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Constraining planktic foraminiferal depth habitats for improved polar and subpolar paleoreconstructions

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Abstract. Planktic foraminifera serve as critical proxy substrates in paleoceanographic reconstructions. However, the vertical structure of foraminiferal assemblages in the water column remains poorly constrained, particularly in the Pacific Ocean, thus impacting paleoceanographic interpretations from this basin. Here we use depth-stratified plankton tows (0–250 m) collected from the Northern California Current (NCC) to investigate spatiotemporal variability in community composition and depth habitat, with particular emphasis on taxa commonly used in polar and subpolar paleoreconstructions, specifically *Neogloboquadrina pachyderma*, *N. incompta*, and *Turborotalita quinqueloba*. Community composition varied significantly across years but not across latitudes, and comparison to previous NCC studies revealed distinct assemblages across end-member states of the Pacific Decadal Oscillation. Spinose species were most abundant in the upper 25 m of the water column and exhibited consistently shallower average living depths (ALD; 24-31 m) and narrower vertical distributions (VD; ± 13-19 m) compared to non-spinose taxa (38-94 m ± 23-49 m). *Turborotalita quinqueloba* and *N. pachyderma* displayed greater depth habitat variability across the study interval, whereas *N. incompta* exhibited a more stable, constrained depth habitat. Depth habitats in the NCC were shallower when compared to previous studies from other ocean basins, likely due to distinct genotypes inhabiting the study region compared to previous studies concentrated in the North Atlantic and Arctic Oceans. Results herein highlight the need to develop a nuanced understanding of the ecological and environmental processes that govern foraminiferal distribution in the water column to better refine proxy interpretations, particularly in climatically sensitive polar and subpolar regions.

1 Introduction

Planktic foraminifera are microscopic protists that play a crucial role in marine ecosystems and oceanic carbon cycling, despite only constituting a minor portion of total zooplankton biomass (Holligan and Robertson, 1996; Schiebel and Hemleben, 2005; Knecht et al., 2023; Ziveri et al., 2023). These unicellular organisms secrete calcium carbonate ($CaCO_3$) shells or "tests" that geochemically record the environment in which the organism lived and calcified (Katz et al., 2010; Allen et al. 2016). Similarly, planktic foraminiferal community composition has been shown to track environmental gradients, with

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strong correspondence to sea surface temperatures, where distinct communities typify specific temperature thresholds, constituting foraminiferal "provinces" (Bé and Tolderland, 1971; Kucera, 2007). As temperature gradients shift either seasonally or on longer timescales, the abundance and community composition of foraminifera fluctuates as well (Arnold and Parker, 1999; Kucera et al., 2005; Jonkers et al., 2013; Chaabane et al., 2026).

Upon death, planktic foraminiferal tests sink to the seafloor and, if above the carbonate compensation depth, may be preserved in the deep-sea sedimentary record as microfossils (Berger, 1979). The progressive deposition of these tests into sedimentary layers upon the seafloor over geologic timescales allows for the investigation of changes in past ocean conditions based upon shell abundance and structure, community composition, and shell geochemistry (Ridgwell and Zeebe, 2005; Katz et al., 2010; Jonkers et al., 2013; Allen et al., 2016; Martin, 2017). Thus, the study of fossil planktic foraminifera has served as a cornerstone of paleoceanographic reconstruction, allowing for the investigation of climate phenomena occurring on timescales ranging from decades to millennia (Havard et al., 2026; Herlinger et al., 2026).

While planktic foraminifera are among the most comprehensively studied calcareous microfossils, having appeared in the fossil record starting in the Middle Jurassic (~180 Ma) (Pawlowski et al., 2003; Gradstein et al., 2021), there are still uncertainties regarding their ecology that directly impact the accuracy of paleoenvironmental interpretations drawn from their test geochemistry and paleocommunity composition. For example, planktic foraminifera may prefer to inhabit different portions of the surface ocean water column (Fairbanks et al., 1982; Rebotim et al., 2017; Kretschmer et al., 2018). However, the depth habitats of many taxa – particularly those that are abundant in polar and subpolar regions – are not well constrained. Differences in shell structure, diet, and symbiotic affinities may impact the depth distribution of planktic foraminifera throughout the water column. For example, some taxa have calcitic spines that are hypothesized to aid in buoyancy control, feeding, and relationships with photosynthetic algae in symbiont bearing species (Bé et al., 1977; Anderson et al., 1979; Spero, 1988; Gaskell et al., 2019; Grigoratou et al., 2021). Therefore, the presence of spines or the hosting of algal symbionts may lead a given taxon to inhabit a shallower depth habitat within the euphotic zone. Despite these general observations, great uncertainties remain regarding the controls on and stability of foraminiferal depth habitats.

To accurately use foraminifera geochemistry as proxies to reconstruct past environmental change, it is necessary to have a comprehensive understanding of the preferred depth habitat, and the stability of that depth habitat, for a given species. For example, if a foraminifer is interpreted to have lived in the surface mixed layer but has a true depth habitat in the thermocline, temperature reconstructions from that species may inadvertently underestimate true mixed-layer paleotemperatures. Furthermore, if the depth habitat of a given species migrates to track a specific environmental parameter (e.g., a specific temperature, the top of the pycnocline), reconstructions drawn from the geochemistry of that taxon may underestimate true variability in ocean conditions. Collectively, these ecological unknowns can lead to erroneous paleoclimate interpretations, ultimately limiting the ability to use deep-sea records as time capsules to better understand Earth's climate system.

Studies of modern foraminifera can vastly improve our understanding of the ecology underlying the calcification and subsequent geochemistry of fossil specimens. For example, foraminiferal depth habitat is investigated through two primary

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avenues: 1) observation of species vertical distribution via depth-stratified plankton tows collected from the surface ocean, or 2) inference of depth habitat from test stable oxygen isotope ($\delta^{18}O$) composition (Emiliani, 1971; Sautter and Thunell, 1989; Mortyn and Charles, 2003; 2004; Rebotim et al., 2017; Greco et al., 2019; Lessa et al., 2020). In modern studies, the former method is preferential due to caveats (e.g., recrystallization, dissolution, vital effects) impacting test isotope composition (Fairbanks et al., 1982; Spero and Lea, 1993; Mortyn and Charles, 2003; Katz et al., 2010; Jonkers et al., 2013; Jochum et al., 2019; Davis et al., 2020). Similarly, investigation of foraminiferal community compositions derived from plankton tow sampling over space and time can provide further insight into how planktic foraminiferal communities reflect regional environmental conditions (e.g., Lane et al., 2023). While many studies have characterized the depth habitat and community composition of tropical and subtropical planktic foraminiferal taxa (e.g., Rebotim et al., 2017; Meilland et al., 2019; Lessa et al., 2020), fewer studies have investigated the ecology of polar and subpolar taxa, with most studies conducted in the North Atlantic or Arctic Oceans (e.g., Kohfeld et al., 1996; Stangeew, 2001; Bauch et al., 2002; Greco et al., 2019).

If we are to confidently use polar and subpolar planktic foraminiferal fossil records to investigate climate dynamics in vulnerable high-latitude regions, and in particular the high-latitude Pacific Ocean basin, we must first gain a better understanding of their ecology and how depth habitat varies in time and space. Here we investigate depth-stratified plankton tows collected from throughout the Northern California Current (NCC; **Fig. 1**), a "transitional" foraminiferal province (Kucera, 2007) that welcomes both subtropical/transitional and polar/subpolar taxa depending upon environmental conditions, to explore spatiotemporal variability in community composition and preferred depth habitats of the species present. The average living depth (ALD) and vertical distribution (VD) of abundant species are quantified using methods developed by Rebotim et al. (2017) and where possible, these methods are applied to previous studies investigating taxa common to polar and subpolar environments, namely *Neogloboquadrina pachyderma*, *N. incompta*, and *Turborotalita quinqueloba* (e.g., Ortiz et al., 1995; Kohfeld et al., 1996; Stangeew, 2001; Kuroyanagi and Kawahata, 2004; Pados and Spielhagen, 2014; Iwasaki et al., 2017), to assess depth habitat stability globally. We also explore changes in community composition with depth and across time, including comparison to prior plankton tow studies conducted in the NCC. Through these efforts, the preferred depth habitats of polar and subpolar taxa are quantified, and their stability is assessed in an effort to better understand the ecology of these taxa that are crucial to paleoclimate reconstructions in high latitude regions.

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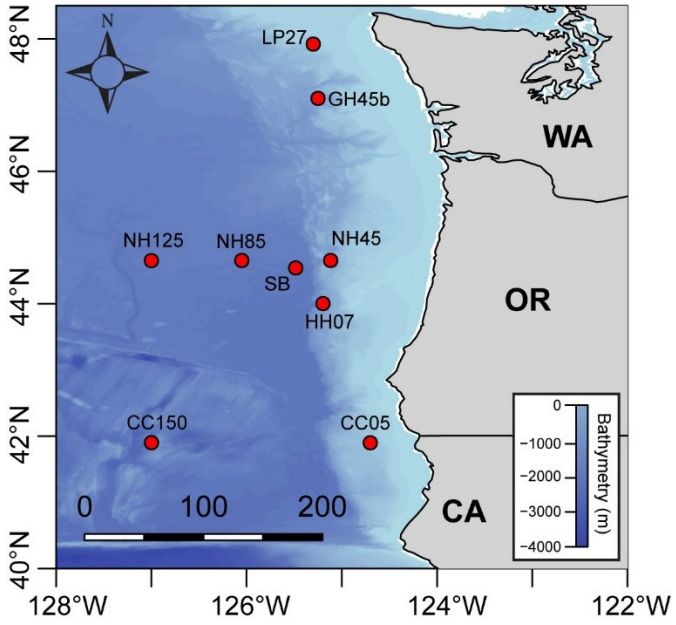

Figure 1. Depth-stratified plankton tow collection sites in the Northern California Current (NCC). Note that some sites were sampled repeatedly over several years. Scale bar is in kilometers.

2 Hydrographic setting

The NCC is a part of the California Current System (CCS) located in the North Pacific Gyre (Checkley and Barth, 2009; NOAA, accessed 2025). Due to its status as an eastern boundary current, the CCS is relatively shallow, slow, and broad compared to the western boundary current in the North Pacific Gyre, the Kuroshio Current. The CCS brings cool waters from the northern latitudes down the western coast of North America, extending from Vancouver Island (50°N) to Baja, California (27°N) (NOAA, accessed 2025). The NCC, which flows from approximately 48°N to 40°N, travels above a relatively narrow, deep continental shelf (0 to 200 m) and a steep continental slope that transitions into deep (>2500 m) water ~25–50 km offshore. The NCC welcomes a variety of phytoplankton that are dependent upon the coastal upwelling of nutrients from deeper waters (Huyer et al., 2005; Barth et al., 2007). Upwelling is caused by seasonal wind variability that brings cooler, more nutrient-rich waters to the surface during spring and summer months, with downwelling occurring in fall and winter months (Huyer et al., 2005; Bograd et al., 2009; Checkley and Barth, 2009).

In addition to seasonal variation, recurring climate variability caused by the Pacific Decadal Oscillation (PDO) and El Niño Southern Oscillation (ENSO) further modulates environmental gradients in time and space (Alexander et al., 2002; Di Lorenzo et al., 2013; Frischknecht et al., 2015). Environmental conditions are linked to PDO being in either a warm, "positive" phase or a cool, "negative" phase, with the most recent six years (2020-2026) producing consistently negative values indicative of a cool phase (National Centers for Environmental Information, 2025). During PDO cool phases, the NCC sources a greater quantity of cool, saline water from the Gulf of Alaska. Conversely, warm phases result in less water being sourced

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from the Gulf of Alaska, leading to warmer, less saline surface waters; these changes in source water influences the biological productivity of the region (Mantua et al., 1997; Field et al., 2006; Keister et al., 2011; Gordon et al., 2021). ENSO similarly impacts local hydrography, with El Niño leading to warmer, less saline surface waters and La Niña leading to enhanced coastal upwelling of deep, cool, higher salinity waters in the region. Conditions in this region can be further affected by periods of anomalously high SST known as marine heatwaves (MHW), which have been shown to have profound effects on NCC plankton communities (e.g., Wyatt et al., 2022; Lane et al., 2023).

3 Materials and Methods

3.1 Plankton tow sampling

Depth-stratified plankton tows were collected from throughout the NCC during four cruises that occurred between April 2022 and May 2025 (**Table 1, Fig. 1**). Depth stratified tows were collected using a 0.5 m diameter open-close plankton tow net with a Puget Sound collar and a 150 µm mesh size. The net was opened and lowered into the water column at a rate of 30 m/min until it reached the bottom of a given sampling interval (e.g., 250 m of the 150-250 m sampling interval). The net was then pulled upwards at a rate of 10 m/min to the top of the sampling interval (e.g., 150 m of the 150-250 m sample interval), closed, and brought back up to the surface at a rate of 30 m/min. This process was then repeated for each additional interval, most commonly: 0-25 m, 25-50 m, 50-100 m, 100-150 m, and 150-250 m. Once the net was pulled aboard, it was rinsed with seawater, and collected samples were poured into plastic jars, preserved in either an NaOH- or borax-buffered formalin solution, and wrapped in Parafilm until the sample could be further processed back in the laboratory at George Mason University.

3.2 Foraminiferal extraction and assemblage analysis

To extract the foraminifera from each sample, the contents of each preserved plankton tow were poured into a crystallizing dish, and any remaining matter was rinsed out of the jar using NaOH-buffered deionized (DI) water (pH ~8.5). The plankton tow contents were swirled in a circular motion, causing the denser material to accumulate at the center of the glass dish. The density of foraminiferal tests relative to other materials in the tow allowed nearly all foraminifera to collect within the center of the dish. Using a pipette, subsamples were removed from the center, placed into a glass petri dish, and observed under stereoscope. Snorkel arms connected to a fume extractor were positioned next to the stage while each petri dish was examined and foraminifera removed to avoid inhalation of formalin fumes. A fine-tipped paint brush was used to remove all individual specimens from the petri dish. Specimens were rinsed by placing them into a smaller petri dish of deionized water for no more than 30 minutes (to avoid dissolution) and subsequently stored on micropaleontological slides. This process was repeated with replicate subsamples until all foraminifera were removed from the plankton tow sample.

