	43704909.05

Table A3 (continued).

43	*G. inflata*	90.00	32721.31	226.26	2944918.11	43704909.05
43	*T. sacculifer*	16.00	281556.35	677.79	4504901.60	43704909.05
44	*N. incompta*	2.00	37789.94	242.13	75579.89	3503674.64
46	*G. cultrata*	4.00	241867.79	648.12	967471.18	12201607.51
46	*G. ruber albus*	64.00	31840.46	227.25	2037789.33	12201607.51
5	*G. bulloides*	54.00	86944.77	379.02	4695017.82	34575150.13
5	*G. inflata*	8.00	43777.40	255.56	350219.22	34575150.13
5	*N. pachyderma*	36.00	56386.54	298.18	2029915.42	34575150.13
51	*G. calida*	4.00	23366.58	217.69	93466.32	56405927.08
51	*N. glutinata*	32.00	38490.15	252.04	1231684.86	56405927.08
52	*G. calida*	2.00	16258.18	182.67	32516.36	29812839.47
52	*N. incompta*	4.00	67724.20	341.48	270896.79	29812839.47
52	*G. inflata*	4.00	62177.22	311.89	248708.87	29812839.47
52	*G. radians*	2.00	41496.03	356.46	82992.06	29812839.47
53	*G. cultrata*	2.00	163687.57	530.26	327375.14	29630670.07
53	*Unknown*	4.00	29132.28	217.72	116529.12	29630670.07
53	*G. uvula*	2.00	26793.19	194.27	53586.38	29630670.07
59	*G. ruber ruber*	52.00	21983.22	191.95	1143127.59	2956996.31
59	*B. variabilis*	8.00	46289.64	332.44	370317.15	2956996.31
61	*G. cultrata*	8.00	62444.54	316.75	499556.33	29743578.16
61	*O. universa*	44.00	309540.63	649.82	13619787.57	29743578.16
61	*H. pelagica*	20.00	98416.68	448.56	1968333.60	29743578.16
61	*G. tenellus*	36.00	31480.82	212.14	1133309.49	29743578.16
61	*B. variabilis*	8.00	42261.55	313.15	338092.42	29743578.16
67	*G. ruber albus*	2.00	52043.19	286.12	104086.39	104086.39
69	*Benthic*	2.00	28348.53	214.03	56697.07	15859601.21
69	*N. incompta*	4.00	63125.00	321.54	252500.01	15859601.21
69	*O. universa*	4.00	177564.13	470.14	710256.54	15859601.21
69	*G. siphonifera*	8.00	102385.23	428.00	819081.85	15859601.21

Table A3 (continued).

74	*G. cultrata*	8.00	153450.26	509.37	1227602.09	62908895.23
74	*N. dutertrei*	2.00	90925.49	393.16	181850.99	62908895.23
74	*G. inflata*	6.00	48537.60	284.24	291225.59	62908895.23
74	*O. universa*	8.00	293351.28	709.37	2346810.22	62908895.23
74	*G. truncatulinoides*	2.00	78933.59	367.67	157867.19	62908895.23
10	*N. glutinata*	4.00	54208.37	300.36	216833.48	12772341.99
10	*G. inflata*	6.00	29709.46	210.75	178256.75	12772341.99
13	*Benthic*	2.00	54704.29	346.74	109408.57	2244649.80
13	*G. inflata*	7.00	38768.98	255.15	271382.84	2244649.80
14	*G. crassiformis*	2.00	24072.86	191.44	48145.73	10410850.19
14	*N. glutinata*	14.00	36339.62	240.49	508754.72	10410850.19
14	*G. ruber albus*	4.00	62429.35	315.86	249717.41	10410850.19
14	*G. ruber ruber*	2.00	44801.13	260.52	89602.27	10410850.19
14	*G. uvula*	1.00	26574.47	207.55	26574.47	10410850.19
15	*Benthic*	1.00	32163.98	218.92	32163.98	1500528.11
15	*G. bulloides*	3.00	45732.72	270.16	137198.15	1500528.11
15	*N. dutertrei*	1.00	35894.37	240.40	35894.37	1500528.11
15	*G. inflata*	7.00	32931.24	226.97	230518.66	1500528.11
15	*T. quinqueloba*	3.00	16642.97	158.95	49928.90	1500528.11
15	*G. ruber albus*	1.00	50135.47	285.52	50135.47	1500528.11
16	*N. incompta*	14.00	29682.55	219.89	415555.73	2167636.06
16	*G. inflata*	3.00	27688.32	209.51	83064.97	2167636.06
17	*N. dutertrei*	2.00	55196.41	296.52	110392.81	3512016.38
17	*N. glutinata*	15.00	37107.66	240.90	556614.89	3512016.38
17	*N. incompta*	53.00	31574.60	221.77	1673453.56	3512016.38
17	*G. inflata*	4.00	28679.65	208.73	114718.61	3512016.38
17	*T. quinqueloba*	11.00	24670.61	194.46	271376.76	3512016.38
19	*G. falconensis*	1.00	62335.18	305.42	62335.18	62335.18

Table A3 (continued).

37	*O. riedeli*	3.00	26319.30	199.48	78957.90	1006576.48
37	*G. ruber albus*	2.00	33464.15	234.32	66928.30	1006576.48
37	*G. ruber ruber*	9.00	39822.22	243.51	358399.95	1006576.48
38	*G. bulloides*	1.00	38330.67	251.42	38330.67	3502608.38
38	*G. ruber ruber*	17.00	52532.99	281.96	893060.84	3502608.38
38	*T. sacculifer*	1.00	96127.41	456.58	96127.41	3502608.38
39	*G. cultrata*	1.00	59054.38	334.07	59054.38	10698794.99
39	*O. universa*	4.00	307909.82	632.55	1231639.29	10698794.99
39	*G. radians*	1.00	70537.18	372.38	70537.18	10698794.99
39	*G. rubescens*	1.00	34448.39	221.16	34448.39	10698794.99
39	*T. sacculifer*	3.00	159282.79	503.49	477848.38	10698794.99
41	*G. conglobatus*	1.00	99208.59	382.43	99208.59	2961913.02
41	*O. universa*	1.00	253317.65	571.95	253317.65	2961913.02
41	*G. uvula*	1.00	39410.52	243.28	39410.52	2961913.02
54	*N. glutinata*	15.00	29089.75	212.04	436346.27	12567088.52
54	*G. rubescens*	2.00	10510.71	129.31	21021.42	12567088.52
55	*G. inflata*	1.00	46057.76	273.59	46057.76	484782.21
55	*G. ruber albus*	6.00	41051.00	251.16	246305.99	484782.21
6	*G. inflata*	1.00	37097.33	241.43	37097.33	3565311.64
60	*N. glutinata*	29.00	25741.07	202.83	746491.14	20366151.18
60	*H. pelagica*	16.00	53063.51	312.32	849016.11	20366151.18
60	*T. quinqueloba*	1.00	20049.78	178.73	20049.78	20366151.18
60	*G. ruber albus*	44.00	42677.11	255.83	1877792.66	20366151.18
60	*G. rubescens*	4.00	17172.02	164.53	68688.07	20366151.18
60	*T. sacculifer*	8.00	44895.68	264.00	359165.47	20366151.18
60	*G. ungulata*	2.00	74024.77	356.77	148049.54	20366151.18
60	*G. uvula*	1.00	32425.52	221.90	32425.52	20366151.18
60	*B. variabilis*	2.00	26173.48	260.90	52346.96	20366151.18
62	*Benthic*	1.00	46614.69	252.39	46614.69	7603619.32

Table A3 (continued).

62	*O. universa*	8.00	116922.51	417.54	935380.10	7603619.32
62	*G. rubescens*	1.00	12199.71	138.82	12199.71	7603619.32
63	*G. cultrata*	2.00	191343.49	576.67	382686.98	5109042.51
63	*G. tenellus*	1.00	39588.31	239.71	39588.31	5109042.51
63	*G. truncatulinoides*	1.00	52261.91	302.22	52261.91	5109042.51
64	*G. inflata*	1.00	32006.02	241.76	32006.02	9877355.82
64	*G. truncatulinoides*	5.00	74410.95	341.54	372054.76	9877355.82
65	*G. cultrata*	1.00	60634.03	321.00	60634.03	5797050.37
65	*O. universa*	3.00	179159.98	491.93	537479.94	5797050.37
72	*H. pelagica*	13.00	105055.67	437.22	1365723.73	36415884.95

Table A4. Keyence counts and average measurements—dead foraminifera

Haul	**Species**	**Count**	**Average surface area (µm²)**	**Max diameter (µm)**	**Total surface area of species (µm²)**	**Total surface area of sample (µm²)**
5	*T. quinqueloba*	254.00	20131.24	184.10	5127451.44	6482567.25
11	*Unknown*	120.00	27453.91	209.37	3255837.61	7378106.91
42	*Unknown*	10.00	43807.78	311.77	398896.56	1593156.01
56	*G. siphonifera*	9.00	80962.26	472.20	1031674.60	4670736.87
61	*Unknown*	48.00	23394.26	200.65	1145946.65	14479016.68
72	*G. siphonifera*	53.00	174655.03	577.05	9212884.65	10794813.04
2	*N. dutertrei*	2.00	44821.53	256.42	89643.06	1751416.06
2	*N. glutinata*	4.00	48783.53	282.55	195134.10	1751416.06
2	*N. incompta*	20.00	26388.76	210.43	527775.13	1751416.06

Table A4 (continued).

2	*N. pachyderma*	2.00	35767.52	236.58	71535.03	1751416.06
2	*T. quinqueloba*	22.00	20242.00	182.38	445324.05	1751416.06
2	*Unknown*	14.00	30143.19	213.21	422004.69	1751416.06
42	*N. incompta*	6.00	32321.95	227.42	193931.68	1593156.01
42	*T. quinqueloba*	38.00	23150.42	194.96	879715.88	1593156.01
42	*G. ruber albus*	4.00	30152.97	225.35	120611.89	1593156.01
43	*G. cultrata*	8.00	62517.45	332.87	500139.58	2537977.52
43	*N. glutinata*	2.00	17935.03	176.72	35870.07	2537977.52
43	*N. incompta*	6.00	40284.97	263.10	241709.83	2537977.52
43	*G. ruber albus*	30.00	33845.69	229.82	1015370.85	2537977.52
43	*G. ruber ruber*	12.00	50803.78	268.26	609645.37	2537977.52
43	*Unknown*	6.00	22540.30	190.11	135241.83	2537977.52
44	*N. dutertrei*	2.00	47425.77	271.14	94851.55	358263.25
44	*G. inflata*	4.00	28512.57	209.60	114050.30	358263.25
44	*G. ruber albus*	2.00	27024.06	207.11	54048.13	358263.25
44	*G. ruber ruber*	4.00	23828.32	197.49	95313.29	358263.25
46	*Benthic*	4.00	32710.78	222.71	130843.13	2517709.47
46	*N. glutinata*	4.00	58009.39	338.47	232037.55	2517709.47
46	*N. incompta*	8.00	30718.00	225.00	245744.00	2517709.47
46	*G. inflata*	8.00	18840.29	185.98	150722.34	2517709.47
46	*O. riedeli*	60.00	21641.12	191.02	1298467.35	2517709.47
46	*G. ruber ruber*	20.00	9718.46	132.84	194369.12	2517709.47
46	*Unknown*	8.00	33190.75	233.03	265526.00	2517709.47
5	*N. incompta*	24.00	29789.45	211.69	714946.86	6482567.25
5	*Unknown*	30.00	21338.96	183.67	640168.95	6482567.25
51	*O. riedeli*	2.00	20669.03	191.72	41338.07	194539.23
51	*G. ruber albus*	2.00	14958.01	156.67	29916.03	194539.23
51	*G. ruber ruber*	10.00	8831.42	120.22	88314.25	194539.23
51	*Unknown*	2.00	17485.44	171.48	34970.89	194539.23

Table A4 (continued).

52	*Benthic*	12.00	71231.82	327.39	854781.81	1799651.93
52	*N. glutinata*	2.00	44825.44	276.24	89650.87	1799651.93
52	*G. ruber albus*	2.00	36173.85	240.40	72347.69	1799651.93
52	*G. ruber ruber*	20.00	24688.62	201.80	493772.40	1799651.93
52	*G. tenellus*	2.00	50949.59	269.11	101899.19	1799651.93
52	*Unknown*	6.00	31199.99	221.59	187199.96	1799651.93
53	*Benthic*	74.00	92932.66	367.09	6877016.50	7234283.36
53	*N. glutinata*	4.00	19259.51	173.77	77038.02	7234283.36
53	*G. ruber ruber*	6.00	46704.81	270.48	280228.84	7234283.36
59	*Benthic*	56.00	35158.36	229.66	1968868.25	2318236.89
59	*N. incompta*	4.00	36514.08	252.84	146056.31	2318236.89
59	*G. ruber albus*	4.00	50828.08	286.82	203312.33	2318236.89
61	*Benthic*	144.00	35068.43	243.06	5049854.47	14479016.68
61	*G. calida*	40.00	34935.65	249.87	1397425.97	14479016.68
61	*N. glutinata*	52.00	26343.60	205.66	1369867.26	14479016.68
61	*G. inflata*	4.00	37133.78	249.91	148535.14	14479016.68
61	*G. ruber albus*	60.00	26921.18	208.39	1615271.02	14479016.68
61	*G. ruber ruber*	92.00	21812.29	183.68	2006731.10	14479016.68
61	*G. rubescens*	36.00	22437.70	186.25	807757.02	14479016.68
61	*G. siphonifera*	4.00	234407.01	693.71	937628.06	14479016.68
67	*Benthic*	8.00	55005.03	267.08	440040.21	440040.21
69	*H. pelagica*	4.00	88131.98	420.61	352527.93	870748.36
69	*G. ruber albus*	2.00	28008.30	223.20	56016.61	870748.36
69	*G. ruber ruber*	20.00	18914.41	182.43	378288.28	870748.36
69	*Unknown*	2.00	41957.77	278.54	83915.55	870748.36
74	*Benthic*	2.00	36939.37	238.67	73878.73	2935707.57
74	*G. calida*	10.00	54125.89	282.79	541258.93	2935707.57
74	*N. glutinata*	4.00	29794.52	218.60	119178.06	2935707.57
74	*N. incompta*	2.00	34995.19	239.71	69990.38	2935707.57

Table A4 (continued).