All specimens from each plankton tow were identified to the species level using a dissecting stereoscope, and species concepts followed those outlined in *Planktic Foraminifers in the Modern Ocean* (Schiebel and Hemleben, 2017). Specimens

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smaller than 100 µm that did not possess distinguishable characteristics of a given species were deemed unidentifiable and counted as "juveniles." The raw assemblage counts from each plankton tow can be found in Hupp et al. (2026).

Table 1. Metadata from each site sampled in this study including date sampled, site abbreviation, latitude, longitude, and depth intervals sampled.

Year	Site	Latitude (N)	Longitude (W)	Intervals Sampled (m)
April 1st, 2022	SB	44°33'36"	125°28'12"	0-25, 25-50, 50-100, 100-150, 150-200, 200-300
May 9th, 2022	CC150	41°54'03"	126°59'56"	0-25, 25-50, 50-100, 100-150, 150-250
May 11th, 2022	HH07	44°00'00"	125°11'59"	0-25, 25-50, 50-100, 100-150, 150-250
May 12th, 2022	NH125	44°39'00"	127°00'00"	0-25, 25-50, 50-100, 100-150, 150-250
May 14th, 2022	GH45b	47°05'59"	125°15'00"	0-25, 25-50, 50-100, 100-150, 150-250
May 25th, 2023	CC05	41°54'00"	124°41'59"	0-25, 25-50, 50-100, 100-150, 150-250
May 26th, 2023	RR06	42°30'00"	125°00'40"	0-25, 25-50, 50-100, 100-150, 150-250
May 28th, 2023	HH07	44°00'00"	125°11'59"	0-25, 25-50, 50-100, 100-150, 150-250
May 29th, 2023	NH85	44°39'06"	126°03'00"	0-25, 25-50, 50-100, 100-150, 150-250
June 2nd, 2023	GH45b	47°05'59"	125°15'00"	0-25, 25-50, 50-100, 100-150, 150-250
June 3rd, 2023	LP27	47°55'11"	125°18'00"	0-25, 25-50, 50-100, 100-150, 150-250
May 17th, 2025	HH07	44°00'00"	125°11'59"	0-25, 25-50, 50-100, 100-150
May 18th, 2025	NH45	44°39'06"	125°07'00"	0-25, 25-50, 50-100, 100-150, 150-250
May 19th, 2025	NH85	44°39'06"	126°03'00"	0-25, 25-50, 50-100, 100-150, 150-250

3.3 Depth habitat determination

To determine the ALD and VD, assemblage counts were first normalized to tow volume to determine the abundance of individuals per cubic meter of each species within a given depth interval. Tow volumes were determined by using the equation for the volume (v) of a cylinder (**Eq. (1)**):

$$v = \pi r^2 h \quad (1)$$

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where the height (h) was adjusted to reflect the depth interval of each tow (e.g., 100 m for the 150-250 m interval) and the radius (r) remained a constant 0.25 m. Abundance (a) was then calculated as individuals/m^3 using the following equation (**Eq. (2)**):

$$a = \frac{\#\ \text{of individuals}}{\text{tow volume in } m^3} \quad (2)$$

Once abundance was determined, it was used to weigh the mean depths of the sampling intervals so that the weighted average of those values would reflect the ALD of a particular species, calculated via the following equations from Rebotim et al. (2017; **Eq. (3)**):

$$ALD = \frac{\Sigma\ (Ci * Di)}{\Sigma\ Ci} \quad (3)$$

where D_i represents a depth interval and C_i represents the concentration of species within the given D_i. The ALD was not determined for species with less than five individuals at a given site due to insufficient population size. Once ALD was quantified, VD was determined using the methods from Rebotim et al. (2017; **Eq. (4)**):

$$VD = \frac{\Sigma\ (|ALD - Di| * Ci)}{\Sigma\ Ci} \quad (4)$$

These calculations were applied to the depth interval samples specific to this study (e.g., **Fig. S1**).

3.4 Statistical Analysis

The data collected from this study were evaluated at several scales to examine differences in 1) community composition by site, 2) community composition by depth, 3) depth habitat via ALD and VD, and 4) communities and depth habitats of this study compared to previous NCC studies. Thus, different statistical techniques were employed for each of these data investigation categories, which are described in each subsection below.

3.4.1. Community Composition by Site and by Depth

Community compositional data was evaluated as normalized abundance (i.e., individuals/m^3) and relative abundance (%) of each species per site. Community diversity was assessed using species richness and the Shannon H. Index (SH), which accounts for both species richness and evenness (Shannon, 1948; Hill, 1973). SH values were determined using PAleontological STatistics (PAST, version 4.03) software. The SH values from each site per year were compared to each other using a Kruskal-Wallis and Pairwise Mann Whitney U/Wilcoxon Rank Sum test due to the data's non-normality and small sample sizes. The *kruskal.test()* and *pairwise.wilcox.test()* functions in base R were used for these calculations. Sites from the most heavily sampled year, 2023, were split into three binned groups based upon latitude: 41-43°N, 43-45°N, and 47-49°N, and both aforementioned statistical tests were again performed in base R to test for differences across latitudinal bins.

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To evaluate compositional changes across depth, both richness and SH values were compared between adjacent depth intervals using a Wilcoxon Signed-Rank test, where values from each depth interval were paired based on site (e.g., HH07 2022 0-25 m was paired with HH07 2022 25-50 m to compare 0-25 m vs. 25-50 m depth intervals). Intervals with no matching pair were excluded, such as in cases where a given depth interval was barren or not sampled. The *wilcox.test()* function in base R was used for these calculations, with the mu argument set to 0. All statistical tests used a 95% confidence level, and all statistical analyses and plots were conducted or created using R unless stated otherwise.

Multivariate approaches including non-metric Multi-Dimensional Scaling (nMDS), PERmutational Multivariate ANalysis of VAriance (PERMANOVA), and SIMilarity PERcentage (SIMPER) were used to further explore the data. Communities were grouped temporally at the site-level by year and spatially by latitudinal bin or depth, and PERMANOVA was applied via the *adonis2()* function in the *vegan* R package to assess variance. The Bray-Curtis dissimilarity metric was used for this analysis as opposed to Euclidean distance because of its ability to handle ecological data with an abundance of zeros. Unless stated otherwise, the Bray-Curtis dissimilarity metric was chosen when applicable for the following statistical tests. When met with statistically significant PERMANOVA results, nMDS and SIMPER were applied. The *metaMDS()* and *simper()* functions from the *vegan* package were used for each of these analyses, respectively. These multivariate analyses discussed above were used to 1) address whether there was statistically significant variance between sites grouped by year/latitude/depth (PERMANOVA), 2) investigate how sites may cluster in multivariate space when grouped by year/depth (nMDS), and 3) identify which species contributed the most toward the dissimilarities between groups (SIMPER).

3.4.2 Depth Habitat via ALD and VD

While ALD and VD were calculated following methods established by Rebotim et al. (2017), potential relationships between ALD and VD were assessed using weighted least squares regression. ALD and VD values were weighted by how many individuals contributed to the calculation, under the assumption that an ALD/VD estimation based upon 300 individuals may be more representative of a given species depth habitat compared to an estimate based upon a population of 30 individuals. The potential for correlation between ALD and VD was assessed using data from all sites and species, and at the species-specific scale, although species-specific correlations were only explored for species that had five or more site observations (n = 5 taxa). ALD and VD data were weighted and analyzed using the *lm()* function in base R. Furthermore, the 95% range of calculated ALD and VD values for each study taxon was determined by bootstrapping the weighted and unweighted ALD and VD values across all sites (**Table 2**), bootstrapped at the 95% level using the *boot()* function in base R with 2,000 resamples.

3.4.3 Comparison to prior foraminiferal studies from the NCC

Two prior studies have investigated planktic foraminiferal communities collected via plankton tow in the NCC. Lane et al. (2023) characterized planktic foraminiferal abundances in the upper 100 m of the water column by analyzing plankton tow samples collected along the National Oceanic and Atmospheric Administration (NOAA) Newport Hydrographic Line at 44.6°N; this study explored how planktic foraminiferal assemblages fluctuated along a shelf to offshore transect across years

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representative of both marine heatwave and non-MHW conditions. Ortiz et al. (1995, 1995) are the only prior studies to subsample the water column to investigate planktic foraminiferal assemblage changes with depth in the NCC. Ortiz et al. (1995) examined community composition across discrete depth intervals in the upper 200 m of the water column, whereas Ortiz et al. (1996) characterized the depth distribution and isotope geochemistry of deeper-dwelling foraminifers living above 800 m depth; both of these studies examine data from the same sites, sampled at the same time, but focused upon analysis of different depths. In these studies, the authors examined four sites, sampled during a single cruise (41-43°N) in 1990 using depth-stratified plankton tows.

To facilitate comparison of observations from this study to those from previous planktic foraminiferal studies in the NCC (i.e., Ortiz et al., 1995; 1996; Lane et al., 2023), raw count data was extracted from each prior study and assessed alongside raw counts derived from this study. Due to differences in sampling sites, data from multiple sites were combined to establish a regional "assemblage" reflective of each sampling year. Then, to summarize community composition found within each study, raw counts from each individual study were summed to produce one overall community composition for the data collected therein. For Lane et al. (2023), raw counts from all MHW years and non-MHW years were summed separately to produce two community compositions. To summarize the overall community composition found within the NCC across all four studies, all raw counts were added together, and the relative abundance of each taxon was again determined. These steps were repeated to reflect species grouped by foraminiferal province. A PERMANOVA was used to assess the statistical significance of differences in community composition between this study and those of Ortiz et al. (1995, 1996) where community composition for each site sampled in both studies was characterized via relative abundance. An additional pairwise PERMANOVA was used to compare results from this study to the MHW and non-MHW years from Lane et al. (2023), where community composition was compared between groups (i.e., non-MHW, MHW, this study).

For comparison to depth habitat estimates from the studies of Ortiz et al. (1995, 1996), ALD and VD calculation methods of Rebotim et al. (2017) were applied to the depth-stratified raw abundance values for 7 taxa found in both studies (*G. glutinata, O. universa, G. bulloides, T. quinqueloba, N. incompta, N. pachyderma,* and *G. scitula*). Statistical differences in ALD values between studies were assessed using the *wilcox.test()* function with the mu argument set to 0.

3.5 Meta-Analysis of Depth Habitat Studies

A meta-analysis of 14 depth-stratified plankton tow studies from polar, subpolar, and transitional regions was conducted using the ALD and VD calculation methods established by Rebotim et al. (2017) to facilitate the comparisons for three key polar and subpolar species (*N. pachyderma*, *N. incompta*, and *T. quinqueloba*) found in this study (**Table S1**). For one study (Greco et al., 2019), ALD and VD were already calculated using these methods; however, most studies (e.g., Carstens and Wefer, 1992; Ortiz et al., 1995; 1996; Kohfeld et al., 1996; Jensen, 1998; Stangeew, 2001; Kuroyanagi and Kawahata, 2004; Gersonde, 2012; Pados and Spielhagen, 2014; Iwasaki et al., 2017) reported foraminiferal abundance in individuals/m^3 and required the application of methods from Rebotim et al. (2017) to determine ALD and VD. Kretschmer et al. (2018) also synthesized data from several studies without publicly available data (e.g., Mortyn and Charles, 2003; Simstich et al., 2003;

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Bergami et al., 2009); however, ALD and VD values calculated in Kretscmer et al. (2018) did not necessarily use all available data from the synthesized studies. Some prior depth habitat studies (e.g., Bauch et al., 2002; Field, 2004; Fraile et al., 2008) did not provide their data in a form that allowed for direct ALD and VD calculation, and thus, they were not included in this meta-analysis.

Within these 14 studies, seven included depth intervals below 300 m (e.g., Carstens and Wefer, 1992; Jensen, 1998; Stangeew, 2001; Pados and Spielhagen, 2014), exceeding the lower limit of this study. To assess whether the more restricted sampling range of this study (0-250/300 m) impacted the observed ALD and VD, results informed by the full depth ranges from all studies were compared to results excluding depths > 300 m. Note that although Mortyn and Charles (2003) sampled to 440 m, ALD and VD values were taken from Kretschmer et al. (2018), so the data could not be manipulated to exclude values > 300 m.

4 Results

4.1 Community Composition by Site

Throughout the 14 samples collected (n = 6,305 specimens), 13 different species were identified, including *Globigerina bulloides, G. falconensis, Globigerinella siphonifera, Globigerinita glutinata, G. uvula, Globigerinoides ruber, Globoconella inflata, Globorotalia scitula, Neogloboquadrina dutertrei, N. incompta, N. pachyderma, Orbulina universa,* and *Turborotalita quinqueloba* (**Fig. 2**). Across the entire study, subpolar species *T. quinqueloba* and polar species *N. pachyderma* were the dominant major taxa, constituting 49.6% and 31.4% of all specimens identified, respectively (**Fig. 3**). Minor taxa *N. incompta* (subpolar), *G. falconensis* (subtropical), and *G. uvula* (subpolar) constituted 2-9% of all study specimens. Trace taxa (≤ 1%) included three transitional taxa (*G. bulloides*, *G. glutinata*, and *G. scitula*) and three subtropical taxa (*O. universa*, *G. ruber, G. siphonifera*, and *N. dutertrei*) as well as *G. inflata*, the preferred province of which has not yet been conclusively identified.

Community composition was consistently dominated by either *T. quinqueloba* or *N. pachyderma*, with sites of greater foraminiferal abundance favouring the former (**Fig. 3a**). Sites with the highest abundance values (16-36 individuals/m^3) were primarily sampled in May 2022, with the exception of RR06 sampled in 2023 (17 individuals/m^3). Overall, approximately 73% of the 6,305 individuals examined in this study were collected from sites sampled in May 2022. The community composition of sites sampled during 2022 was dominated by subpolar taxa (**Fig. 3b**). In 2023, *N. pachyderma* became the dominant taxon and generally increased in relative abundance as latitude increased; however, for the two northernmost sites sampled, *T. quinqueloba* was the predominant species. In 2025, the *T. quinqueloba*-dominant trend halted abruptly; all three sites sampled during this year were composed of >82% *N. pachyderma*, with site NH85 reaching nearly 90%, demonstrating the prevalence of this polar taxon in 2025.

When using SH values as measures of site diversity, all 2025 samples had distinctly lower diversity, with SH values less than 0.65 (**Fig. 4a**). Comparatively, assemblages from 2022 and 2023 were more diverse, with SH values consistently greater than 0.9 apart from GH45b in 2023 (SH = 0.64). The highest SH value was associated with the community at CC150

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290 in 2022 (SH = 1.45), with five additional sites from 2022 and 2023 reporting SH values over 1.0. These differences in SH values from each site were examined latitudinally (**Fig. 4b**); this comparison showed a general decrease in diversity as latitude increased, particularly for the 2022 and 2023 years. However, a Kruskal-Wallis test found no statistically significant differences in SH values between years and latitudinal bins (2023 only).

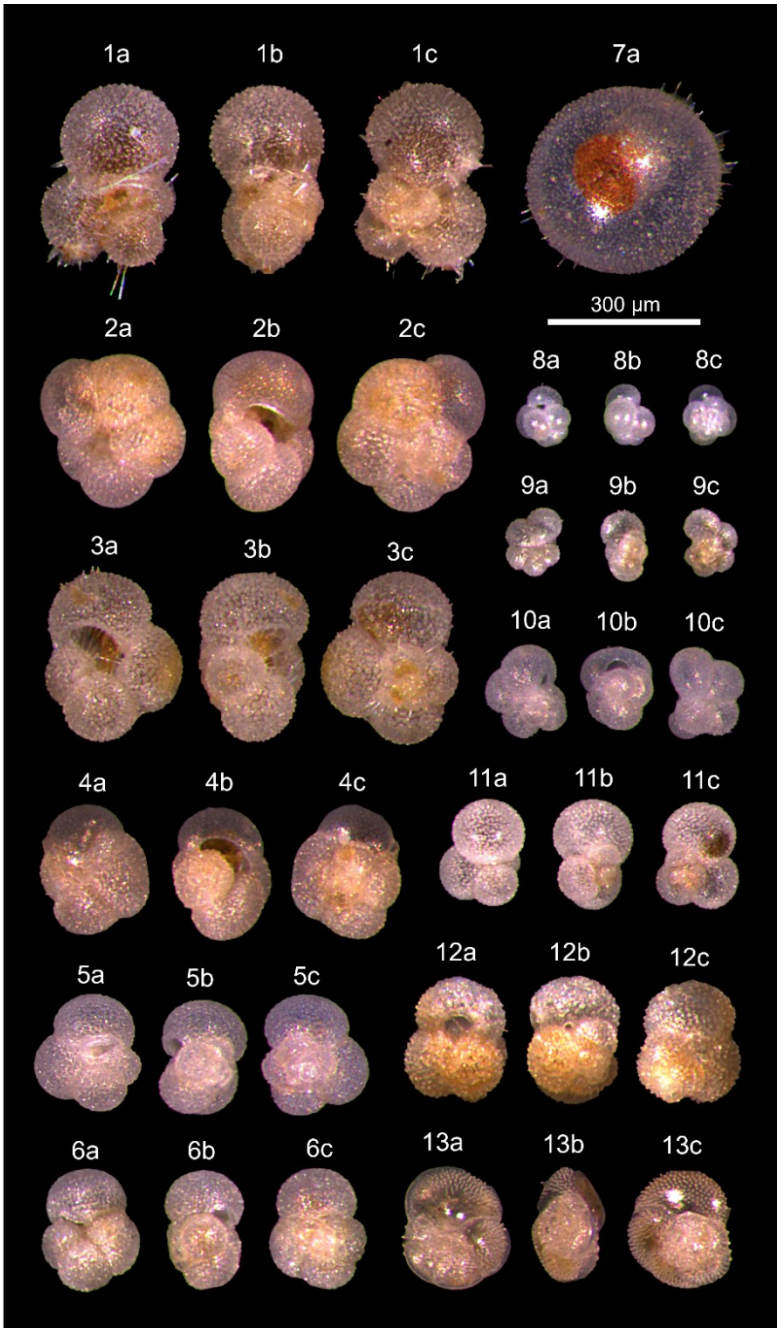

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Figure 2. Species found in this study, imaged with a stereoscope and shown in **(a)** ventral view, **(b)** side view, and **(c)** dorsal view. Species shown include: **(1)** *Globigerina falconensis**, **(2)** *Neogloboquadrina dutertrei*, **(3)** *Globigerina bulloides**, **(4)** *Globoconella inflata*, **(5)** *Neogloboquadrina pachyderma*, **(6)** *Neogloboquadrina incompta*, **(7)** *Orbulina universa**, **(8)** *Globigerinita uvula*, **(9)** *Turborotalita quinqueloba**, **(10)** *Globigerinella siphonifera*, **(11)** *Globigerinita glutinata*, **(12)** *Globigerinoides ruber**, **(13)** *Globorotalia scitula*. Asterisk denotes spinose species, although spines may not be visible. All species were identified using *Planktic Foraminifers in the Modern Ocean* (Schiebel and Hemleben, 2017).

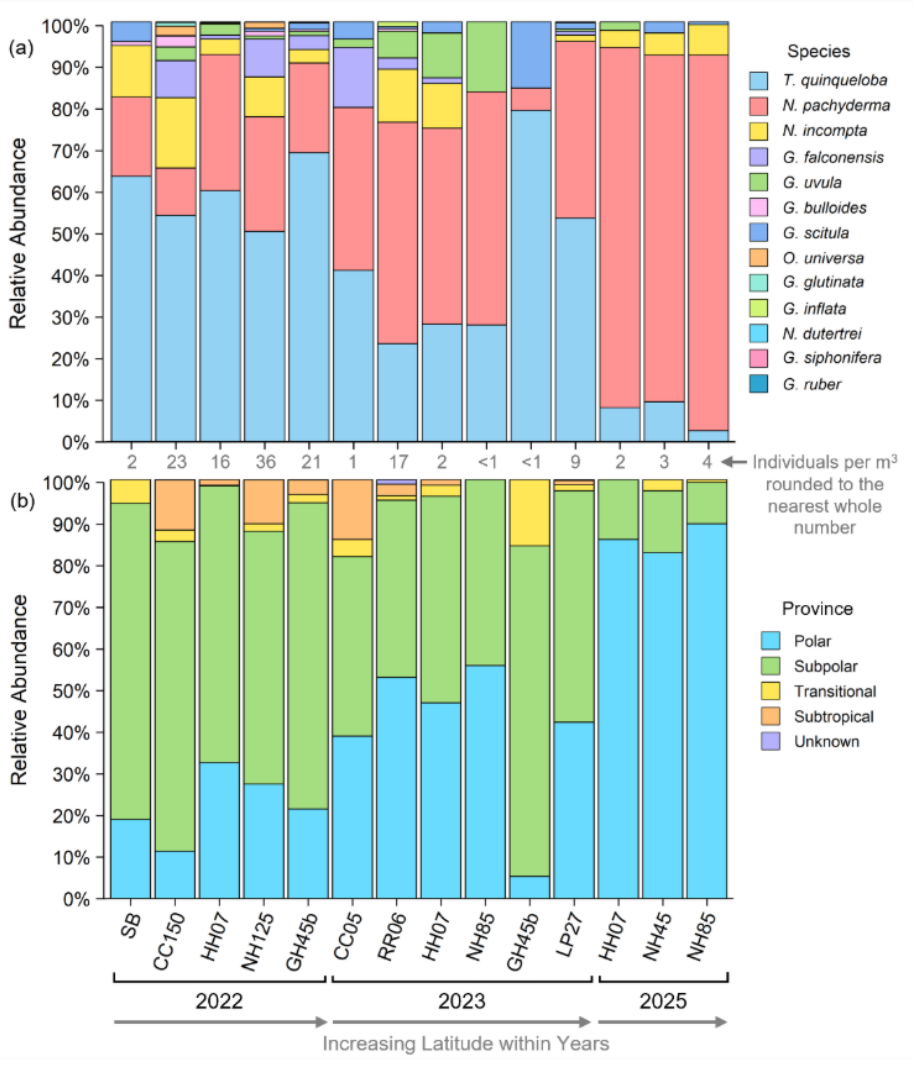

Figure 3. Community composition at each site for the upper 250 m of the water column, colored by **(a)** species and **(b)** foraminiferal province. Sites are organized primarily by year (increasing left to right) and secondarily by latitude (increasing left to right) within the temporal bounds. Note that site SB is listed first in 2022 because it was sampled in April compared to the following 2022 samples which were collected in May. Foraminiferal abundance in individuals per m^3 is listed below each site name.

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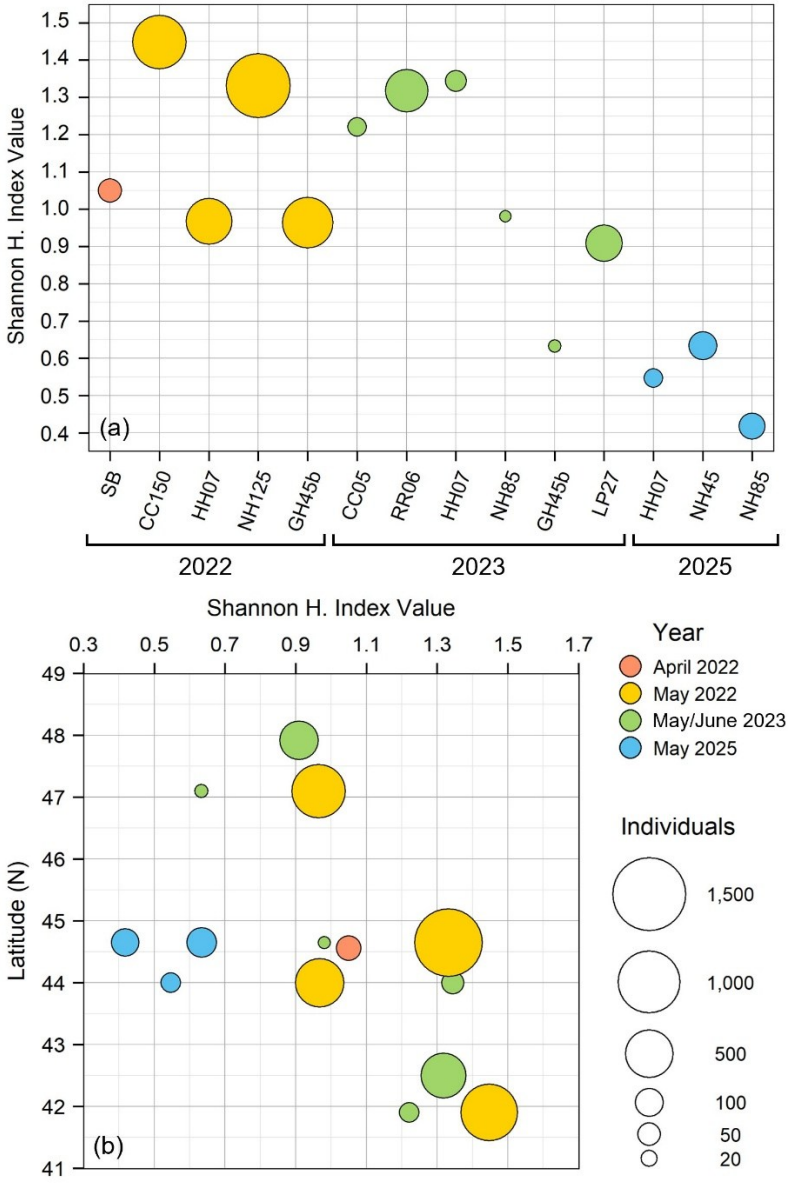

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Figure 4. (a) Shannon H. Index values per site, organized primarily by year (increasing left to right) and secondarily by latitude (increasing left to right). Note that site SB is listed first in 2022 because it was sampled in April compared to the following 2022 samples which were collected in May. **(b)** Shannon H. Index values per site versus latitude. Point size in both panels is directly proportional to the total number of individuals that were found at a given site.

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Community composition varied significantly among sites grouped by year (PERMANOVA, p = 0.002) but not between sites grouped by latitude (p = 0.333). Therefore, nMDS and SIMPER were only applied to the community composition data grouped by year. The nMDS plot (stress = 0.031) showed distinct clusters for the May 2022 and May 2025 sites, signifying 325 similarities within these groups, while May/June 2023 sites were spread more evenly throughout the plot, signifying dissimilarity (**Fig. 5**). SIMPER analysis revealed *T. quinqueloba* and *N. pachyderma* to be the primary contributors to differences in community composition among years, collectively contributing over 66%, 88%, and 81% to the dissimilarity metrics for the 2022-2023, 2022-2025, and 2023-2025 comparisons, respectively (**Table S2**). Sites sampled in 2022 were consistently characterized by higher relative abundances of *T. quinqueloba,* whereas sites from 2025 had higher relative 330 abundances of *N. pachyderma*.