74	*H. pelagica*	2.00	41654.00	293.14	83307.99	2935707.57
74	*G. ruber albus*	26.00	31022.71	218.63	806590.52	2935707.57
74	*G. ruber ruber*	28.00	21992.64	196.65	615793.83	2935707.57
74	*G. rubescens*	4.00	15097.75	150.93	60391.00	2935707.57
74	*Unknown*	8.00	70664.77	313.07	565318.13	2935707.57
9	*G. bulloides*	4.00	48111.37	290.82	192445.49	2239675.18
9	*N. incompta*	28.00	33712.89	234.08	943961.06	2239675.18
9	*T. quinqueloba*	36.00	22804.93	191.94	820977.43	2239675.18
9	*Unknown*	12.00	23524.27	200.51	282291.21	2239675.18
10	*Benthic*	10.00	47065.80	265.34	470657.96	6551536.94
10	*N. incompta*	46.00	28985.15	211.20	1333316.72	6551536.94
10	*N. pachyderma*	36.00	33338.84	225.64	1200198.30	6551536.94
10	*T. quinqueloba*	112.00	22510.82	183.64	2521212.03	6551536.94
10	*Unknown*	48.00	20833.64	183.79	1000014.88	6551536.94
10	*G. uvula*	1.00	26137.03	192.83	26137.03	6551536.94
11	*N. incompta*	73.00	39186.45	245.24	2860610.69	7378106.91
11	*G. inflata*	2.00	31194.93	215.85	62389.86	7378106.91
11	*N. pachyderma*	24.00	43389.71	263.71	1041352.95	7378106.91
11	*T. quinqueloba*	6.00	26319.30	200.13	157915.79	7378106.91
12	*N. dutertrei*	2.00	68453.26	336.21	136906.53	3396671.99
12	*N. incompta*	59.00	38883.96	251.04	2294153.40	3396671.99
12	*G. inflata*	2.00	43561.72	259.37	87123.44	3396671.99
12	*N. pachyderma*	3.00	33468.20	242.82	100404.60	3396671.99
12	*T. quinqueloba*	11.00	21870.89	183.14	240579.78	3396671.99
12	*Unknown*	23.00	23369.75	193.31	537504.24	3396671.99
13	*G. bulloides*	1.00	48203.44	290.83	48203.44	723197.47
13	*N. dutertrei*	3.00	44375.84	262.96	133127.53	723197.47
13	*N. incompta*	6.00	41485.91	256.75	248915.44	723197.47
13	*T. quinqueloba*	3.00	17246.47	166.40	51739.42	723197.47

Table A4 (continued).

13	*Unknown*	10.00	24121.16	186.87	241211.64	723197.47
14	*G. bulloides*	2.00	61229.43	309.24	122458.86	914358.68
14	*N. dutertrei*	4.00	65874.19	318.84	263496.77	914358.68
14	*N. incompta*	6.00	38845.07	246.15	233070.39	914358.68
14	*G. inflata*	3.00	56154.32	282.57	168462.95	914358.68
14	*N. pachyderma*	1.00	49029.72	270.84	49029.72	914358.68
14	*T. quinqueloba*	4.00	19460.00	174.96	77839.99	914358.68
15	*N. incompta*	10.00	26489.41	200.18	264894.14	291019.02
15	*Unknown*	1.00	26124.88	205.78	26124.88	291019.02
16	*G. bulloides*	3.00	65547.12	329.04	196641.37	1335200.14
16	*N. dutertrei*	1.00	38640.52	256.37	38640.52	1335200.14
16	*N. glutinata*	7.00	36151.28	244.05	253058.96	1335200.14
16	*N. pachyderma*	16.00	29278.09	207.82	468449.50	1335200.14
16	*T. quinqueloba*	7.00	23526.28	191.22	164683.96	1335200.14
16	*Unknown*	7.00	30532.26	219.25	213725.83	1335200.14
17	*G. bulloides*	1.00	33804.38	235.21	33804.38	457355.53
17	*N. pachyderma*	4.00	30256.26	209.53	121025.03	457355.53
17	*Unknown*	12.00	25210.51	197.79	302526.12	457355.53
18	*G. bulloides*	2.00	111644.38	428.63	223288.75	5083692.26
18	*N. dutertrei*	19.00	56064.25	290.13	1065220.76	5083692.26
18	*N. glutinata*	4.00	41623.62	256.54	166494.48	5083692.26
18	*N. incompta*	40.00	42056.43	252.06	1682257.04	5083692.26
18	*N. pachyderma*	8.00	46908.59	263.62	375268.73	5083692.26
18	*T. quinqueloba*	31.00	28073.76	208.64	870286.62	5083692.26
18	*Unknown*	19.00	29912.83	218.10	568343.75	5083692.26
18	*G. uvula*	2.00	66266.06	304.84	132532.13	5083692.26
19	*Benthic*	6.00	43345.03	269.98	260070.15	1522694.77
19	*N. dutertrei*	9.00	46949.18	262.88	422542.61	1522694.77
19	*N. incompta*	18.00	37426.93	241.05	673684.74	1522694.77

Table A4 (continued).

19	*T. quinqueloba*	6.00	27732.88	214.86	166397.27	1522694.77
37	*Benthic*	49.00	49603.67	278.69	2430579.96	2736295.75
37	*N. incompta*	7.00	32155.74	225.95	225090.15	2736295.75
37	*T. quinqueloba*	1.00	19520.75	177.55	19520.75	2736295.75
37	*Unknown*	2.00	30552.44	223.15	61104.88	2736295.75
38	*N. glutinata*	2.00	34721.79	237.97	69443.58	1056854.73
38	*N. incompta*	6.00	35810.83	233.52	214865.00	1056854.73
38	*G. inflata*	2.00	32520.92	233.52	65041.84	1056854.73
38	*T. quinqueloba*	1.00	15993.90	160.05	15993.90	1056854.73
38	*O. riedeli*	17.00	21067.88	185.07	358153.89	1056854.73
38	*G. ruber albus*	1.00	78274.40	363.20	78274.40	1056854.73
38	*Unknown*	10.00	25508.21	200.04	255082.12	1056854.73
39	*G. conglomerata*	1.00	57359.30	290.04	57359.30	3544356.55
39	*N. incompta*	15.00	30770.25	224.30	461553.74	3544356.55
39	*G. inflata*	39.00	36984.00	237.26	1442375.95	3544356.55
39	*T. quinqueloba*	1.00	28679.65	218.98	28679.65	3544356.55
39	*G. ruber albus*	9.00	41474.77	250.69	373272.91	3544356.55
39	*G. ruber ruber*	7.00	18474.02	172.35	129318.16	3544356.55
39	*G. tenellus*	1.00	32479.91	216.92	32479.91	3544356.55
39	*Unknown*	34.00	29979.91	217.82	1019316.92	3544356.55
4	*G. bulloides*	3.00	89468.60	382.29	268405.81	2062488.02
4	*N. incompta*	24.00	39464.77	250.55	947154.53	2062488.02
4	*N. pachyderma*	7.00	52627.78	291.12	368394.49	2062488.02
4	*T. quinqueloba*	5.00	27098.28	214.94	135491.40	2062488.02
4	*Unknown*	8.00	42880.22	268.38	343041.78	2062488.02
40	*G. bulloides*	4.00	69137.30	336.07	276549.19	2396692.10
40	*N. incompta*	14.00	33766.94	232.41	472737.12	2396692.10
40	*G. inflata*	1.00	32898.40	225.30	32898.40	2396692.10

Table A4 (continued).

40	*T. quinqueloba*	1.00	20353.77	183.51	20353.77	2396692.10
40	*G. ruber albus*	11.00	47378.11	282.29	521159.24	2396692.10
40	*G. ruber ruber*	4.00	92085.11	382.41	368340.45	2396692.10
40	*Unknown*	26.00	27102.07	215.42	704653.93	2396692.10
41	*N. incompta*	7.00	45493.75	250.37	318456.23	1834732.18
41	*G. inflata*	9.00	38728.62	241.01	348557.56	1834732.18
41	*G. ruber albus*	15.00	51067.46	276.97	766011.89	1834732.18
41	*G. ruber ruber*	1.00	19548.09	174.75	19548.09	1834732.18
41	*Unknown*	15.00	25477.23	197.21	382158.41	1834732.18
54	*G. cultrata*	1.00	58753.64	314.86	58753.64	2062474.31
54	*O. universa*	3.00	157122.93	448.49	471368.80	2062474.31
54	*H. pelagica*	2.00	88321.84	373.70	176643.69	2062474.31
54	*G. ruber albus*	17.00	32632.69	219.36	554755.78	2062474.31
54	*G. ruber ruber*	14.00	21842.70	181.47	305797.81	2062474.31
54	*G. siphonifera*	1.00	59081.72	325.24	59081.72	2062474.31
54	*G. tenellus*	9.00	22956.48	177.51	206608.32	2062474.31
54	*Unknown*	12.00	19122.05	168.82	229464.55	2062474.31
55	*G. calida*	3.00	23954.36	213.51	71863.07	2299199.80
55	*G. cultrata*	2.00	145134.35	444.21	290268.69	2299199.80
55	*N. glutinata*	1.00	27642.76	209.95	27642.76	2299199.80
55	*N. incompta*	1.00	28142.65	224.70	28142.65	2299199.80
55	*H. pelagica*	6.00	107869.94	448.89	647219.63	2299199.80
55	*G. radians*	1.00	110003.59	482.02	110003.59	2299199.80
55	*G. ruber ruber*	16.00	16701.32	163.46	267221.08	2299199.80
55	*G. siphonifera*	1.00	204855.01	630.03	204855.01	2299199.80
55	*G. tenellus*	5.00	20982.02	176.12	104910.08	2299199.80
55	*Unknown*	15.00	36471.55	239.52	547073.24	2299199.80
56	*G. calida*	3.00	47553.36	296.23	142660.08	4670736.87
56	*G. cultrata*	2.00	169904.38	475.20	339808.76	4670736.87

Table A4 (continued).

56	*N. glutinata*	1.00	33655.53	237.66	33655.53	4670736.87
56	*N. incompta*	2.00	42158.27	257.90	84316.53	4670736.87
56	*H. pelagica*	8.00	53005.41	315.43	424043.27	4670736.87
56	*G. ruber albus*	4.00	37729.19	238.88	150916.76	4670736.87
56	*G. ruber ruber*	60.00	33077.29	217.90	1984637.35	4670736.87
56	*G. tenellus*	1.00	23703.77	194.59	23703.77	4670736.87
56	*Unknown*	11.00	38889.90	265.81	427788.85	4670736.87
56	*G. uvula*	1.00	27531.37	210.78	27531.37	4670736.87
6	*G. bulloides*	3.00	114056.78	435.58	342170.35	2965217.11
6	*N. incompta*	26.00	39378.47	248.25	1023840.17	2965217.11
6	*N. pachyderma*	2.00	66921.55	333.28	133843.11	2965217.11
6	*T. quinqueloba*	20.00	25284.14	203.63	505682.81	2965217.11
6	*Unknown*	25.00	38387.23	253.22	959680.68	2965217.11
60	*Benthic*	5.00	34567.47	228.70	172837.35	603120.21
60	*G. calida*	1.00	21227.98	202.81	21227.98	603120.21
60	*G. cultrata*	1.00	39065.81	258.28	39065.81	603120.21
60	*N. incompta*	1.00	30985.32	223.20	30985.32	603120.21
60	*G. inflata*	3.00	19146.10	171.78	57438.29	603120.21
60	*G. ruber ruber*	10.00	18498.85	179.07	184988.46	603120.21
60	*Unknown*	6.00	16096.17	163.15	96577.00	603120.21
62	*N. incompta*	1.00	42893.41	267.21	42893.41	860225.50
62	*H. pelagica*	1.00	19806.31	193.71	19806.31	860225.50
62	*G. ruber albus*	4.00	34451.43	223.98	137805.71	860225.50
62	*G. ruber ruber*	3.00	32334.10	237.89	97002.29	860225.50
62	*G. siphonifera*	4.00	75944.42	376.62	303777.69	860225.50
62	*G. tenellus*	2.00	27103.05	202.08	54206.09	860225.50
62	*Unknown*	8.00	25591.75	200.47	204734.01	860225.50
63	*G. calida*	4.00	47100.73	280.09	188402.92	2379976.67
63	*N. incompta*	1.00	29199.11	224.42	29199.11	2379976.67

Table A4 (continued).