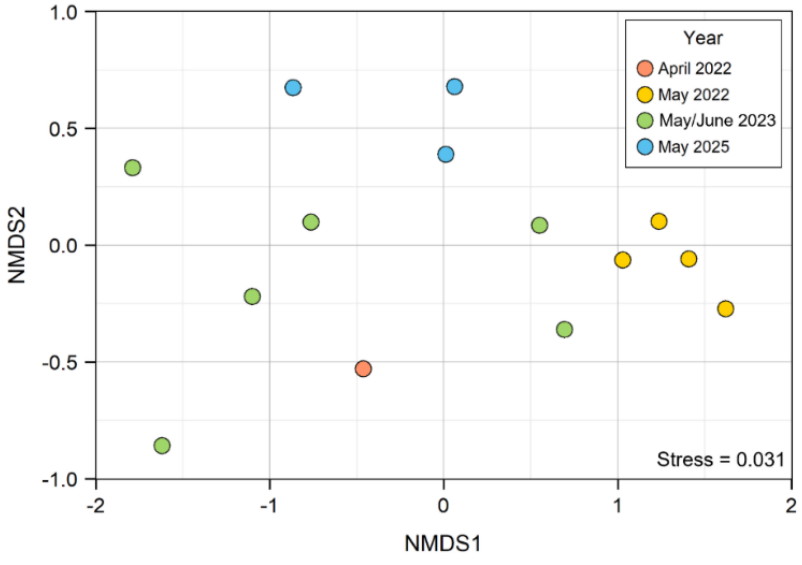

Figure 5. nMDS plot of study sites informed by community composition (0-250/300 m) relative abundance values and colored 335 by time of sampling. Stress of the fit was 0.031.

4.2 Community Composition by Depth

Community composition displayed distinct patterns across depths (**Fig. 6**). Across the shallower depths (<25 m), community composition was dominated by the spinose taxon *T. quinqueloba*, whereas deeper depths hosted more non-spinose 340 species such as *N. pachyderma*, *N. incompta*, and *G. scitula.* When community composition across discrete depth intervals was averaged across all sites, spinose taxa accounted for the majority (75%) of the 0-25 m assemblage (**Fig. 7**). However, this

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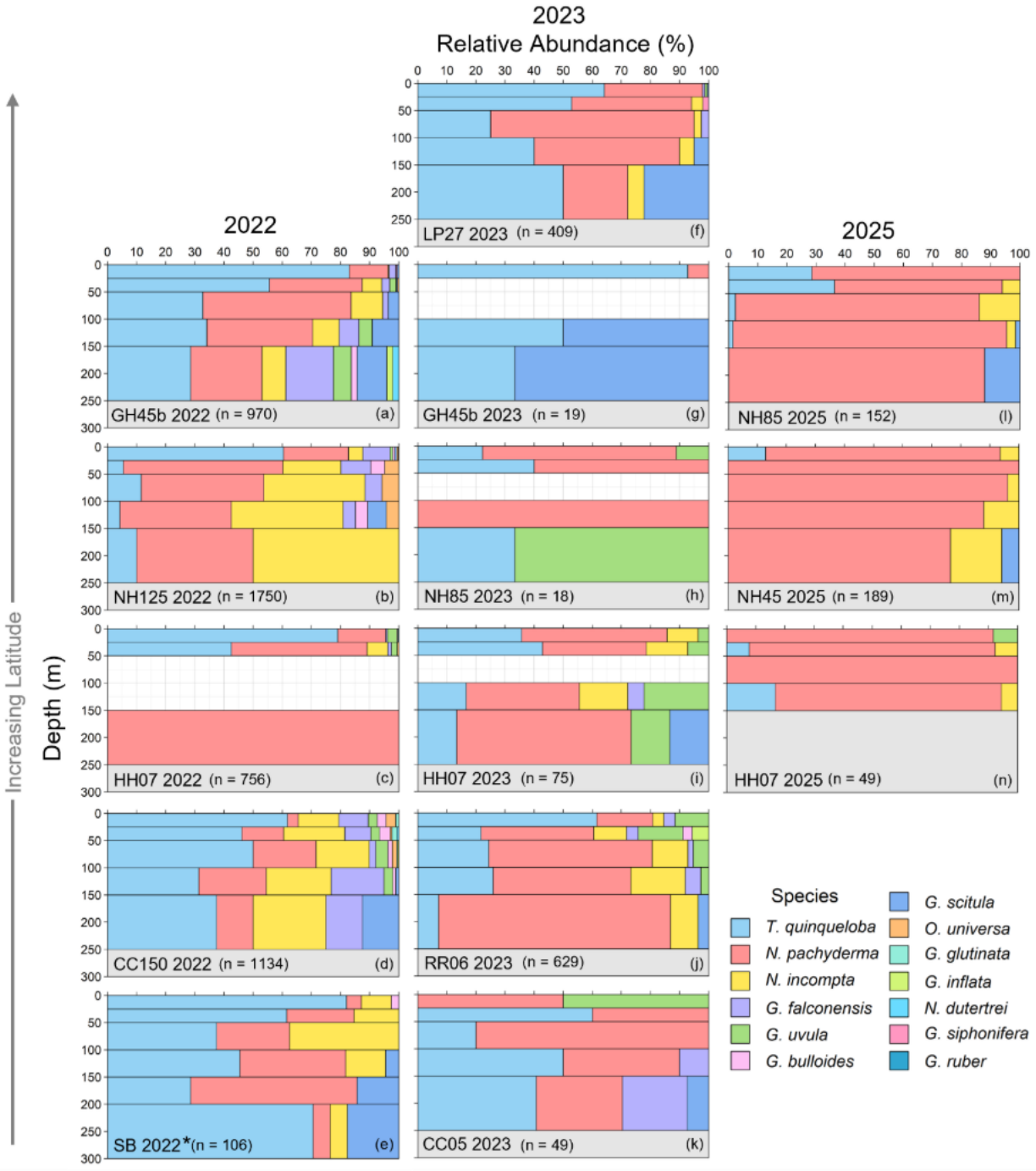

Figure 6. Community composition by depth at each of the 14 sites sampled, organized in columns by year. Panels are organized secondarily by latitude, with latitude increasing from bottom to top. Note that site SB is listed first in the 2022 column because it was sampled in April compared to the following 2022 samples which were collected in May. Grey bars indicate depth intervals that were not measured, whereas missing bars denote depth intervals where no specimens were present. (n=X) denotes the number of individuals found at each respective site.

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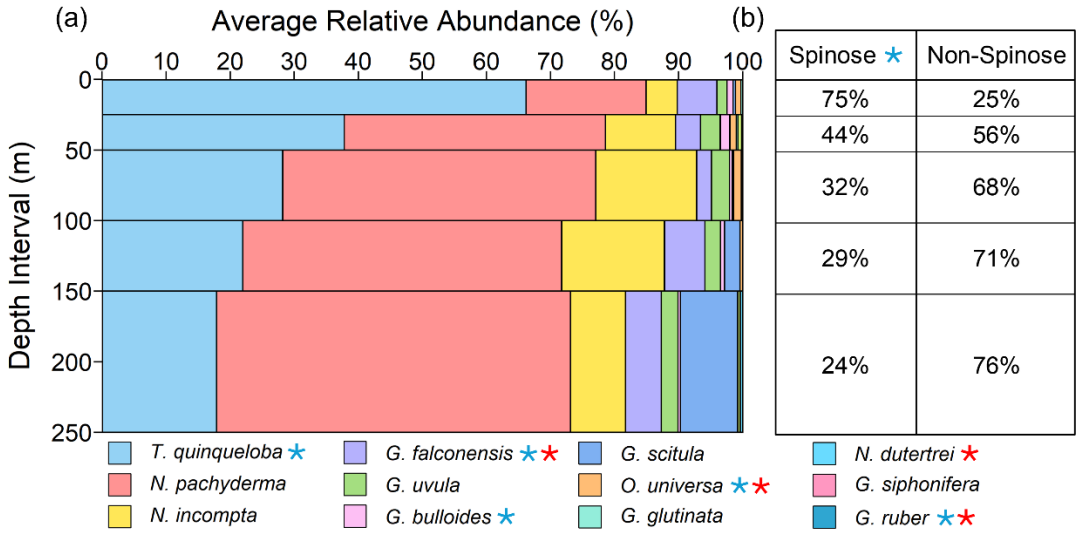

(b)

Spinose ★	Non-Spinose
75%	25%
44%	56%
32%	68%
29%	71%
24%	76%

Figure 7. (a) Average community composition by depth encompassing all 14 sites sampled (n = 6,305 specimens), with % average relative abundance for each taxon calculated as the average of all % relative abundance values found throughout this study at the given depth interval. **(b)** Average community composition of spinose taxa (denoted with blue asterisk) and non-spinose tax per depth interval, rounded to the nearest whole number. Red asterisk denotes species with confirmed algal symbionts.

value dropped to 44% for the 25-50 m interval and progressively decreased at deeper depths. By 150-250 m, spinose species only account for 24% of the assemblage, with non-spinose taxa composing the remaining 76%.

SH and richness values were calculated for each viable depth interval at each site as measures of diversity (**Fig. 8**). SH values ranged from as low as 0 (indicating depth intervals that contained only one species, i.e., 1 *N. pachyderma* found in the 150-250 m interval of HH07 in May 2022) to as high as 1.845, and richness values ranged from as low as 0 (indicating depth intervals that contained no specimens) to as high as nine different species. A paired Wilcoxon Signed Rank test revealed significant differences for two depth interval comparisons with respect to species richness: a positive value at the 25-50 m vs. 50-100 m comparison ($p = 0.023$), and a negative value at the 50-100 m vs. 100-150 m comparison ($p = 0.043$) (**Fig. 8a, b**). The sign of these values indicated that richness was significantly higher in the 25-50 m depth interval compared to the 50-100 m depth interval, and that richness was significantly lower in the 50-100 m depth interval compared to the 100-150 m depth interval, respectively. The SH values from the 50-100 m vs. 100-150 m comparison yielded the only significant differences ($p = 0.027$), where the negative sign indicated that SH values were significantly lower for the 50-100 m depth interval compared to the 100-150 m depth interval (**Fig. 8d**), consistent with a noticeable decrease in SH across the 50-100 m interval (**Fig. 8c**).

It is difficult to identify clustering in the nMDS plot comparing community composition across depth intervals from all years (stress = 0.102; **Fig. 9a**). When separated by year, the nMDS ordination shows a clear depth-related community

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succession in 2022 (stress = 0.088; **Fig. 9b**). This pattern was less distinct in 2023 and was largely absent in the 2025 data (**Fig. 9c, d**). Lastly, a PERMANOVA was applied to the relative abundances from each depth interval, and no significant variance was found in community composition when examined across adjacent intervals for all years (p = 0.074).

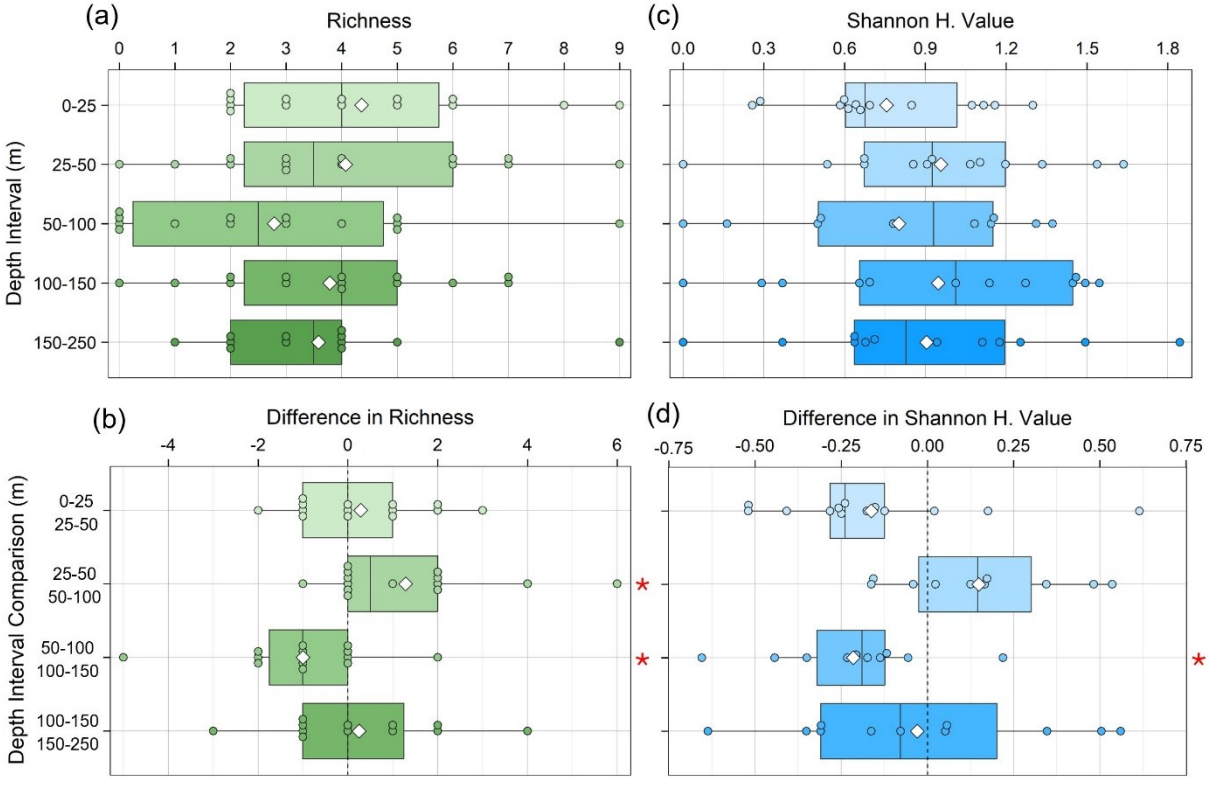

Figure 8. (a) Box and whisker plots showing species richness values at each depth interval at each site. Note that depths 150-200 m and 200-300 m from site SB were excluded due to differing sampling intervals. White diamonds represent the unweighted mean values. **(b)** Richness value differences (shallower interval – deeper interval) between depth intervals at each site. Asterisks to the right denote statistically significant differences between depths, calculated using a paired Wilcoxon Signed Rank Test. Data points with no matching pair were excluded in these calculations. **(c)** Panel structured the same as (a), but showing SH values. Depths 150-200 m and 200-300 m from site SB were once again excluded, and any depths that contained no specimen were excluded as well. **(d)** Structured the same as (b), but with SH values. Asterisk again denotes a statistically significant difference between depth intervals.

4.3 Depth Habitat Constrained via ALD and VD

Of the 13 different species observed in the study, only 10 had five or more individuals at any given site, which was used as the minimum population size cutoff for determining ALD and VD calculations as per Rebotim et al. (2017; **Table 2**). Over half of the ALD and VD calculations were made based upon population sizes of < 30 individuals, and nearly 30% were

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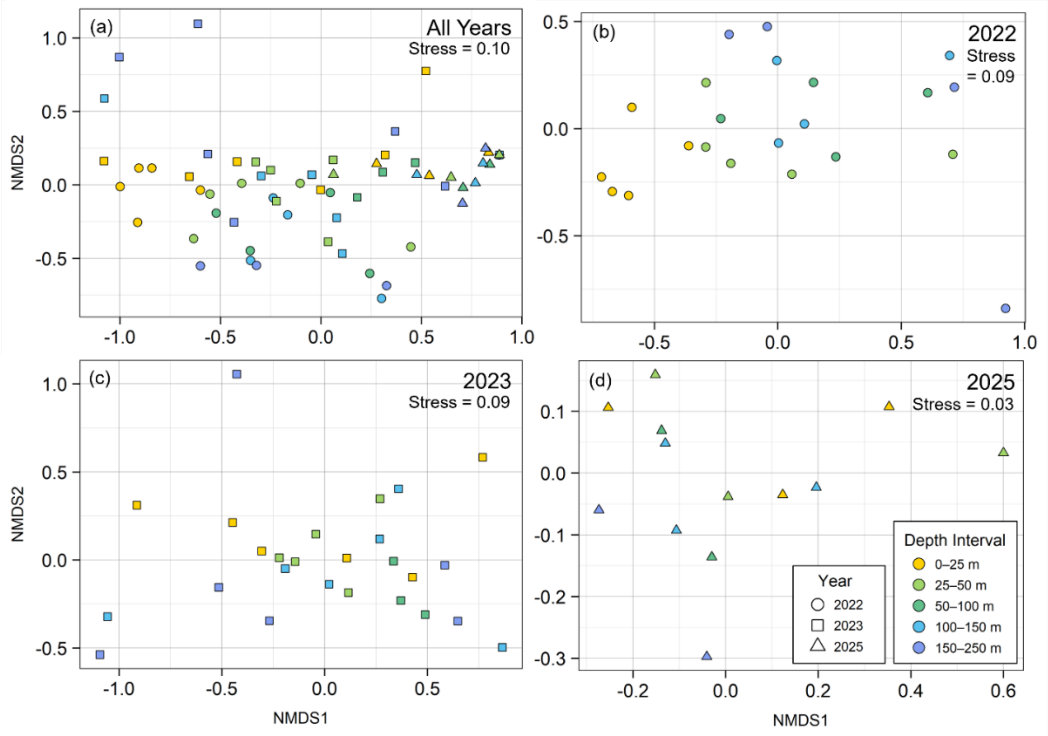

Figure 9. (a) nMDS plot of community composition across depth intervals from all sites informed by relative abundance values, colored by depth interval, and shaped by year. Stress of the fit was 0.102. nMDS plots, with data points colored and shaped according by depth and year, respectively, are also shown for **(b)** 2022, **(c)** 2023, and **(d)** 2025. Stress of fit for each model is shown in the upper right corner of each panel.

made based on population sizes of ≤ 10 individuals. Because larger population sizes may be more representative of true depth habitat at a given site compared to those with smaller population sizes, mean ALD and VD values were calculated by weighing each metric by the number of individuals that contributed to the calculation, with the largest being 876 *T. quinqueloba* at NH125 in 2022 and the smallest being five specimens in multiple instances. The weighted ALD was taken for each of the 10 evaluated taxa, and 95% bootstrapped (n = 2000 replicates) confidence intervals were applied to determine a summarized regional ALD and VD range (**Table 2; Fig. 10**). Although weighted ALD values fell between 23-50 m for most taxa, *G. scitula* was the exception with a deeper ALD of 93.6 m. VD followed a similar trend, as most values fell within a smaller range of 13-27 m while *G. scitula* had a much larger VD (48.8 m). Additionally, *G. inflata* had an apparent VD of 0, due to this species being found at only one site within a single depth interval. Of the 10 species where ALD and VD were calculated, four species were spinose (*T. quinqueloba, G. bulloides, O. universa,* and *G. falconensis*) and six were non-spinose (*G. glutinata, G. inflata, G. uvula, N. incompta, N. pachyderma,* and *G. scitula*). Nearly all non-spinose taxa were found to have deeper ALDs compared to the spinose species (**Fig. 10**), with the exception being *G. glutinata*, whose depth habitat estimate was based on only 10

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410 individuals from a single site (**Table 2**). To examine the relationship between ALD and VD, a weighted linear regression was used to find the best-fitting model for the full dataset as well as for individual species with at least five separate ALD/VD observations (i.e., found in high enough abundance at ≥ 5 sites; **Fig. 11**). Of these five species, only *T. quinqueloba, N. pachyderma,* and *G. uvula* produced statistically significant weighted linear models, whereas *N. incompta* and *G. falconensis* did not.

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Table 2. Summary table of average ALD and VD values calculated by methods described in Rebotim et al. (2017). "Weighted
420 by # Individuals" shows weighted ALD and VD averages when weighing each individual ALD and VD estimate by the number of individuals that contributed to the calculation. "Unweighted" shows the ALD and VD averages without the weighing scheme. "Sites" refers to the number of sites that had ALD and VD estimates for the given taxa, and "Zone" refers to the grouping based on environmental conditions as described in the Discussion section. Confidence intervals (95%) were bootstrapped with 2,000 resamples. Asterisk denotes spinose taxa, and cross symbol denotes taxa with confirmed algal
425 symbionts.

	Weighted by # of Individuals				Unweighted					
Species	**ALD**	95% CI	**VD**	95% CI	**ALD**	95% CI	**VD**	95% CI	**Sites**	**Zone**
Globigerinita glutinata	24		14		24		14		1	Shallow Surface
*Turborotalita quinqueloba**	24	18-35	13	7-23	38	26-57	23	15-32	12	Shallow Surface
*Globigerina bulloides**	27	25-29	17	17.0-17.3	27	25-29	17	17.0-17.3	2	Shallow Surface
Orbulina universa†*	29	19-38	16	11-21	29	19-38	16	11-21	2	Shallow Surface
Globigerina falconensis†*	31	21-73	19	10-34	62	28-112	24	15-33	6	Shallow Surface
Globoconella inflata	38		0		38		0		1	Deep Surface
Globigerinita uvula	41	28-55	23	15-33	46	25-62	27	12-42	6	Deep Surface
Neogloboquadrina incompta	47	39-70	27	22-33	57	47-68	31	22-39	10	Deep Surface
Neogloboquadrina pachyderma	49	34-68	27	20-37	57	44-70	34	26-42	13	Deep Surface
Globorotalia scitula	94	55-167	49	32-65	102	62-169	53	34-65	5	Subsurface

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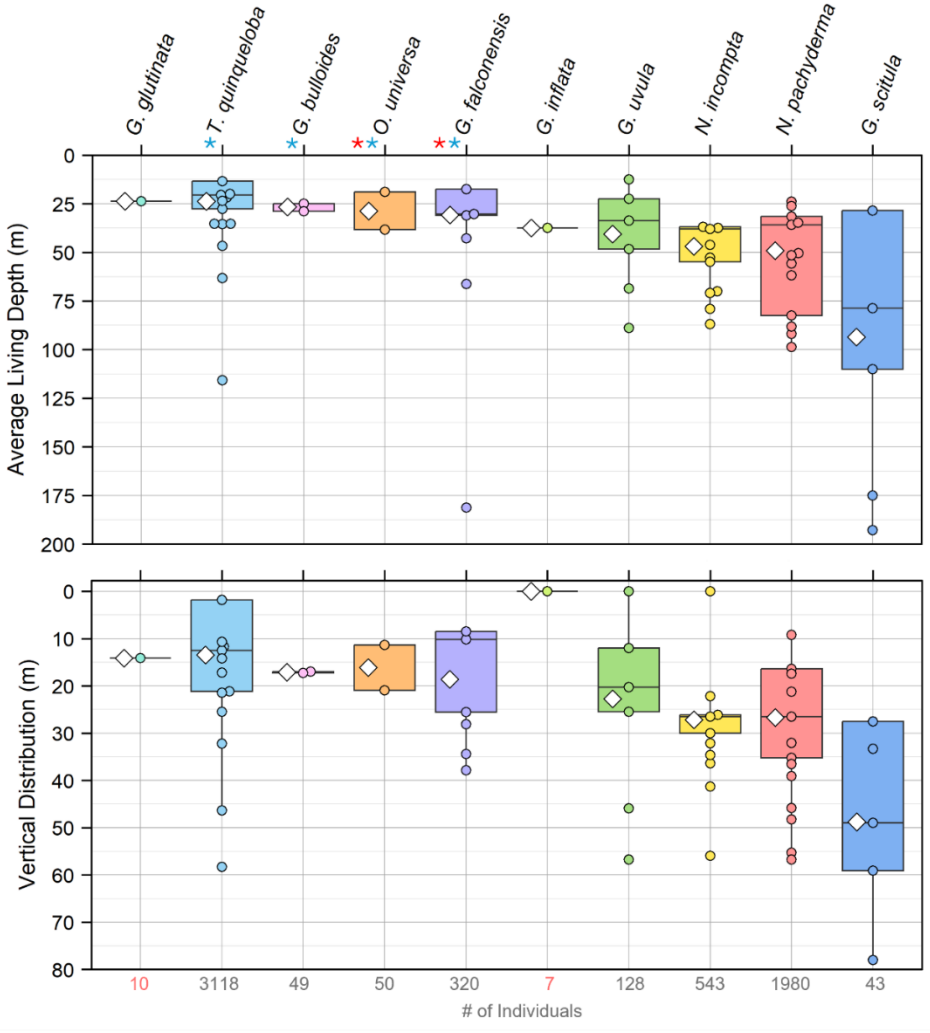

Figure 10. (a) Weighted ALD values for all species with five or more individuals present at any given site. Species are organized from left to right by the weighted mean ALD, denoted by the white diamond. A blue asterisk signifies spinose species while a red asterisk signifies species with confirmed algal symbionts. **(b)** Weighted VD values for all species with five or more individuals present at any given site. Species are organized from left to right by the weighted mean ALD, and the weighted mean VD is denoted by a white diamond. The gross number of individuals that contributed to the ALD and VD calculations is located below each species distribution. Note the red values for *G. glutinata* and *G. inflata*: these ALD and VD estimations were included with the understanding that they may not be fully representative of the preferred depth habitat of these taxa due to small sample size.

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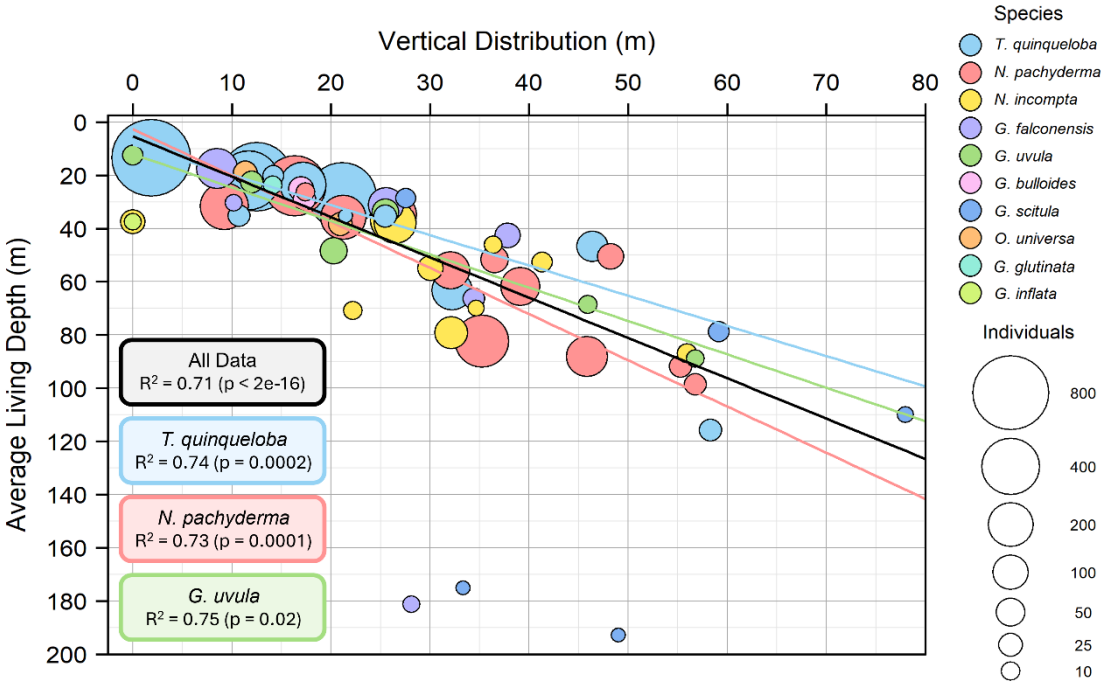

Figure 11. Weighted scatterplot of ALD and VD for all species with five or more individuals present at any given site. Points weighted by the number of individuals that contributed to the calculation. Weighted linear regression (WLR) models were calculated for the top five most abundant species throughout the study (species key listed in abundance order), and the statistically significant ($\alpha = 0.05$) relationships were plotted. The black line represents the WLR model fitted to all data points ($R^2 = 0.71$); the blue line represents the WLR model fitted to only the *T. quinqueloba* data ($R^2 = 0.74$); the red line represents the WLR model fitted to only the *N. pachyderma* data ($R = 0.73$); and the green line represents the weighted linear regression model fitted to only the *G. uvula* data ($R = 0.75$).