63	*O. universa*	2.00	218616.65	530.25	437233.30	2379976.67
63	*H. pelagica*	5.00	38032.97	265.30	190164.83	2379976.67
63	*G. ruber albus*	9.00	38234.13	241.63	344107.21	2379976.67
63	*G. ruber ruber*	3.00	59678.14	290.90	179034.42	2379976.67
63	*G. siphonifera*	3.00	252030.17	643.65	756090.51	2379976.67
63	*Unknown*	12.00	21312.03	180.31	255744.36	2379976.67
64	*G. cultrata*	2.00	61751.93	348.87	123503.86	5108568.62
64	*N. incompta*	5.00	50069.85	280.85	250349.27	5108568.62
64	*O. universa*	3.00	139494.71	449.67	418484.14	5108568.62
64	*N. pachyderma*	1.00	70719.45	360.41	70719.45	5108568.62
64	*H. pelagica*	2.00	185583.86	622.73	371167.73	5108568.62
64	*G. ruber albus*	55.00	36886.62	234.43	2028764.10	5108568.62
64	*G. ruber ruber*	6.00	37405.16	237.84	224430.96	5108568.62
64	*G. siphonifera*	12.00	77634.19	362.85	931610.22	5108568.62
64	*G. tenellus*	14.00	31679.24	215.58	443509.35	5108568.62
64	*Unknown*	11.00	19630.11	170.88	215931.26	5108568.62
64	*G. uvula*	1.00	30098.29	208.51	30098.29	5108568.62
65	*N. incompta*	1.00	31179.74	236.14	31179.74	3916605.73
65	*G. inflata*	1.00	24994.83	191.09	24994.83	3916605.73
65	*H. pelagica*	4.00	77381.29	347.19	309525.16	3916605.73
65	*G. ruber albus*	56.00	30268.19	211.38	1695018.74	3916605.73
65	*G. ruber ruber*	7.00	51361.00	271.27	359526.97	3916605.73
65	*G. rubescens*	4.00	17421.65	157.76	69686.60	3916605.73
65	*G. siphonifera*	5.00	125331.38	443.54	626656.92	3916605.73
65	*G. tenellus*	13.00	31649.90	217.31	411448.65	3916605.73
65	*Unknown*	15.00	23732.73	190.62	355991.00	3916605.73
65	*G. uvula*	1.00	32577.12	217.61	32577.12	3916605.73
72	*G. calida*	4.00	92776.74	420.25	371106.97	10794813.04
72	*G. ruber albus*	10.00	41560.43	255.19	415604.33	10794813.04

Table A4 (continued).

72	*G. ruber ruber*	2.00	56958.32	287.03	113916.63	10794813.04
72	*G. tenellus*	2.00	37504.39	240.55	75008.79	10794813.04
72	*Unknown*	6.00	101048.61	424.56	606291.66	10794813.04
14	*Unknown*	0.00	0.00	0.00	0.00	914358.68
40	*O. riedeli*	0.00	0.00	0.00	0.00	2396692.10
53	*G. ruber albus*	0.00	0.00	0.00	0.00	7234283.36
74	*G. siphonifera*	0.00	0.00	0.00	0.00	2935707.57
2	*G. bulloides*	0.00	0.00	0.00	0.00	1751416.06
42	*G. bulloides*	0.00	0.00	0.00	0.00	1593156.01
42	*N. glutinata*	0.00	0.00	0.00	0.00	1593156.01
42	*G. inflata*	0.00	0.00	0.00	0.00	1593156.01
42	*O. riedeli*	0.00	0.00	0.00	0.00	1593156.01
42	*G. ruber ruber*	0.00	0.00	0.00	0.00	1593156.01
42	*G. siphonifera*	0.00	0.00	0.00	0.00	1593156.01
43	*G. calida*	0.00	0.00	0.00	0.00	2537977.52
43	*N. dutertrei*	0.00	0.00	0.00	0.00	2537977.52
43	*G. inflata*	0.00	0.00	0.00	0.00	2537977.52
43	*T. sacculifer*	0.00	0.00	0.00	0.00	2537977.52
44	*N. incompta*	0.00	0.00	0.00	0.00	358263.25
46	*G. cultrata*	0.00	0.00	0.00	0.00	2517709.47
46	*G. ruber albus*	0.00	0.00	0.00	0.00	2517709.47
5	*G. bulloides*	0.00	0.00	0.00	0.00	6482567.25
5	*G. inflata*	0.00	0.00	0.00	0.00	6482567.25
5	*N. pachyderma*	0.00	0.00	0.00	0.00	6482567.25
51	*G. calida*	0.00	0.00	0.00	0.00	194539.23
51	*N. glutinata*	0.00	0.00	0.00	0.00	194539.23
52	*G. calida*	0.00	0.00	0.00	0.00	1799651.93
52	*N. incompta*	0.00	0.00	0.00	0.00	1799651.93
52	*G. inflata*	0.00	0.00	0.00	0.00	1799651.93

Table A4 (continued).

52	*G. radians*	0.00	0.00	0.00	0.00	1799651.93
53	*G. cultrata*	0.00	0.00	0.00	0.00	7234283.36
53	*Unknown*	0.00	0.00	0.00	0.00	7234283.36
53	*G. uvula*	0.00	0.00	0.00	0.00	7234283.36
59	*G. ruber ruber*	0.00	0.00	0.00	0.00	2318236.89
59	*B. variabilis*	0.00	0.00	0.00	0.00	2318236.89
61	*G. cultrata*	0.00	0.00	0.00	0.00	14479016.68
61	*O. universa*	0.00	0.00	0.00	0.00	14479016.68
61	*H. pelagica*	0.00	0.00	0.00	0.00	14479016.68
61	*G. tenellus*	0.00	0.00	0.00	0.00	14479016.68
61	*B. variabilis*	0.00	0.00	0.00	0.00	14479016.68
67	*G. ruber albus*	0.00	0.00	0.00	0.00	440040.21
69	*Benthic*	0.00	0.00	0.00	0.00	870748.36
69	*N. incompta*	0.00	0.00	0.00	0.00	870748.36
69	*O. universa*	0.00	0.00	0.00	0.00	870748.36
69	*G. siphonifera*	0.00	0.00	0.00	0.00	870748.36
74	*G. cultrata*	0.00	0.00	0.00	0.00	2935707.57
74	*N. dutertrei*	0.00	0.00	0.00	0.00	2935707.57
74	*G. inflata*	0.00	0.00	0.00	0.00	2935707.57
74	*O. universa*	0.00	0.00	0.00	0.00	2935707.57
74	*G. truncatulinoides*	0.00	0.00	0.00	0.00	2935707.57
10	*N. glutinata*	0.00	0.00	0.00	0.00	6551536.94
10	*G. inflata*	0.00	0.00	0.00	0.00	6551536.94
13	*Benthic*	0.00	0.00	0.00	0.00	723197.47
13	*G. inflata*	0.00	0.00	0.00	0.00	723197.47
14	*G. crassiformis*	0.00	0.00	0.00	0.00	914358.68
14	*N. glutinata*	0.00	0.00	0.00	0.00	914358.68
14	*G. ruber albus*	0.00	0.00	0.00	0.00	914358.68

Table A4 (continued).

14	*G. ruber ruber*	0.00	0.00	0.00	0.00	914358.68
14	*G. uvula*	0.00	0.00	0.00	0.00	914358.68
15	*Benthic*	0.00	0.00	0.00	0.00	291019.02
15	*G. bulloides*	0.00	0.00	0.00	0.00	291019.02
15	*N. dutertrei*	0.00	0.00	0.00	0.00	291019.02
15	*G. inflata*	0.00	0.00	0.00	0.00	291019.02
15	*T. quinqueloba*	0.00	0.00	0.00	0.00	291019.02
15	*G. ruber albus*	0.00	0.00	0.00	0.00	291019.02
16	*N. incompta*	0.00	0.00	0.00	0.00	1335200.14
16	*G. inflata*	0.00	0.00	0.00	0.00	1335200.14
17	*N. dutertrei*	0.00	0.00	0.00	0.00	457355.53
17	*N. glutinata*	0.00	0.00	0.00	0.00	457355.53
17	*N. incompta*	0.00	0.00	0.00	0.00	457355.53
17	*G. inflata*	0.00	0.00	0.00	0.00	457355.53
17	*T. quinqueloba*	0.00	0.00	0.00	0.00	457355.53
19	*G. falconensis*	0.00	0.00	0.00	0.00	1522694.77
37	*O. riedeli*	0.00	0.00	0.00	0.00	2736295.75
37	*G. ruber albus*	0.00	0.00	0.00	0.00	2736295.75
37	*G. ruber ruber*	0.00	0.00	0.00	0.00	2736295.75
38	*G. bulloides*	0.00	0.00	0.00	0.00	1056854.73
38	*G. ruber ruber*	0.00	0.00	0.00	0.00	1056854.73
38	*T. sacculifer*	0.00	0.00	0.00	0.00	1056854.73
39	*G. cultrata*	0.00	0.00	0.00	0.00	3544356.55
39	*O. universa*	0.00	0.00	0.00	0.00	3544356.55
39	*G. radians*	0.00	0.00	0.00	0.00	3544356.55
39	*G. rubescens*	0.00	0.00	0.00	0.00	3544356.55
39	*T. sacculifer*	0.00	0.00	0.00	0.00	3544356.55
41	*G. conglobatus*	0.00	0.00	0.00	0.00	1834732.18
41	*O. universa*	0.00	0.00	0.00	0.00	1834732.18

Table A4 (continued).

41	*G. uvula*	0.00	0.00	0.00	0.00	1834732.18
54	*N. glutinata*	0.00	0.00	0.00	0.00	2062474.31
54	*G. rubescens*	0.00	0.00	0.00	0.00	2062474.31
55	*G. inflata*	0.00	0.00	0.00	0.00	2299199.80
55	*G. ruber albus*	0.00	0.00	0.00	0.00	2299199.80
6	*G. inflata*	0.00	0.00	0.00	0.00	2965217.11
60	*N. glutinata*	0.00	0.00	0.00	0.00	603120.21
60	*H. pelagica*	0.00	0.00	0.00	0.00	603120.21
60	*T. quinqueloba*	0.00	0.00	0.00	0.00	603120.21
60	*G. ruber albus*	0.00	0.00	0.00	0.00	603120.21
60	*G. rubescens*	0.00	0.00	0.00	0.00	603120.21
60	*T. sacculifer*	0.00	0.00	0.00	0.00	603120.21
60	*G. ungulata*	0.00	0.00	0.00	0.00	603120.21
60	*G. uvula*	0.00	0.00	0.00	0.00	603120.21
60	*B. variabilis*	0.00	0.00	0.00	0.00	603120.21
62	*Benthic*	0.00	0.00	0.00	0.00	860225.50
62	*O. universa*	0.00	0.00	0.00	0.00	860225.50
62	*G. rubescens*	0.00	0.00	0.00	0.00	860225.50
63	*G. cultrata*	0.00	0.00	0.00	0.00	2379976.67
63	*G. tenellus*	0.00	0.00	0.00	0.00	2379976.67
63	*G. truncatulinoides*	0.00	0.00	0.00	0.00	2379976.67
64	*G. inflata*	0.00	0.00	0.00	0.00	5108568.62
64	*G. truncatulinoides*	0.00	0.00	0.00	0.00	5108568.62
65	*G. cultrata*	0.00	0.00	0.00	0.00	3916605.73
65	*O. universa*	0.00	0.00	0.00	0.00	3916605.73
72	*H. pelagica*	0.00	0.00	0.00	0.00	10794813.04

Appendix B: Species correlations

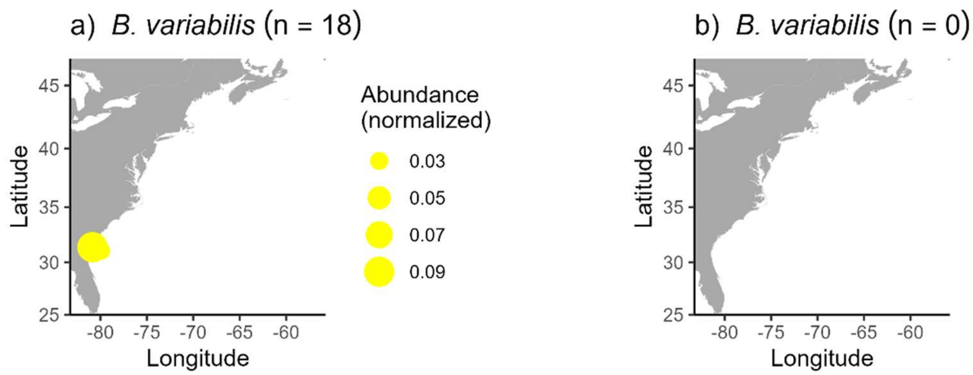

Figure B1. a) Distribution of all *B. variabilis*, living and dead, sized according to concentration. **b)** Size of all dead individuals.