To assess spatiotemporal variation in ALD and VD across the three most prominent polar and subpolar taxa in this study, ALD and VD values for *N. pachyderma, T. quinqueloba*, and *N. incompta* were examined across years (**Fig. 12a-c**) and latitudes (**Fig. 12d-f**). When viewed primarily by year and secondarily by latitude, these values showed clear fluctuation between sites within a given year for *T. quinqueloba* and *N. pachyderma*, though lesser so for *N. incompta*. The latter taxon appeared to have a more constrained and stable depth habitat. Additionally, ALDs generally became shallower as latitude increased for *N. pachyderma* and *T. quinqueloba*, although this was not the case for *N. incompta*.

4.4 Comparison to prior foraminiferal assemblage studies from the NCC

Comparison of NCC community compositions described in Ortiz et al. (1995, 1996), Lane et al. (2023), and this study revealed differences in community composition between studies (**Fig. 13**). Community compositions in this study are most similar to sites sampled by Lane et al. (2023) during non-MHW years, particularly in *N. pachyderma* and *N. incompta*

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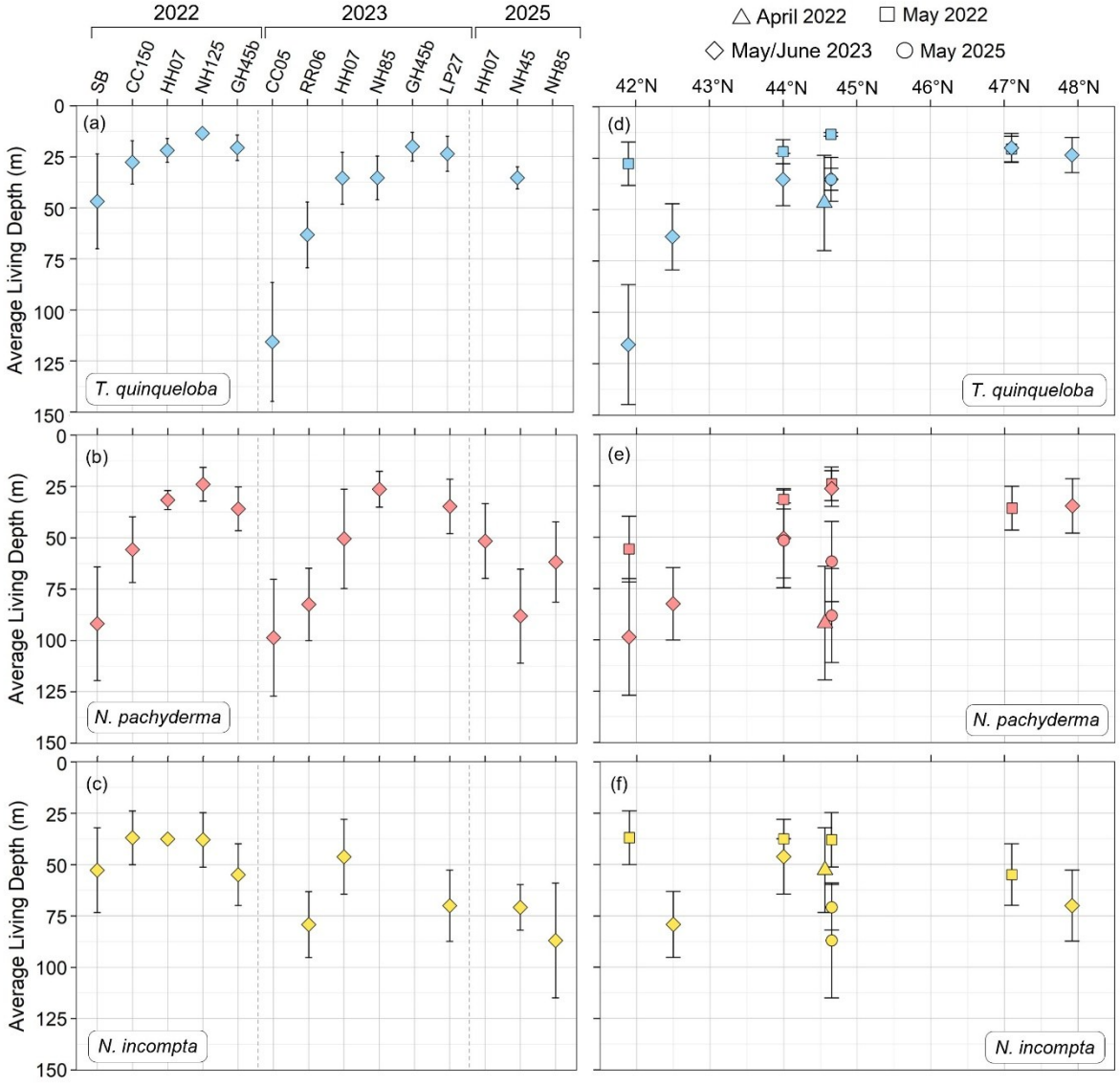

Figure 12. Individual ALD and VD values per site, organized by year (left column) and latitude (right column), colored by species. ALD values are the central points (diamonds in the left column, various shapes in the right column depending upon the year) and VD values are represented as bars above and below the ALD values. Dotted grey lines in the left column represent breaks between years. Note that site SB is listed first in the 2022 column because it was sampled in April compared to the following 2022 samples which were collected in May. Also note that points stacked on top of one another in the right column are due to repeated sampling at the same latitude during different years.

abundances (**Fig. 13b**). During the MHW years investigated in Lane et al. (2023), *N. pachyderma* was nearly or completely absent (**Fig. 13a**), with its highest relative abundance never exceeding 10%. Ortiz et al. (1995) also reported low relative

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abundances of *N. pachyderma* (< 2%) in the upper 200 m of the water column, with a notably large relative abundance of *N. dutertrei* (~35%). When community composition of sites sampled in this study were directly compared to the sites sampled in Ortiz et al. (1995) via PERMANOVA, significant differences were found ($p = 0.002$). When this analysis was repeated using assemblages inclusive of depths below 200 m (i.e., Ortiz et al., 1996), differences were still found to be significant ($p = 0.001$). However, when the community composition of years sampled during this study were compared to MHW and non-MHW years sampled by Lane et al. (2023), results were insignificant at the 95% confidence level (e.g., $p = 0.55$ for comparison between this study and MHW years).

Depth habitats for *G. glutinata, O. universa, G. bulloides, T. quinqueloba, N. incompta, N. pachyderma,* and *G. scitula* were compared to ALD and VD values calculated using data from Ortiz et al. (1995, 1996) (**Fig. S2**). Four of these taxa (*G. glutinata, O. universa, G. bulloides,* and *G. scitula*) had no more than 50 individuals that contributed to their ALD and VD calculations in this study; however, Ortiz et al. (1990) found these taxa in substantially greater numbers, allowing for further insight into the depth habitat of these species when they are more abundant. The ALD and VD values from this study closely matched those of Ortiz et al. (1995), and no statistically significant differences were found in species-specific comparisons between the studies. However, when data from Ortiz et al. (1996) is considered (0-800 m as opposed to 0-200 m examined in Ortiz et al., 1995), significant differences in depth habitat are found for *N. pachyderma* ($p = 0.0039$) and *G. scitula* ($p = 0.0304$). Aside from these two species, ALD values derived from this study appeared to be consistently shallower than those of Ortiz et al., (1995, 1996) except for minor differences in the reconstructed depth habitat of *N. incompta* (**Fig. S2**).

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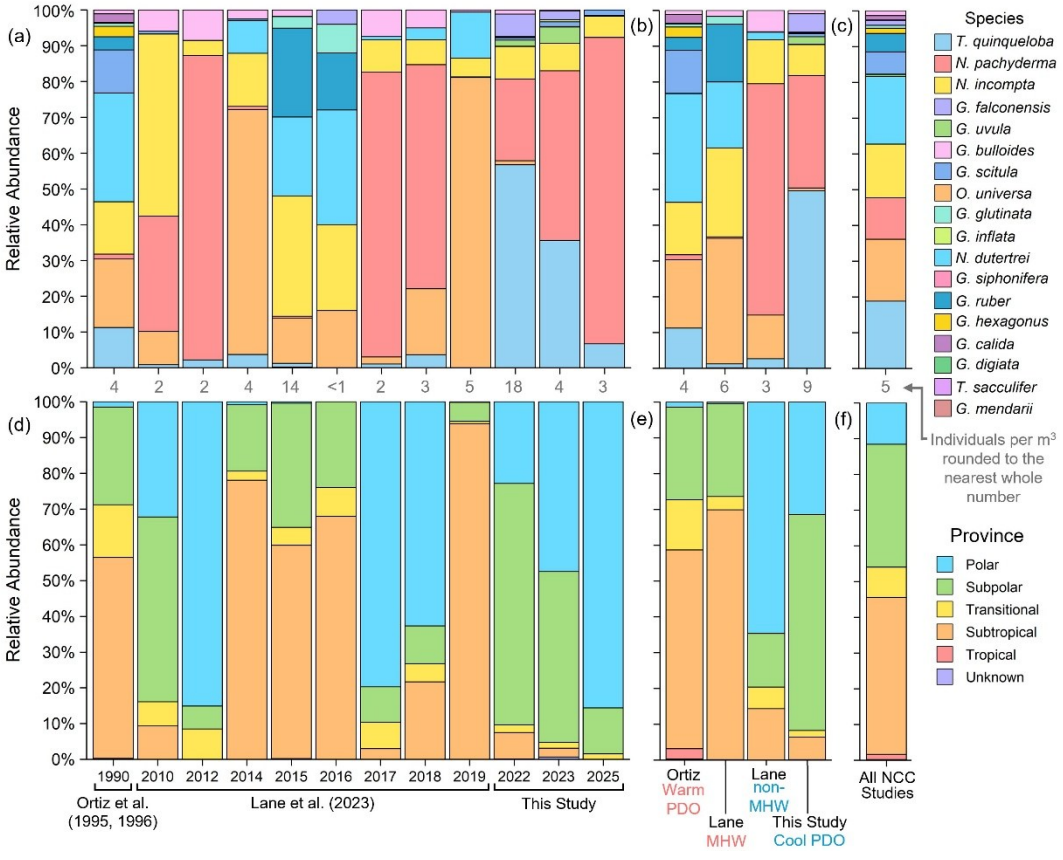

Figure 13. Community composition by year (**a, d**) based upon data from Ortiz et al. (1995, 1996), Lane et al. (2023), and this study. Overall community composition from each study (**b, e**) with data from Lane et al. (2023) separated and summarized based upon MHW years and non-MHW years. Summary community composition in the NCC combining raw data from all three studies (**c, f**). Colors for panels (**a-c**) indicate relative abundance of individual species, whereas colors for panels (**d-f**) denote relative abundance of taxa associated with each foraminiferal province. Foraminiferal abundance (individuals/m^3) is shown below panels a-c.

4.5 Meta-Analysis of Depth Habitat Studies

When assessing the ALD and VD values derived from multiple studies, the differences in sampling depth intervals were taken into consideration. ALD and VD data from prior studies were examined using all depths sampled in each study (**Fig. S3a-c**) as well as values calculated only using depths shallower than 300 m (**Fig. S3d-f**). While all ALD-VD regressions were found to be statistically significant regardless of inclusion of deeper depth intervals, the data considering all depth intervals produced stronger R^2 values. This comparison revealed that while the general spread of the individual ALD and VD values for *T. quinqueloba* and *N. incompta* were not greatly affected by the absence of the depths >300 m (**Fig. S3a, d, c, f**), the values for *N. pachyderma* experienced a notable VD decrease despite the ALD remaining relatively the same (**Fig. S3b,**

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e). Therefore, further assessment of ALD and VD in the meta-analysis included all depth intervals sampled in the respective studies without removing depths >300 m as to not artificially skew values toward shallower depths.

When plotting the average ALD and VD values of *N. pachyderma*, *N. incompta*, and *T. quinqueloba* from each applicable study, values for *N. pachyderma* and *N. incompta* obtained herein aligned well with values constrained in other globally-distributed studies (**Fig. 14; Table S1**). For *N. pachyderma*, VDs from each study ranged from ~10-160 m, whereas ALD values clustered within a range of ~50-225 m (**Fig. 14b, e**). This study observed values on the shallow end of those ranges, at 57 m (unweighted) and 49 m (weighted) for ALD and 34 m (unweighted) and 27 m (weighted) for VD. Similarly, ALD and VD values for *N. incompta* across all examined studies ranged from ~45-110 m and 20-70 m, respectively (**Fig. 14c, f)**, with this study reporting values again on the shallow end at 57 m (unweighted) and 47 m (weighted) for ALD and 31 m (unweighted) and 27 m (weighted) for VD. Despite being on the shallower end of depth habitat estimates from other studies, *N. pachyderma* and *N. incompta* still fell within the overall ranges of data from preexisting studies.

Conversely, the *T. quinqueloba* ALD and VD values from this study appeared to be distinctly shallower than estimates from prior studies (**Fig. 14a, d**). Among all prior studies examined, the mean ALD and VD of *T. quinqueloba* ranged from 63-133 m and ~20-80 m, respectively. The mean ALD values found in this study were 25-39 m shallower than those of the closest mean ALD value from another study, which was Ortiz et al. (1995) with an ALD of 63 m (**Table S2**). The unweighted ALD mean from this study was 38 m while the weighted ALD mean was even shallower at 24 m, reflecting the weight of the large number of juvenile specimens in the 0-25 m. Although the VD of *T. quinqueloba* was within the range of values from other studies (~20-80 m) when unweighted (23 m), it too fell outside of the range from other studies when weighted, as the value fell to below 13 m.