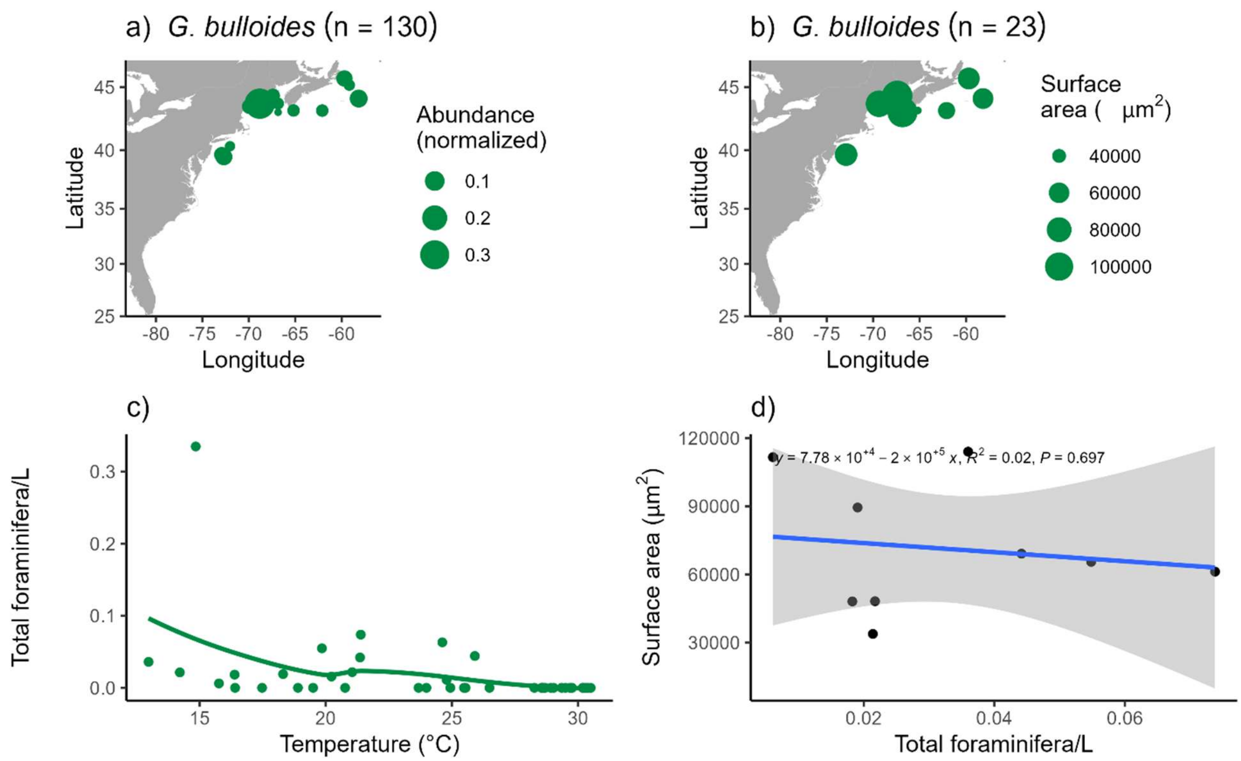

Figure B2. a) Distribution of all *G. bulloides*, living and dead, sized according to concentration. **b)** Size of all dead individuals. **c)** Temperature distribution of *G. bulloides*. **d)** Linear model of total species abundance versus average surface area of dead individuals.

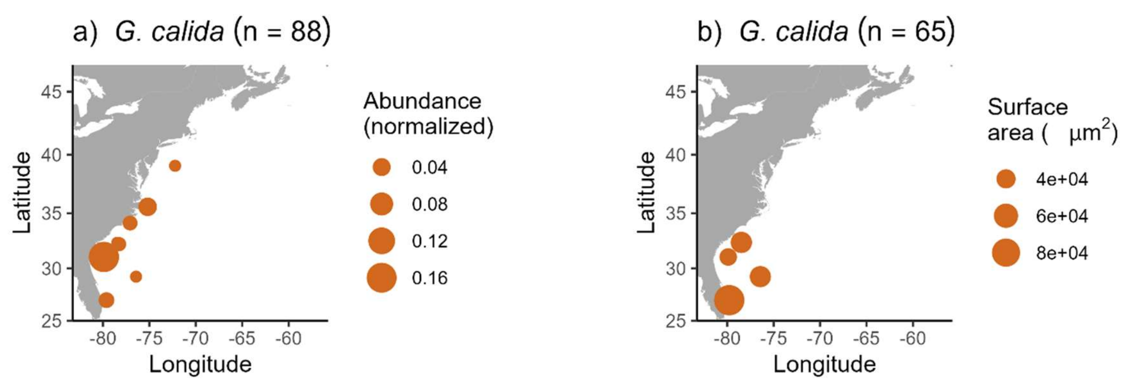

Figure B3. a) Distribution of all *G. calida*, living and dead, sized according to concentration. **b)** Size of all dead individuals.

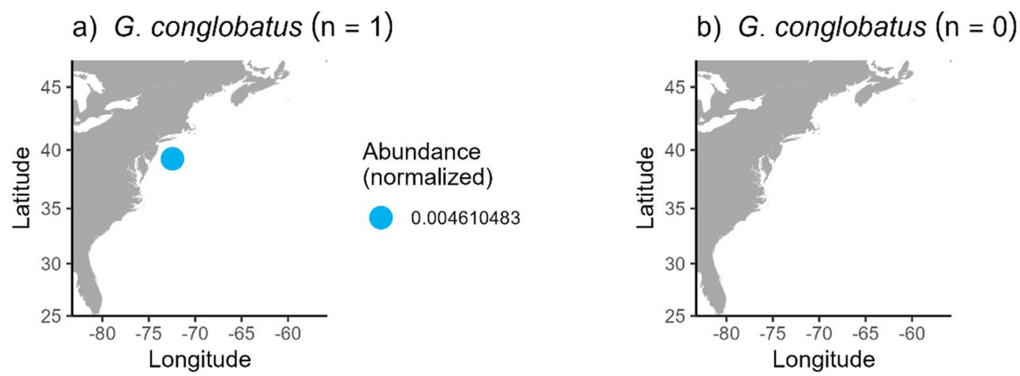

Figure B4. a) Distribution of all *G. conglobatus*, living and dead, sized according to concentration. **b)** Size of all dead individuals.

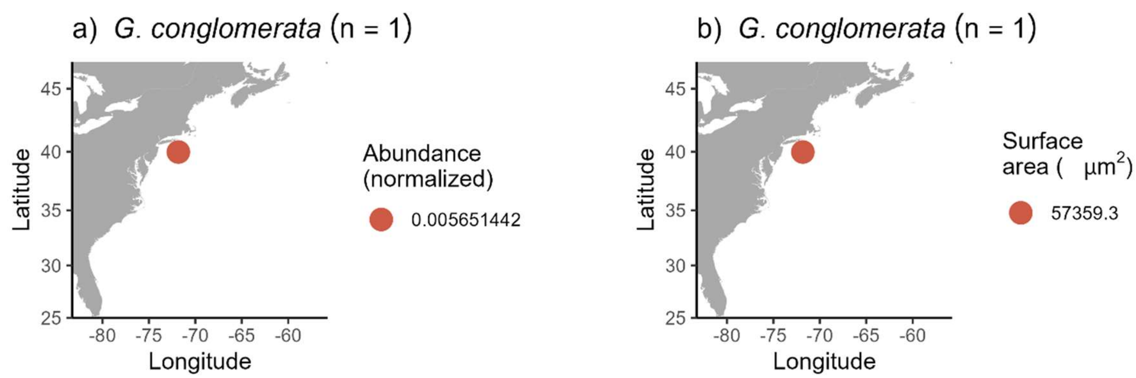

Figure B5. a) Distribution of all *G. conglomerata*, living and dead, sized according to concentration. **b)** Size of all dead individuals.

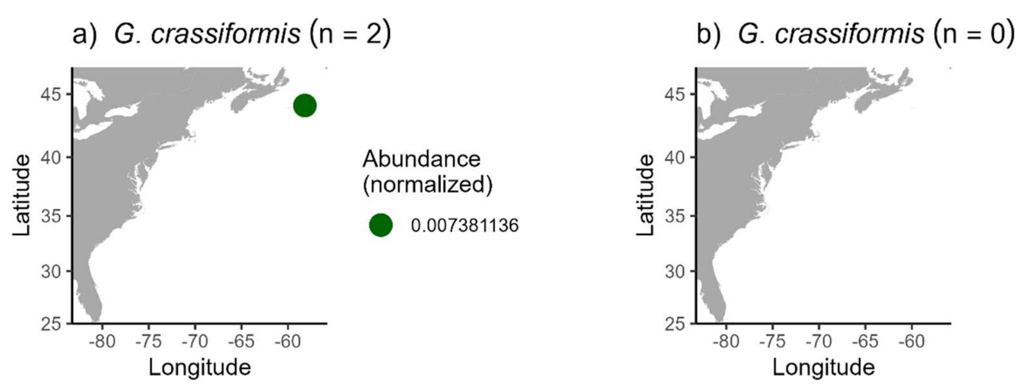

Figure B6. a) Distribution of all *G. crassiformis*, living and dead, sized according to concentration. **b)** Size of all dead individuals.

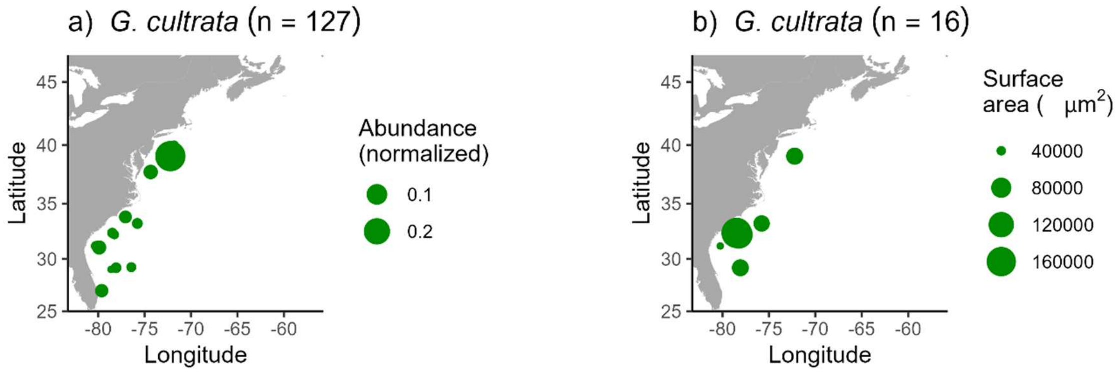

Figure B7. a) Distribution of all *G. cultrata*, living and dead, sized according to concentration. **b)** Size of all dead individuals.

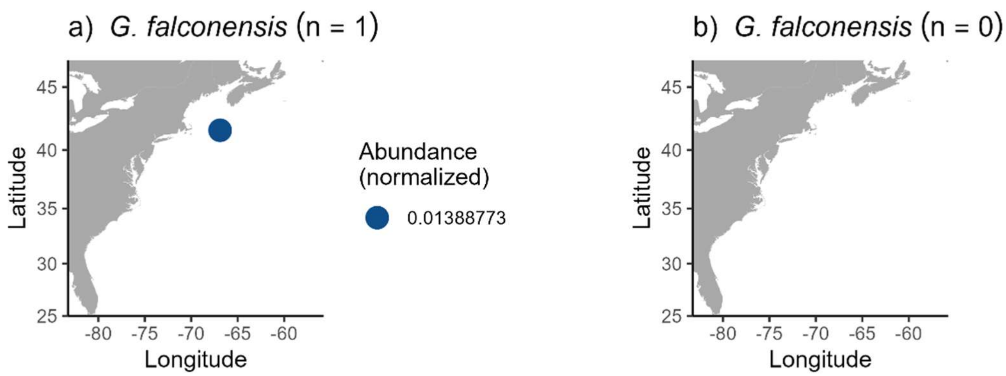

Figure B8. a) Distribution of all *G. falconensis*, living and dead, sized according to concentration. **b)** Size of all dead individuals.

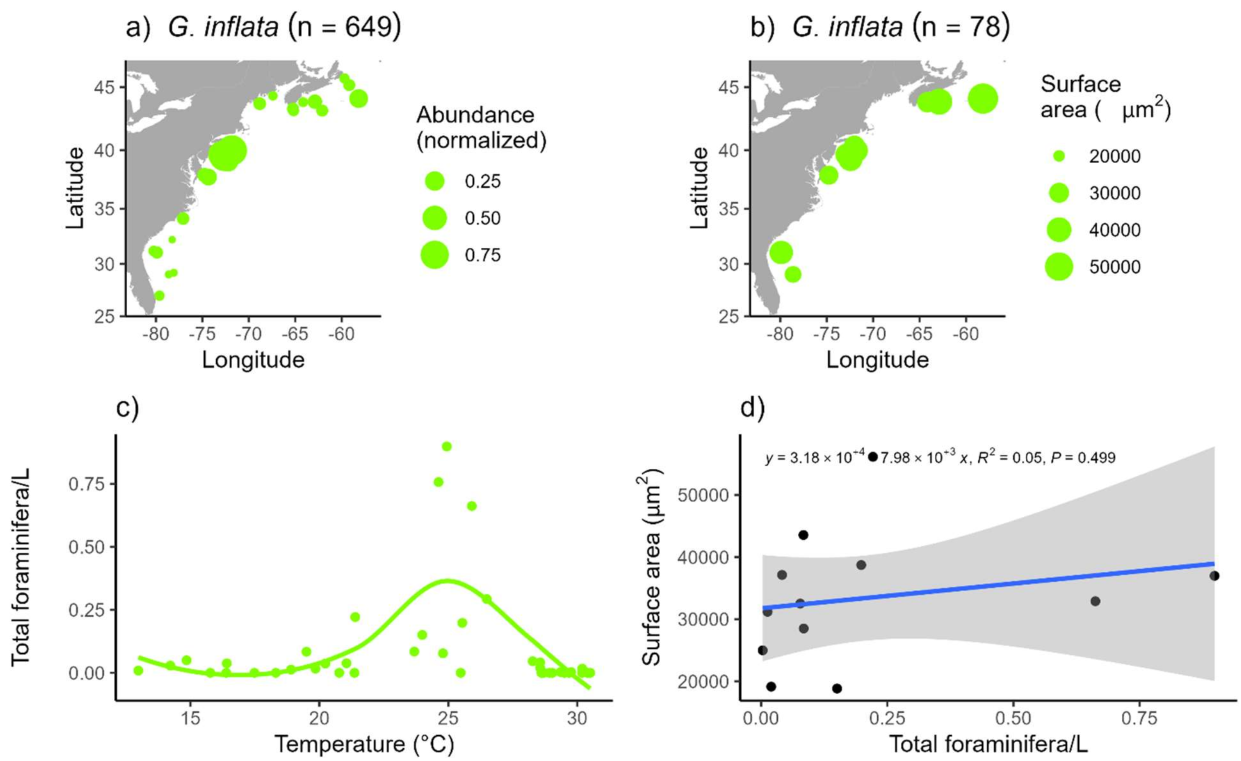

Figure B9. a) Distribution of all *G. inflata*, living and dead, sized according to concentration. **b)** Size of all dead individuals. **c)** Temperature distribution of *G. inflata*. **d)** Linear model of total species abundance versus average surface area of dead individuals.

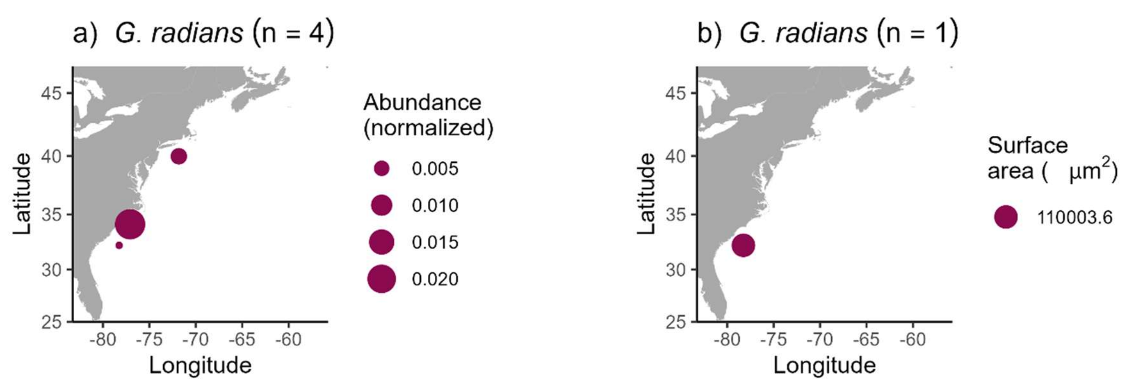

Figure B10. a) Distribution of all *G. radians*, living and dead, sized according to concentration. **b)** Size of all dead individuals.

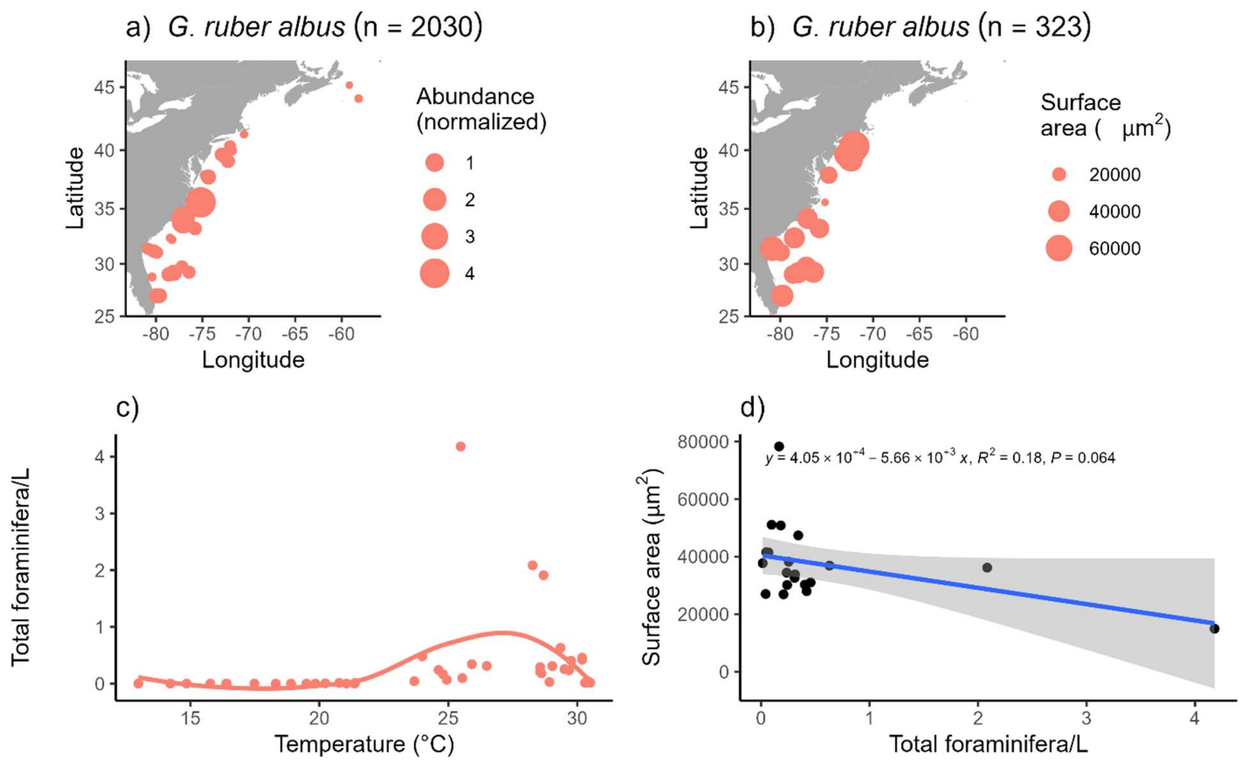

Figure B11. a) Distribution of all *G. ruber albus*, living and dead, sized according to concentration. **b)** Size of all dead individuals. **c)** Temperature distribution of *G. ruber albus*. **d)** Linear model of total species abundance versus average surface area of dead individuals.

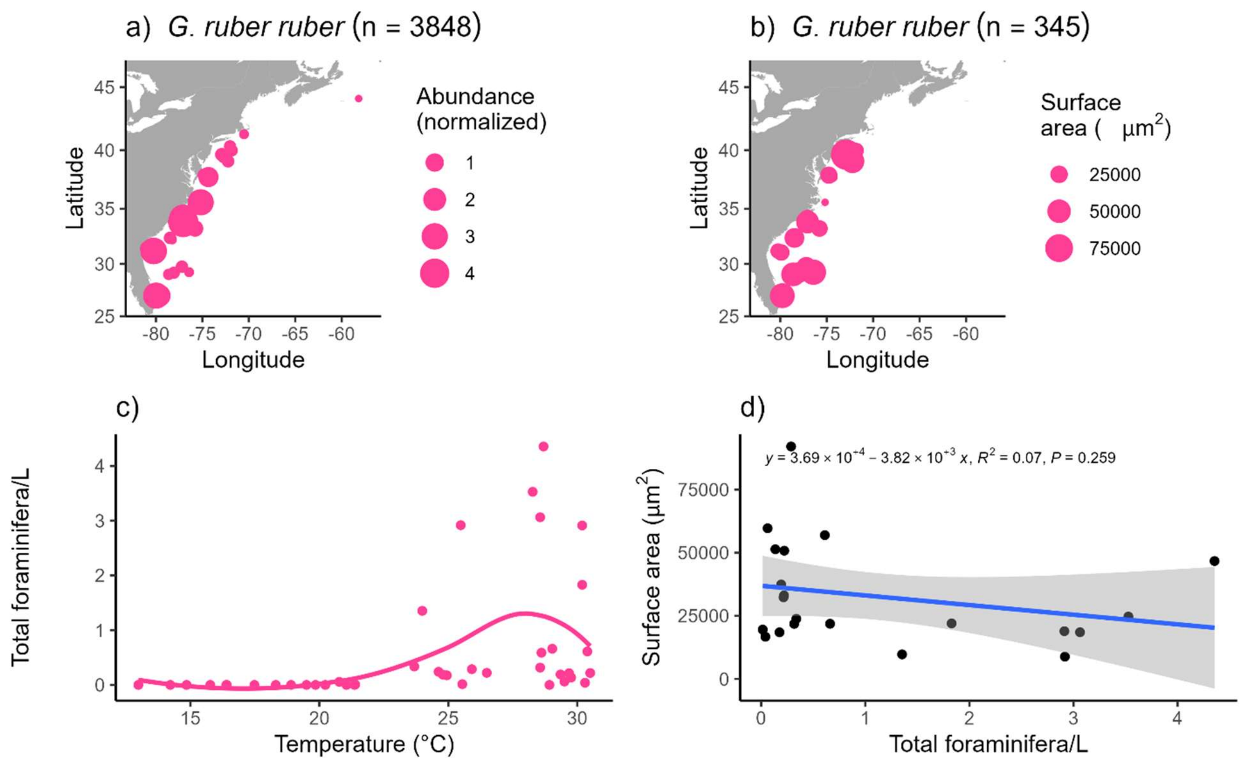

Figure B12. a) Distribution of all *G. ruber ruber*, living and dead, sized according to concentration. **b)** Size of all dead individuals. **c)** Temperature distribution of *G. ruber ruber*. **d)** Linear model of total species abundance versus average surface area of dead individuals.

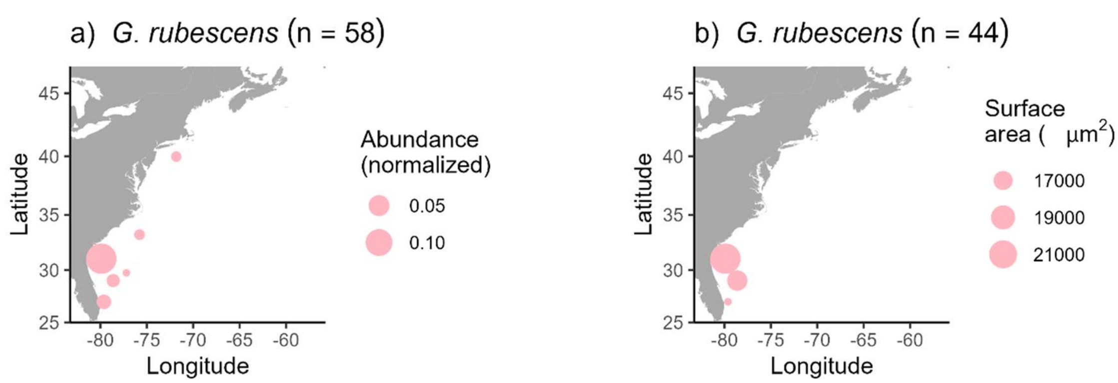

Figure B13. a) Distribution of all *G. rubescens*, living and dead, sized according to concentration. **b)** Size of all dead individuals.