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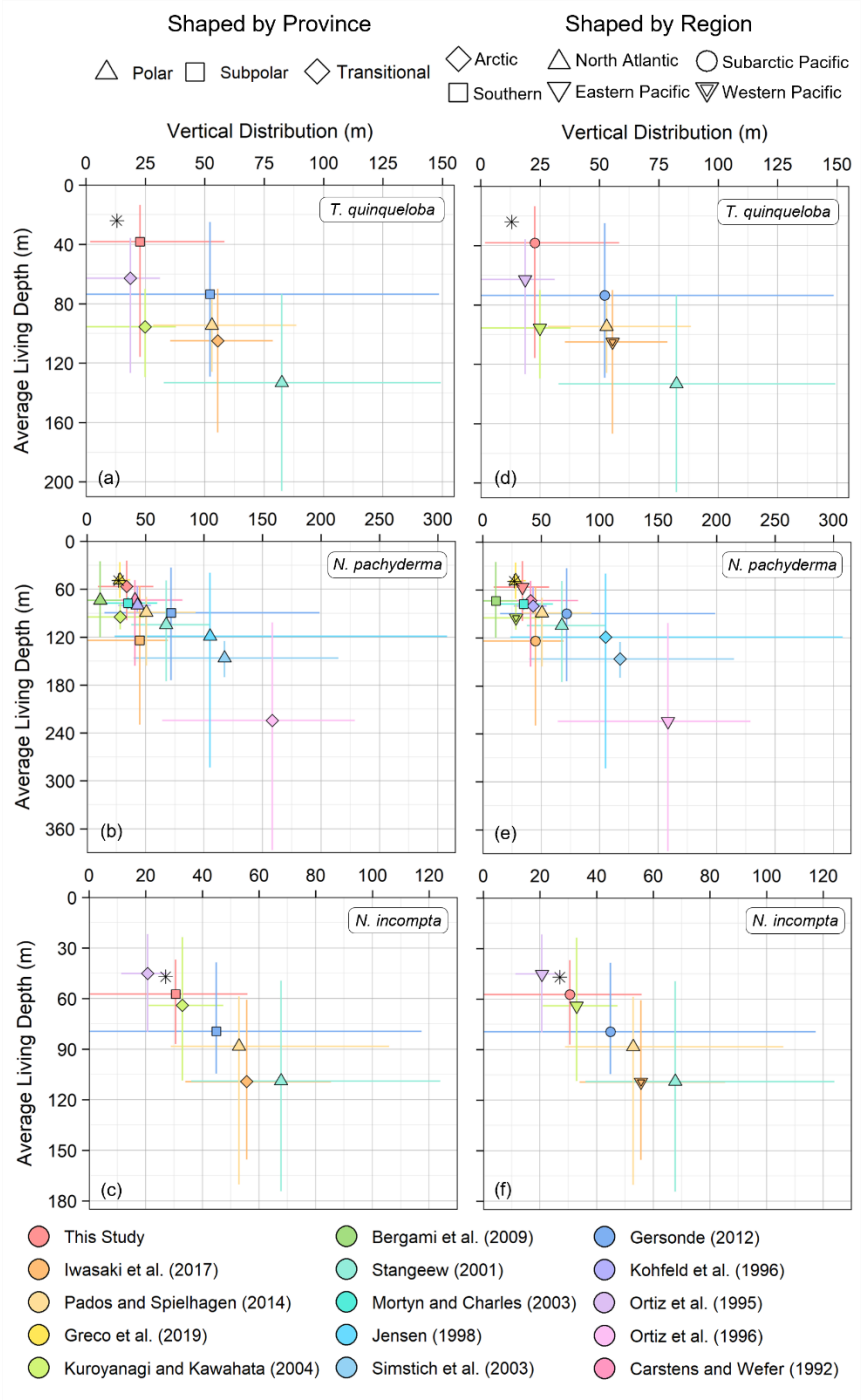

Figure 14. Average ALD and VD values taken for **(a, d)** *T. quinqueloba,* (**b, e**) *N. pachyderma*, and (**c, f**) *N. incompta* from each applicable study as listed in **Table 2**. Points are shaped by province in the left column (**a-c**) and region in the right column (**d-f**). Weighted means from this study are denoted by black star symbols. All points are colored by study.

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Examination of reconstructed depth habitats for a given taxon across foraminiferal provinces and geographic regions revealed interesting patterns (**Fig. 14**). ALD was shallower and VD more constrained for *T. quinqueloba* and *N. incompta* when sampled from transitional regions when compared to studies from polar or subpolar foraminiferal provinces. Additionally, these taxa had generally shallower ALD and smaller VDs in observational studies from the Pacific Ocean basin compared to the Atlantic or Arctic Oceans. However, these comparisons are informed by relatively limited number of studies (n = 6). Regarding *N. pachyderma*, studies from transitional and subpolar foraminiferal provinces yielded narrower VDs compared to studies from polar regions; however, this could be impacted by the number of studies done in each province (i.e., eight studies from polar regions, three from subpolar, and three from transitional). Sites sampled in the Pacific Ocean also produced narrower VDs for *N. pachyderma* compared to those from the North Atlantic and Arctic Oceans. Across all three taxa, ALDs from the Eastern Pacific Ocean also appeared to be shallower than the ALDs found in the Western Pacific Ocean.

5. Discussion

5.1 Spatiotemporal Variability in NCC Planktic Foraminiferal Communities

Investigation of site-level assemblages characterized in this study provide insight into spatiotemporal variability in foraminiferal community composition in the upper ~250 m of the water column. Community composition exhibited pronounced interannual fluctuations (**Fig. 3**) but lacked a consistent latitudinal trend (**Fig. 4**), indicating that environmental variability across years rather than latitudinal gradients was the first order control on assemblage structure observed herein. Although *T. quinqueloba* and *N. pachyderma* were the primary drivers of the dissimilarities between years (**Table S2**), the presence of either taxon at a given site was not indicative of the year during which it was sampled due to both species being the most prolific throughout the entire study period. Despite this, we find a transition from communities dominated by subpolar species to communities dominated by polar species across the three study years (**Fig. 3, 13d**).

Temporal variation in community composition across sites observed in this study may obscure discernible latitudinal trends in community composition and diversity. Upon closer examination of SH values, this idea is seemingly supported. For example, when examining only sites sampled in 2023, the most heavily sampled year, a general decrease in SH value can be observed at increasing latitudes (**Fig. 4b**). For 2022, in which fewer sites were sampled, similar trends also emerge. However, the small sample size across years prevents further exploration of latitudinal trends in this dataset. Similarly, many sites investigated herein exist at similar distances from shore. Prior studies in the NCC have found distinct changes in foraminiferal communities along a shelf to offshore transect (i.e., Lane et al., 2023) indicating that there is further spatial heterogeneity in community composition likely not captured by the samples investigated in this study. Therefore, additional observations (i.e., more sites sampled across additional years, latitudes, and distances offshore) may uncover stronger spatial trends in community composition.

Comparison of communities characterized herein to those from previous studies conducted in the NCC provides perhaps the best insight into how foraminiferal communities change on longer timescales in response to variable environmental

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conditions (**Fig. 13**). Community composition of assemblages investigated in this study are most reflective of cooler water assemblages, congruent with sampling during the cool phase of the PDO. Conversely, the assemblages of Ortiz et al. (1995, 1996) and the MHW years sampled by Lane et al. (2023) reflect conditions associated with the sampling during the warm phase of PDO (NASA, accessed 2020). Comparison of community compositions between this study and that of Ortiz et al. (1995, 1996) yielded statistically significant differences, suggesting that communities in this region have detectably different compositions when sampling across endmembers of decadal-scale climate oscillations. However, interestingly, the assemblages identified by Lane et al. (2023) were not statistically different from assemblages characterized in this study, regardless of whether they were compared to MHW or non-MHW years; this could be due to Lane et al. (2023) characterizing assemblage across a greater longitudinal range than examined in this study, allowing shelf-offshore variability to statistically overshadow variability in assemblages sampled across years and environmental states. It is also noteworthy that the p-value for the comparison between this study and MHW years from Lane et al. (2023) was near the statistical threshold for significance ($p = 0.055$).

The general community composition of this region, summarized by compiling all data from this and prior NCC plankton tow studies, can inform interpretations drawn from sedimentary records in the region (**Fig. 13**). NCC assemblages consist primarily of polar and subpolar taxa during cooler water conditions and subtropical taxa during warm water conditions. We find that foraminiferal abundance in the surface ocean (i.e., individuals/m^3) is relatively consistent across studies, regardless of PDO or MHW conditions. Similarity in community composition and foraminiferal abundance suggests that MHW conditions may be difficult to disentangle from warm PDO phases when examining the fossil record. Post-depositional processes such as preferential dissolution of specific taxa may further complicate the preservation of full assemblages in the sedimentary record and thus obfuscate climatic signals interpreted from fossil assemblages. Weakly calcified or dissolution-prone taxa may be selectively removed during sinking or after deposition to the seafloor, potentially biasing assemblages toward more robust species, obscuring original ecological signals (Berger, 1970; Conan et al., 2002; Taylor et al., 2018). As a result, the community composition preserved in deep-sea sediments may not fully reflect the living community structure, particularly in regions where carbonate dissolution is pronounced or deposition occurs primarily near or below the lysocline (Ziveri et al., 2023). Further investigation into the dissolution susceptibility of common taxa living in transitional, subpolar, and polar foraminiferal provinces will improve our understanding of potential biases influencing paleocommunity reconstruction in these regions.

Sediment trap observations (i.e., Ortiz and Mix, 1992) in the NCC (Sept. 1987-1988) have shown foraminiferal fluxes to be highest in nearshore environments when upwelling is strong, indicating that upwelling conditions may have a stronger control on foraminiferal flux than temperature in this dynamic region. While sediment trap records are valuable for documenting such short-term environmental controls, the plankton tow compilation explored here may provide a better view of how longer-term climate signals, specifically decadal- to subdecadal-scale as opposed to intra-annual, may manifest in sedimentary records. Consistent with this interpretation, transitional taxa were present in every year investigated across the three studies, yet their relative abundance in the region was <5%, indicating that assemblages fluctuate between communities

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dominated by subtropical taxa versus communities dominated by polar and subpolar taxa in response to changing environmental conditions.

Trends were also discernible when examining community composition across depth (**Fig. 6-9**), which corroborated the current understanding of depth habitat preferences for spinose versus non-spinose species (Rebotim et al., 2017). On average, spinose taxa were found to be most abundant in the top 25 m of the water column, whereas non-spinose taxa were more abundant at all depths below 25 m, reaching their highest relative abundance in the 150-250 m depth interval (**Fig. 7**). The presence of spinose species at shallower depths within the water column compared to non-spinose species supports the use of spines as a buoyancy control (Furbish and Arnold, 1997; Gaskell et al., 2019). Water density increases sharply around the 50 m depth in the study region (**Fig. S4**) with spinose species most abundant above this threshold, which may support the theory that spinose taxa use their spines to retain buoyancy (Takahashi and Be, 1984). Furthermore, previous studies have suggested that spines function as a mechanism for prey capture in species with a preference for carnivory, whereas non-spinose taxa are believed to have more generalist, herbivorous eating habits (Bé et al., 1977; Anderson et al., 1979; Hemleben et al., 1989; Grigoratou et al., 2021). The concentration of spinose taxa within the upper 25 m of the water column may further support this interpretation of spine function, as it is within this depth range that a great diversity of other plankton communities are present for foraminifera to prey upon (Jäger et al., 2008; Sutor and Dagg, 2008). Chlorophyll α concentrations are highest in the upper 50 m of the water column in this region (**Fig. S4**), further supporting the interpretation of high food availability as a potential driver of higher abundances of spinose taxa within the uppermost surface ocean.

Though depth habitat was only quantified for two symbiont-bearing species in this study (*O. universa* and *G. falconensis*), both taxa occupy shallow depth habitats within the upper 25 m of the water column. Symbiont-bearing species may prefer to stay at more shallow depths of the water column where 1) environmental conditions are relatively stable and 2) light, nutrients, prey, and CO_2 are most abundant. Symbiont-bearing species may rely on their photosynthetic partners as passive sources of nutrients, allowing them to exhibit more specialized feeding preferences compared to non-symbiont bearing taxa (Bé et al., 1977; Anderson et al., 1979; Hemleben et al., 1989; LeKieffre et al., 2018; Grigoratou et al., 2021). In contrast, asymbiotic species are not constrained to the euphotic zone, allowing for greater variation in depth habitat due to the more homogeneous conditions below the thermocline and halocline. Thus, species adapted to environmental conditions in this layer may be able to occupy greater vertical depths while still being within their optimal ecological range (Chaabane et al., 2026).

Interestingly, no statistically significant differences were found in community composition across adjacent depths when examined using species relative abundance (PERMANOVA, $p = 0.074$). Some years show a gradual transition in community composition with increasing depth (e.g., **Fig. 9b**), whereas other years do not (**Fig. 9c, d**). However, significant differences were observed between depth intervals when examined using diversity metrics such as species richness and SH values (**Fig. 8**). Richness and SH values exhibited generally stable trends with depth aside from a stark decrease in diversity at the 50-100 m interval. While richness appeared to decrease steadily with depth, SH values increased with depth for intervals above 50 m and decreased for intervals below 100 m.