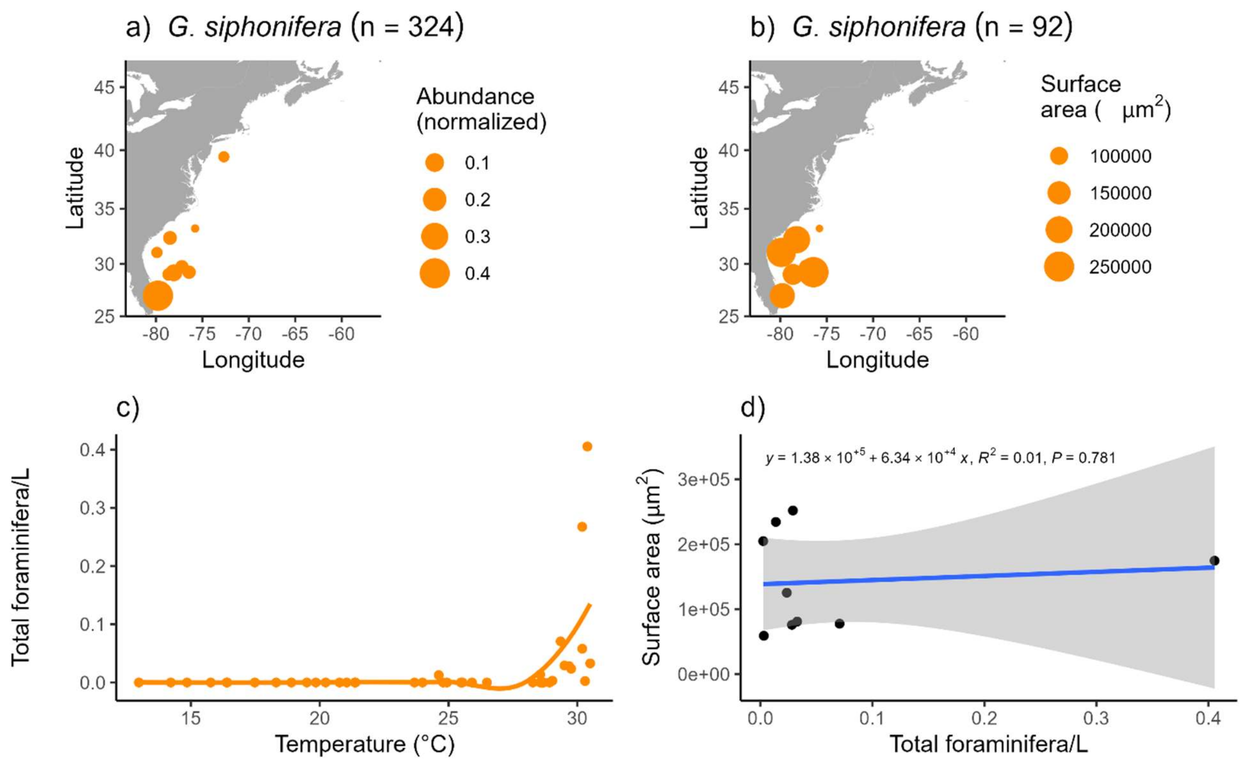

Figure B14. a) Distribution of all *G. siphonifera*, living and dead, sized according to concentration. **b)** Size of all dead individuals. **c)** Temperature distribution of *G. siphonifera*. **d)** Linear model of total species abundance versus average surface area of dead individuals.

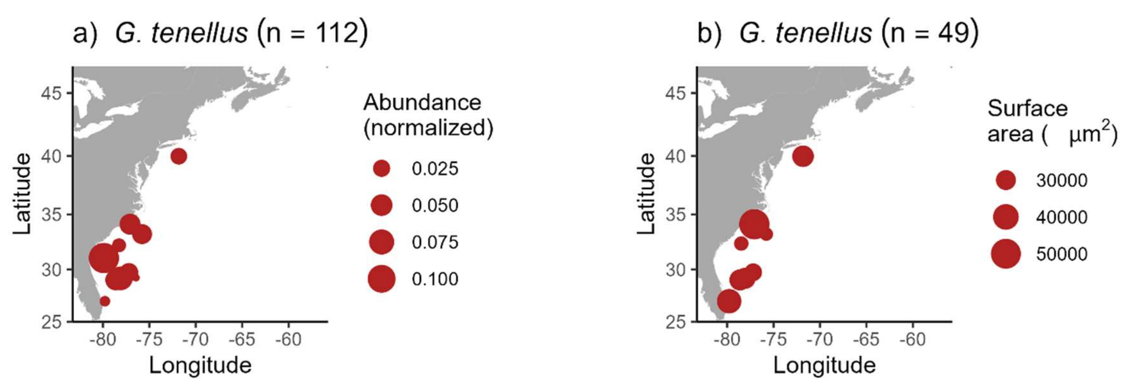

Figure B15. a) Distribution of all *G. tenellus*, living and dead, sized according to concentration. **b)** Size of all dead individuals.

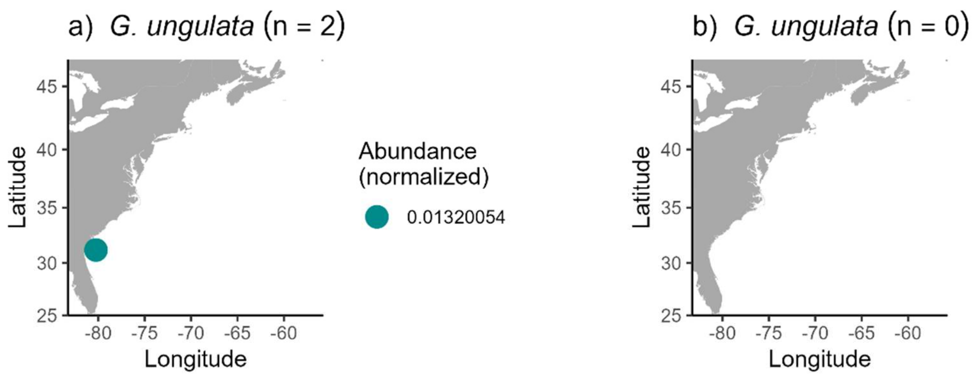

Figure B16. a) Distribution of all *G. ungulata*, living and dead, sized according to concentration. **b)** Size of all dead individuals.

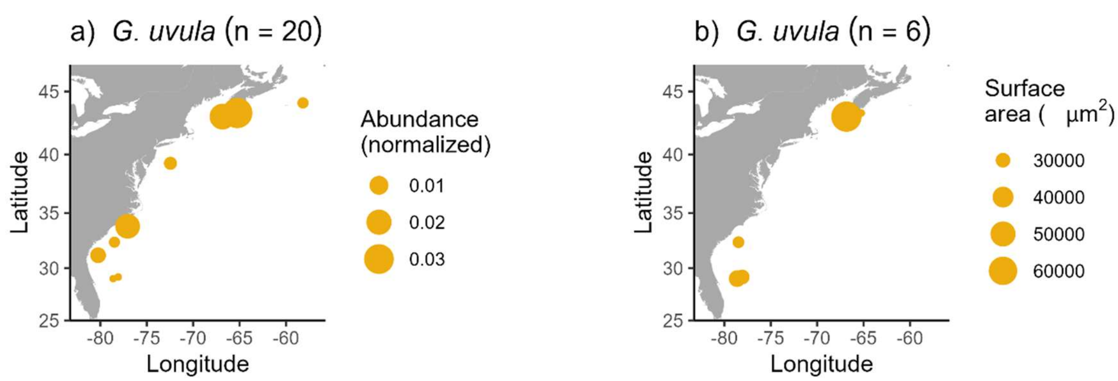

Figure B17. a) Distribution of all *G. uvula*, living and dead, sized according to concentration. **b)** Size of all dead individuals.

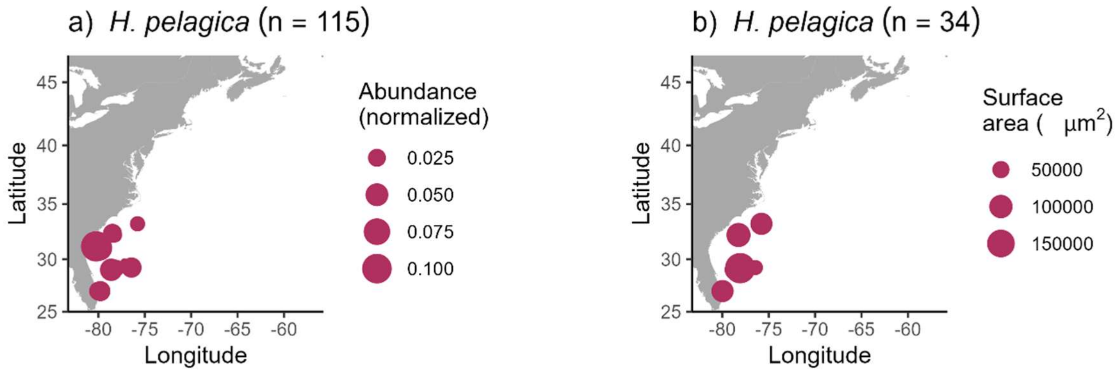

Figure B18. a) Distribution of all *H. pelagica*, living and dead, sized according to concentration. **b)** Size of all dead individuals.

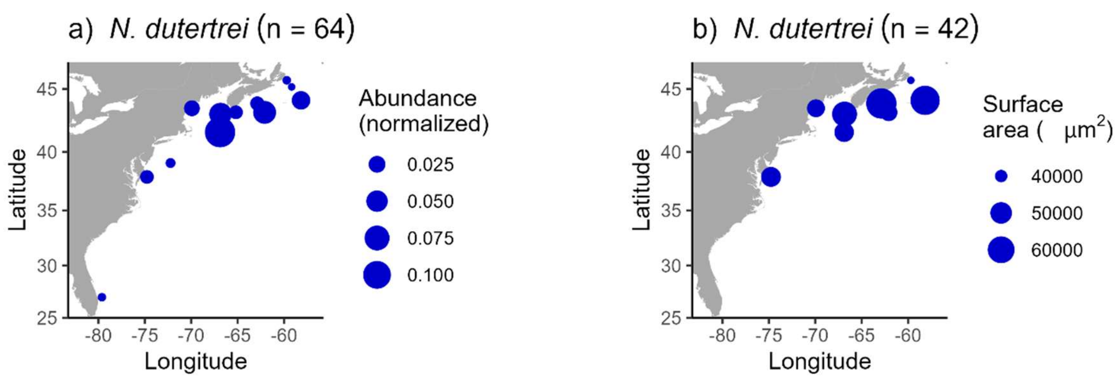

Figure B19. a) Distribution of all *N. dutertrei*, living and dead, sized according to concentration. **b)** Size of all dead individuals.

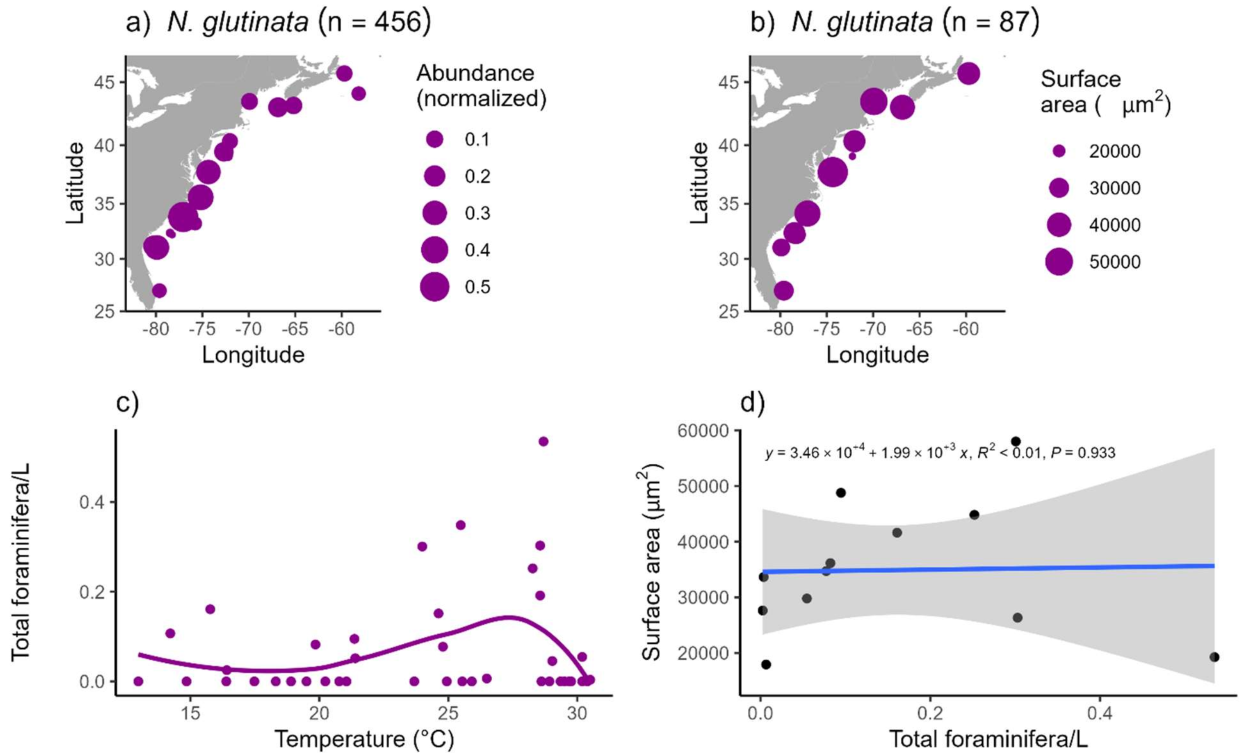

Figure B20. a) Distribution of all *N. glutinata*, living and dead, sized according to concentration. **b)** Size of all dead individuals. **c)** Temperature distribution of *N. glutinata*. **d)** Linear model of total species abundance versus average surface area of dead individuals.

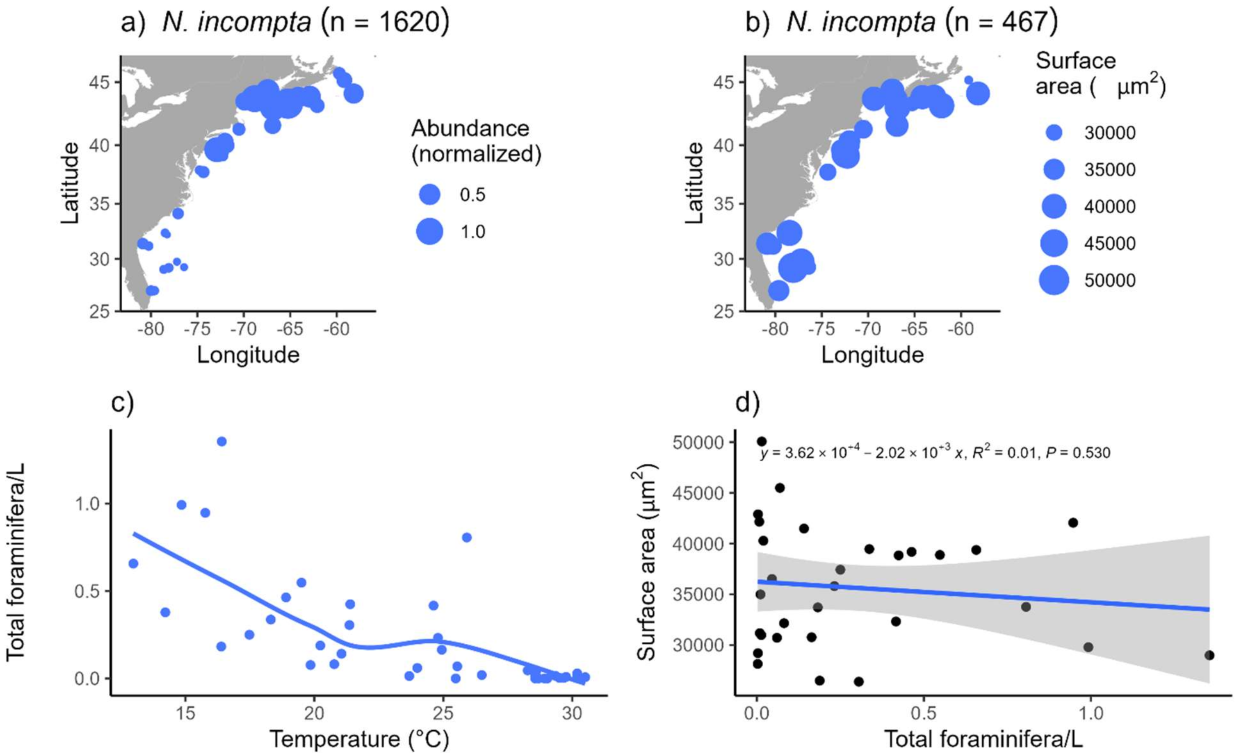

Figure B21. a) Distribution of all *N. incompta*, living and dead, sized according to concentration. **b)** Size of all dead individuals. **c)** Temperature distribution of *N. incompta*. **d)** Linear model of total species abundance versus average surface area of dead individuals.

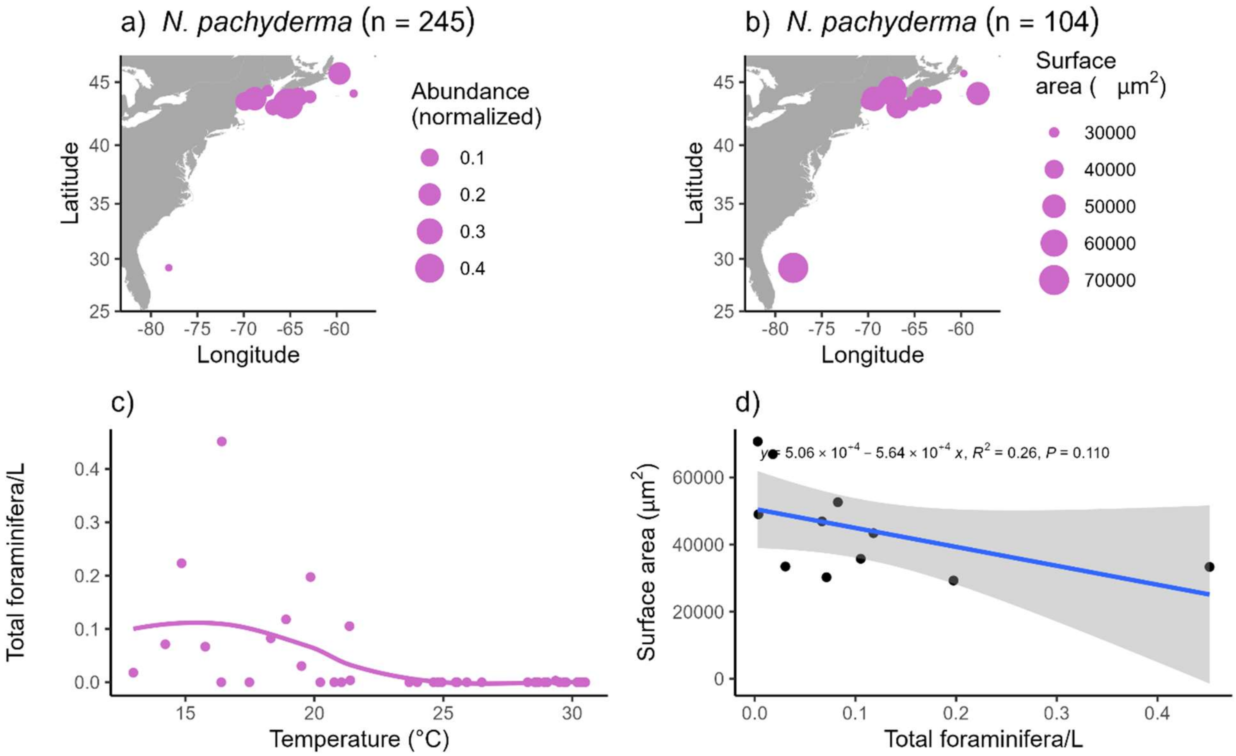

Figure B22. a) Distribution of all *N. pachyderma*, living and dead, sized according to concentration. **b)** Size of all dead individuals. **c)** Temperature distribution of *N. pachyderma*. **d)** Linear model of total species abundance versus average surface area of dead individuals.

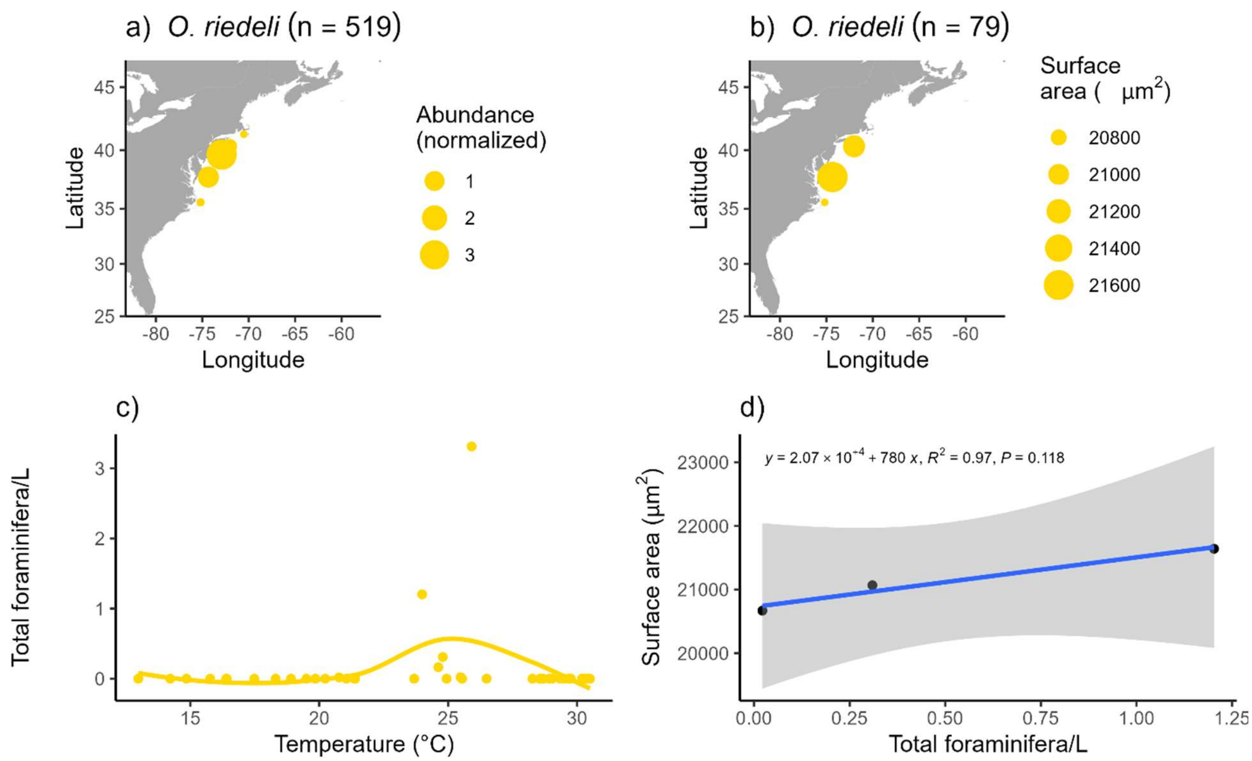

Figure B23. a) Distribution of all *O. riedeli*, living and dead, sized according to concentration. **b)** Size of all dead individuals. **c)** Temperature distribution of *O. riedeli*. **d)** Linear model of total species abundance versus average surface area of dead individuals.

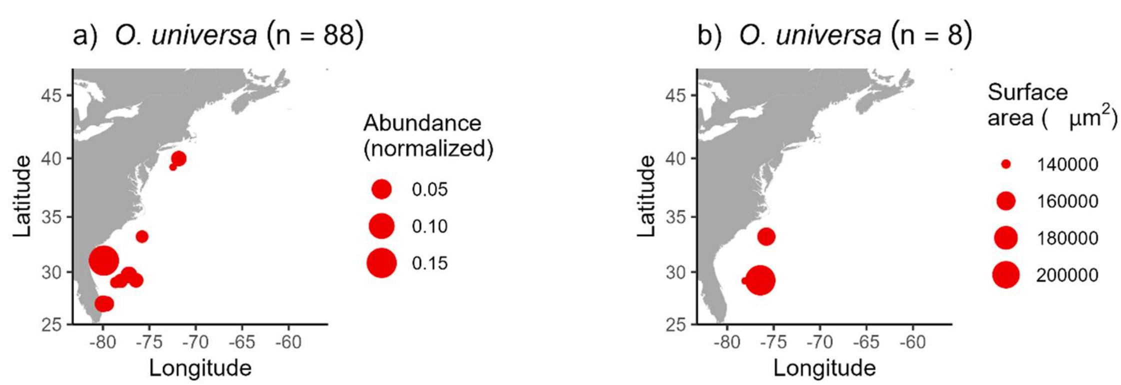

Figure B24. a) Distribution of all *O. universa*, living and dead, sized according to concentration. **b)** Size of all dead individuals.

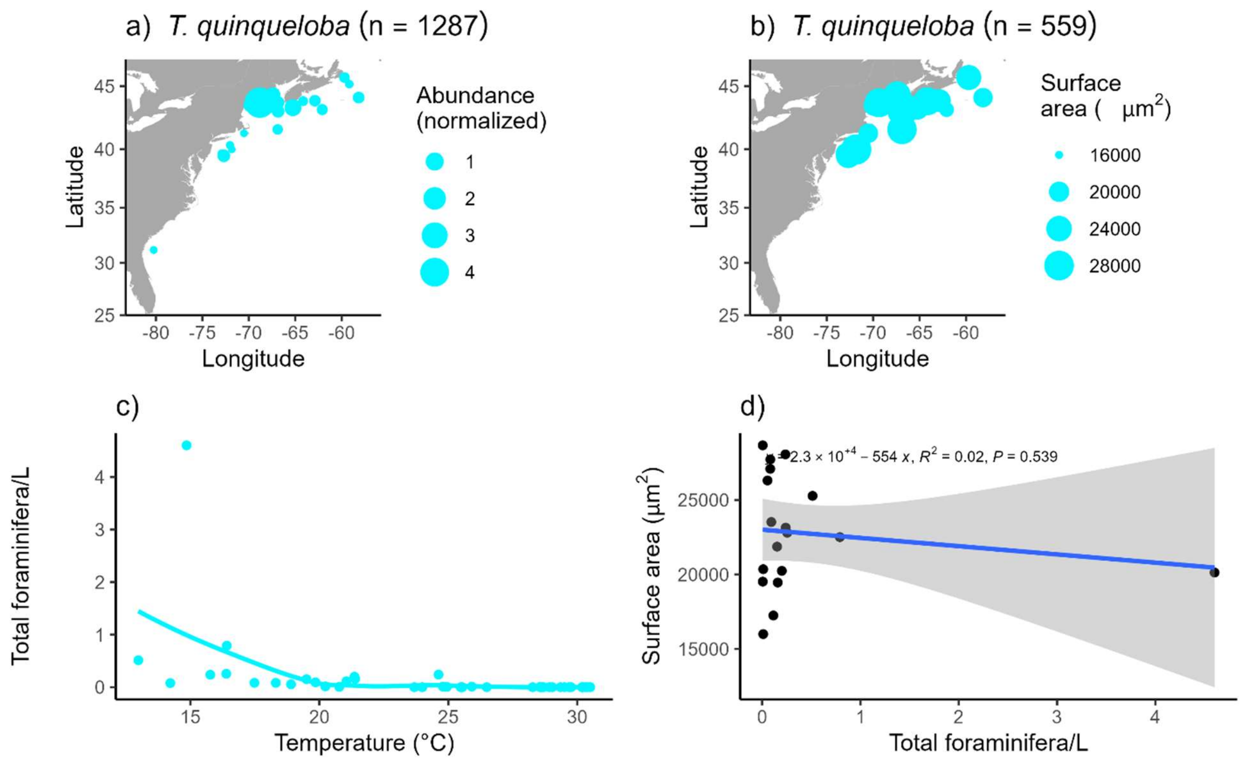

Figure B25. a) Distribution of all *T. quinqueloba*, living and dead, sized according to concentration. **b)** Size of all dead individuals. **c)** Temperature distribution of *T. quinqueloba*. **d)** Linear model of total species abundance versus average surface area of dead individuals.

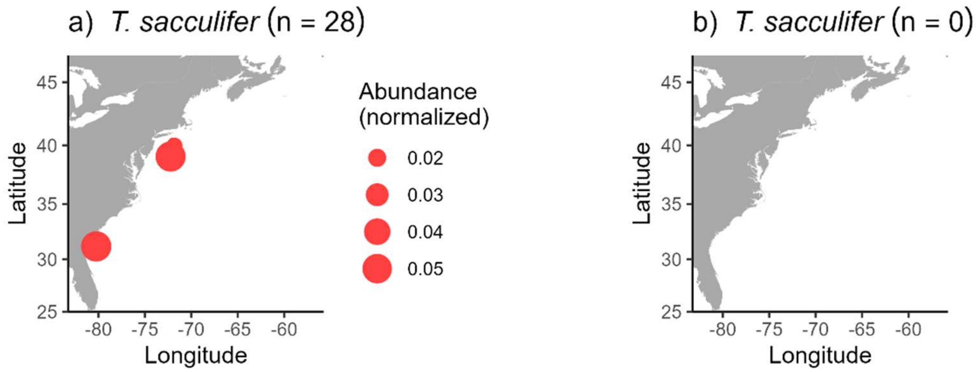

Figure B26. a) Distribution of all *T. sacculifer*, living and dead, sized according to concentration. **b)** Size of all dead individuals.

Appendix C: Statistical analyses

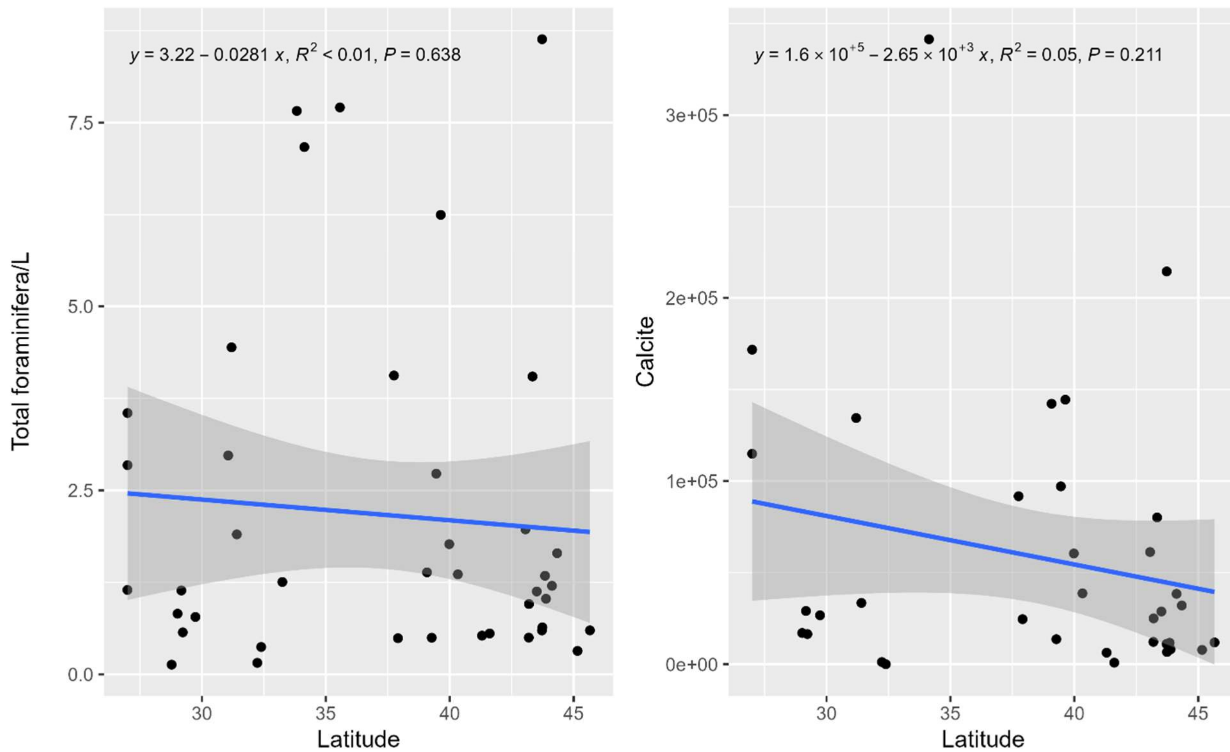

Figure C1. Linear model of latitude versus total foraminifera per liter (normalized, right) and total calcite produced by live foraminifera.

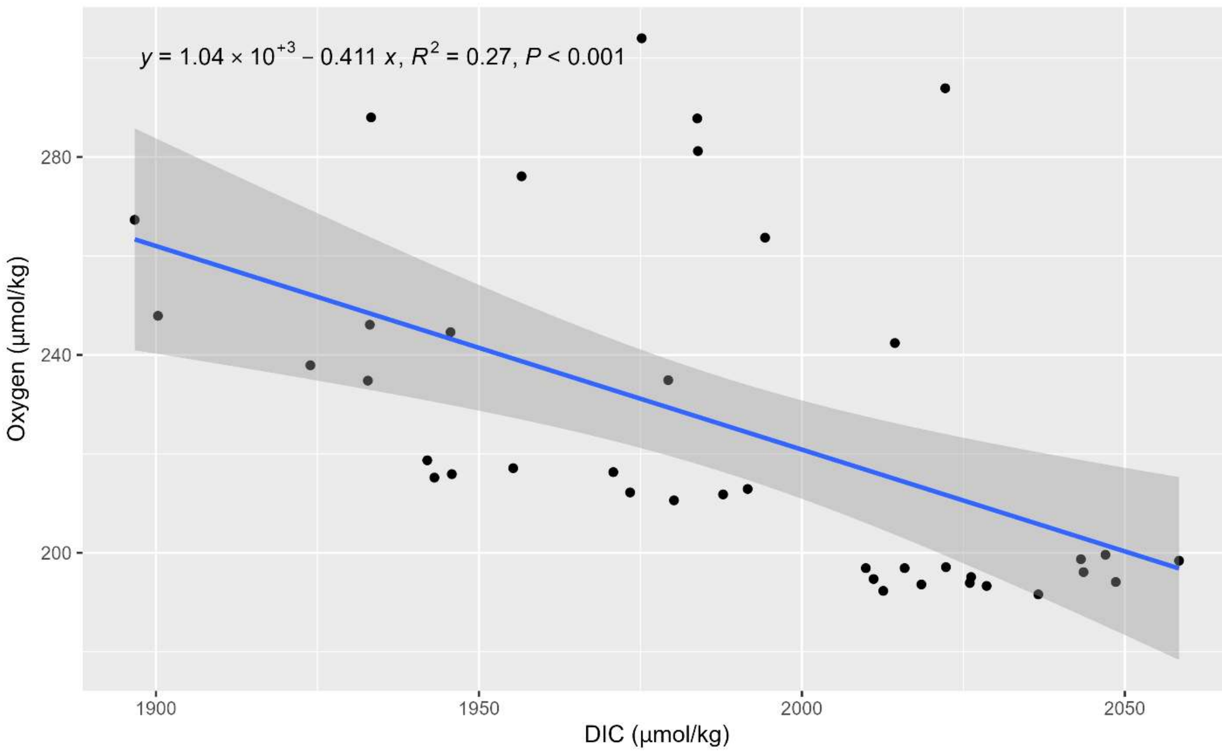

Figure C2. Linear model of DIC versus surface oxygen.

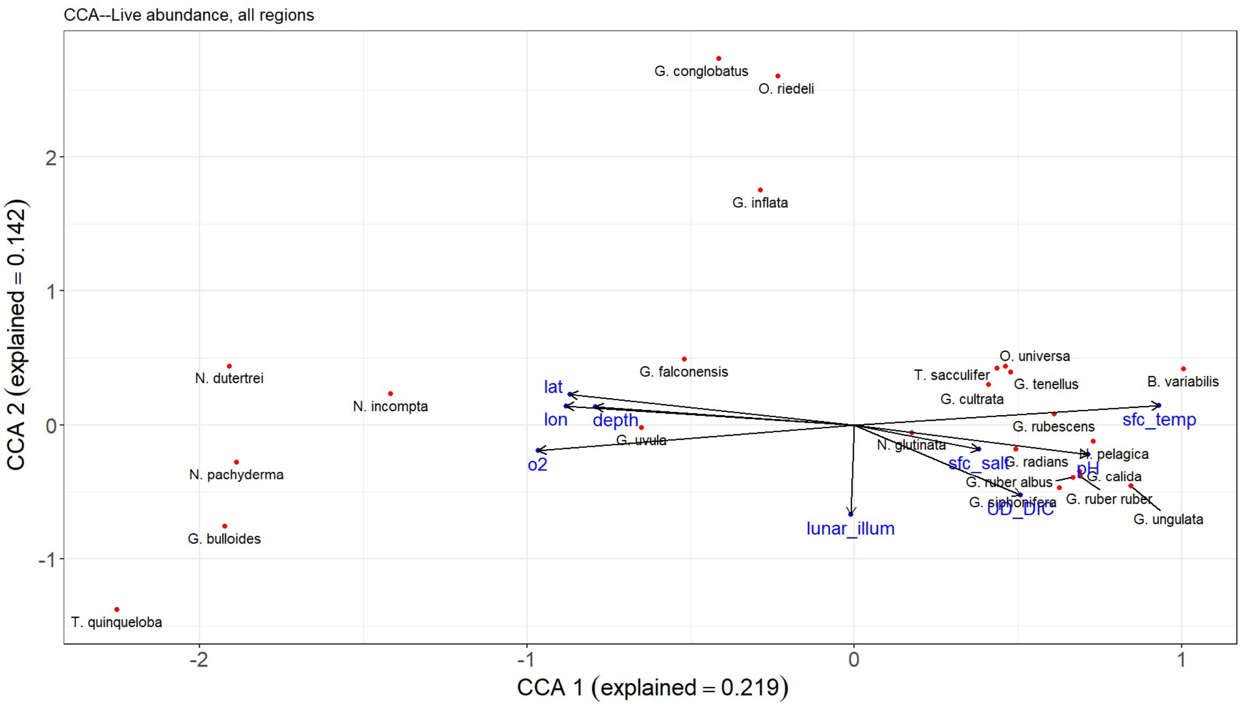

Figure C3. Canonical correlation analysis of the twenty-seven species in the dataset and environmental drivers.

Table C1. Stepwise linear regression results for Shannon and Simpson's diversity indices.

	Shannon diversity index			Simpson's diversity index		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	-20.71	-38.14 – -3.28	**0.021**	-7.70	-14.87 – -0.52	**0.036**
lon	0.05	0.02 – 0.09	**0.004**	0.02	0.01 – 0.04	**0.004**
pH	3.24	0.79 – 5.68	**0.011**	1.24	0.24 – 2.25	**0.017**
Observations	38			38		
R^2 / R^2 adjusted	0.217 / 0.172			0.220 / 0.175		

Table C2. Stepwise linear regression results for total concentration and calcite.

	Total normalized abundance		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	-688.24	-1149.71 – -226.77	**0.005**
UD DIC	0.16	0.05 – 0.26	**0.004**
sfc temp	0.75	0.13 – 1.38	**0.020**
pH	74.31	22.32 – 126.30	**0.007**
ALK	-103342.49	-173948.78 – -32736.20	**0.005**
lunar illum	1.62	-0.59 – 3.83	0.146
Observations	38		
R^2 / R^2 adjusted	0.278 / 0.165		

	Total normalized live surface area (calcite)		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.00	-0.34 – 0.34	1.000
UD DIC	2.36	0.07 – 4.65	**0.044**
sfc temp	1.32	-0.58 – 3.21	0.165
pH	2.64	0.31 – 4.98	**0.028**
ALK	-5.20	-10.52 – 0.12	0.055
Observations	33		
R^2 / R^2 adjusted	0.225 / 0.115		