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Previously published profiles of environmental data from this region may provide insight into potential causes of this anomalous drop in diversity observed at 50-100 m (e.g., **Fig. S4**; Hupp and Fehrenbacher, 2023, 2025). The water column in this region can be subdivided into distinct zones with similar environmental conditions: 1) the surface mixed-layer zone where temperature, primary productivity, and DO are high while salinity is low; 2) the zone of High Environmental Variability (abbreviated as "HEV" hereafter) where the thermocline, halocline, and pycnocline begin, and primary productivity and DO rapidly decrease; and 3) the subsurface zone where temperature and DO are low, there is little to no primary production, and salinity is high. The 50-100 m depth interval coincides with the HEV, suggesting that the precipitous drop in diversity found at this depth is likely due to fewer species being adapted to live under such heterogeneous environmental conditions.

The examination of richness and SH values across depths revealed further insights into changes in community biodiversity beyond the distinct decrease at 50-100 m. On average, assemblages from the 0-25 m depth interval had the highest species richness and the lowest SH values, indicating unevenness in community composition in this interval (**Fig. 8**). Despite over half (~53%) of the individuals found throughout the top 250 m of the water column being located within the shallowest depth interval (n = 3370), the assemblage was largely dominated by one or two specific taxa (e.g., **Fig. 6**) with very few individuals representing each additional species. Together, *T. quinqueloba* and *N. pachyderma* accounted for ~87% of the total community in this depth interval, followed by *N. incompta, G. falconensis,* and *G. uvula* which collectively accounted for ~12%, and finally all additional taxa (*G. bulloides, G. scitula, O. universa, G. glutinata,* and *G. ruber*) comprised the remaining ~1% (**Fig. 7**). The presence of multiple spinose trace taxa at the shallowest depth interval led to higher richness in the uppermost surface ocean, while the low SH values were attributed to repeated dominance of *T. quinqueloba* and *N. pachyderma*.

A particularly anomalous abundance of *T. quinqueloba* occurred at NH125 in May 2022, with 1406 individuals present in the 0-25 m depth interval (**Fig. 6b**). This 'bloom' of *T. quinqueloba* may be related to synchronized reproduction, which is postulated based upon the large quantity of small specimens interpreted to be juveniles. Studies suggest that these reproductive events occur when mature individuals migrate through the water column in accordance with the lunar cycle to orchestrate the release of gametes at a specific depth, thus increasing the likelihood of fusion with increased gamete proximity (Erez et al., 1991; Meilland et al., 2021). In a study by Meilland et al. (2021), these reproductive mechanisms caused the overrepresentation of small specimens of *G. ruber* and *O. universa* in the surface layer around the new moon. A similar mechanism may underpin the observation of abundant, surface-dwelling *T. quinqueloba* found at NH125 in this study; however, we do not find this occurrence to be linked to distinct periods of the lunar cycle during sampling.

Together, these patterns in environmental structure and ecological preference confirm that the vertical distribution of taxa is closely tied to gradients in water column stability, resource availability, reproduction, and physiological constraints (Kuroyanagi and Kawahata, 2004; Lessa et al., 2020). Because ALD and VD are fundamentally derived from where taxa reside within these gradients, variability in factors such as light availability, productivity, and water column stratification likely influence both the depth at which species calcify and the breadth of depths they occupy. As a result, shifts in these environmental variables with depth may translate into measurable differences in ALD and VD among taxa (**Fig. 10; Table 2**).

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All spinose taxa (*T. quinqueloba, G. bulloides, O. universa*, and *G. falconensis*) were deemed to inhabit the shallowest depths of the surface zone, whereas all but two non-spinose species (*G. inflata*, *G. uvula*, *N. incompta,* and *N. pachyderma*) were found deeper in the surface zone. Notably, the ALDs for *N. incompta* and *N. pachyderma* were found to be right above the boundary between the surface zone and HEV zone, suggesting that these taxa can comfortably inhabit either zone. Only *G. scitula* was found to inhabit the subsurface zone.

When considering data from all taxa, a positive relationship is found between ALD and VD (**Fig. 11**) suggesting that taxa occupying deeper portions of the water column may integrate environmental signals over a broader depth range, whereas surface-dwelling taxa record more constrained conditions. This has important implications for the resolution of paleoproxies, as species with broader VDs may produce geochemical signals that represent conditions averaged over a larger portion of the water column—potentially smoothing or dampening apparent environmental variability. Conversely, taxa with narrow VD ranges may provide higher-resolution records of specific environmental conditions, but only within a limited depth range. Understanding these differences is critical when both selecting taxa for paleoreconstructions and when interpreting multi-species proxy records intended to reconstruct surface ocean structure.

5.2 Stability of Polar and Subpolar Planktic Foraminiferal Depth Habitats

Observations herein provide insight into the stability of the depth habitats of subpolar and polar planktic foraminifera, with particular focus on species commonly used for geochemical-based paleoreconstructions: *N. pachyderma, N. incompta,* and *T. quinqueloba*. The depth habitat of *T. quinqueloba* and *N. pachyderma* fluctuate between sites within a given year, with ALD and VD generally decreasing at progressively higher latitudes within the NCC (**Fig. 12**). Conversely, *N. incompta* has a relatively more stable depth habitat. These observations are corroborated by species-specific relationships between ALD and VD where statistically significant relationships were found for *T. quinqueloba*, *N. pachyderma*, and *G. uvula* (**Fig. 11**), but not for *N. incompta* or *G. falconensis*, suggesting that the former three taxa have relatively more variable depth habitats. ALDs determined for *T. quinqueloba* and *N. pachyderma* vary by approximately 100 m and 75 m, respectively (**Fig. 12**). While this variability may be purely environmentally driven, it is worth considering that several morphotypes and genotypes of these taxa exist and can be found in the NCC. While only one genotype of *N. pachyderma* is found in the study region (Darling et al., 2007), several morphotypes of this taxon exist (e.g., El Bani Altuna et al., 2018). It is possible that distinct morphotypes have different ecological preferences, contributing to some of the variability in depth habitat observed in the NCC. Conversely, three genotypes of *T. quinqueloba* inhabit the NCC region (Darling et al., 2003; 2017), each of which could also exhibit distinct depth habitat preferences. Changes in the relative abundance of various genotypes and morphotypes over the study period could drive observed variability across time and space, however further study is needed to better understand the connections between foraminiferal ecology and genetic and morphological variability (e.g., Darling et al., 2003).

Collectively, these observations have important implications for the use of these taxa as paleoceanographic proxy substrates. Spatiotemporal variability in these parameters demonstrate that depth habitats are not fixed and that habitat variability is greater in some taxa than in others. The observed decrease in ALDs with increasing latitude and variability

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between years suggests that *T. quinqueloba* and *N. pachyderma* may migrate throughout the water column to track specific environmental conditions (e.g., specific temperatures) or other physiochemical boundaries. For example, prior studies have suggested that *N. pachyderma* may migrate to depths that are near or just below the pycnocline (Simstich et al., 2003; Kozdon et al., 2009; Jonkers et al., 2009), while others have posited that depth habitat of the neogloboquadrinids is modulated by the depth of the deep chlorophyll maximum due to increased food availability (Kohfeld et al., 1996; Kuroyanagi and Kawahata, 2004; Xiao et al., 2014; Pados and Spielhagen, 2014; Greco et al., 2019). Other researchers have argued that similar mechanisms may underpin the depth habitat of *T. quinqueloba* (Simstich et al., 2003; Jonkers et al., 2010), yet here we find this taxon at consistently shallower depths than coexisting neogloboquadrinids. While robust statistical modeling of depth habitat metrics and co-collected environmental data is required to fully test controls on the variability observed in this study, *N. pachyderma* and *N. incompta* were found to have weighted average ALDs of 49 m and 47 m, respectively, which aligns well with the depth of the regional pycnocline in the NCC (e.g., **Fig. S4**).

Some studies have described *N. incompta* and *N. pachyderma* as sister species and suggest that their shared ecology allows for use of geochemical calibrations developed in one species to be readily applied to the other (e.g., Morley et al. 2024). While we do find similar average ALD for these taxa (**Table 2**), we argue that this is perhaps not an appropriate assumption. Observations herein, particularly 1) differential depth habitats between *N. pachyderma* and *N. incompta* when collected from the same site at the same time and 2) differences in the stability of depth habitat among these taxa indicate that these species, while both nonspinose and genetically related (Darling et al., 2006), have different ecologies. It is possible that these ecological differences impact partitioning of trace elements and isotopes into their tests, requiring the need to establish species-specific calibrations among these two sister taxa and acknowledge differences in the depths that their test geochemistry represents.

Despite inter- and intra-annual variability in depth habitats observed in this study, comparison of depth habitat estimates to those of Ortiz et al. (1995) suggest some consistency over longer timescales. When the depth habitat estimates of this study were compared to those of Ortiz et al. (1995), ALD estimates herein were shallower, though not statistically different for most taxa (**Fig. S2**). Shallower depth habitats observed in this study may also be linked to sampling during the cooler phase of PDO. Given the warmer water conditions during sampling in 1990, polar and subpolar taxa may have migrated deeper in the water column to reach cooler conditions than if sampled during the cool phase of PDO. The only taxa for which Ortiz et al. (1995; 1996) found significantly different depth habitats than found in this study were for *N. pachyderma* and *G. scitula*. We argue that the depth habitat constrained herein for *G. scitula* differs from the prior studies by Ortiz et al. due to differences in the depth ranges explored. *Globorotalia scitula* is known to inhabit deeper waters, and thus, it is not surprising that consideration of deeper depth intervals (i.e., 200-800 m) resulted in a greater abundance of *G. scitula* and therefore a deeper calculated ALD. A similar mechanism may explain differences in the reconstructed depth habitat for *N. pachyderma* among studies. However, when considering depths below 200 m, the ALD derived from Ortiz et al. (1996) was 224 ± 39 m (**Table S1**), the deepest depth habitat estimate of all studies examining this taxon (**Fig. 14b, e**). We argue this is likely to be an artifact of overcounting dead shells that have sunk to greater depths, rather than a true ecological signal of *N. pachyderma* preferring

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such deep environments. Thus, the ALD and VD determined in this study (**Table 2**) should serve as representative depth habitats for the three key study taxa in the NCC.

When comparing the results of this study to ALD and VD calculations derived from data from 14 additional studies, depth habitats differ among ocean basins and foraminiferal provinces (**Fig. 14**). Although the estimates from this study aligned well with those of Ortiz et al. (1995), they were far shallower than estimates from North Atlantic/Arctic regions and polar provinces—particularly regarding *T. quinqueloba*. Prior studies investigating the depth habitat of *N. pachyderma* and *T. quinqueloba* in the North Atlantic and Arctic regions have identified that the presence or absence of sea ice plays an important role in depth habitat regulation of these taxa; when sea ice is present, these taxa tend to inhabit shallower surface waters, whereas the absence of sea ice is often associated with deeper depth habitats (Xiao et al., 2014; Pados and Spielhagen, 2014; Greco et al., 2019). However, historical observations (1985-2015) show that the depth habitats of *T. quinqueloba* are shoaling over time in the Arctic due to enhanced sea-ice export, while *N. pachyderma* habitats have stayed relatively stable over the same time (Greco et al., 2021). Interestingly, all three taxa exhibit some of the shallowest depth habitats among all studies, yet the NCC is devoid of sea ice.

Distinct differences in depth habitat across ocean basins could be due to differential ecologies among genotypes of each species. Prior work has found that the genotypes of *N. pachyderma* (Darling et al., 2007) and *N. incompta* (Darling et al., 2006) living in the NCC differ from those found in the Arctic and North Atlantic Oceans. Similarly, six genotypes of *T. quinqueloba* have been identified globally, with different genotypes found more commonly in certain regions than others (Darling and Wade, 2008). For example, Type IIa, IIc, and IId can be found in the NCC region and Type IId dominates the North Pacific Ocean, whereas Type IIa and IIb populate the Arctic and North Atlantic Oceans (Darling et al., 2017). Results herein suggest that different genetic populations of polar and subpolar foraminifera likely have different ecological preferences resulting in distinct depth habitat affinities. While most studies investigating polar and subpolar planktic foraminifera are conducted in the Arctic and North Atlantic Oceans, we argue that further study is needed to explore both the ecology and geochemistry of genotypes specific to the Pacific Ocean basin.

Beyond genotypic considerations, other factors may impact the anomalously shallow depth habitat of *T. quinqueloba* found in this study. As the most abundant taxon in the study as well as one of the smallest, *T. quinqueloba* test size must be taken into consideration when interpreting how this study relates to previous works. Many previous studies did not identify individuals smaller than 100-125 µm, yet many *T. quinqueloba* tests identified in this study were within this size range and were included in the assemblages as identifiable individuals. Since adults tend to migrate deeper prior to gametogenesis (Erez et al., 1991; Pracht et al., 2019; Meilland et al, 2021), previous studies may have identified these larger individuals while neglecting to identify the juveniles that are often more abundant at shallower depths. This may also explain some of the deeper depth habitat estimates for this taxon at specific sites, which may have been dominated by adults just prior to gametogenesis (e.g., CC05 in 2023; **Fig. 12a**). Due to the possibility that the presence of abundant juveniles in the uppermost surface ocean skewed the ALD values for *T. quinqueloba* toward shallow depth habitats, it would not be appropriate to potentially further

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skew the mean ALD in this direction by weighing it. Therefore, the unweighted depth habitat estimate of 38 ± 23 m may be more accurate as opposed to the weighted value of 24 ± 13 m constrained in this study.

Another factor that must be considered when comparing depth habitat studies is the differing depth intervals sampled (e.g., **Fig. S3**), as including the full sampling range even when sampling spans below the depths at which planktic foraminifera are accepted to dominantly live (~0-250 m) may skew ALD and VD values towards deeper depths due to the overcounting of empty tests falling through the water column. Although tests may have been present at greater depths, this may not be a true reflection of living depth habitat, as the organism itself could already be dead when found at these deeper intervals. Unfortunately, the distinction between live and dead individuals is most discernible directly following collection, and it can be difficult to evaluate months to years after collection. For example, the vibrant color of the cytoplasm indicating live individuals is most apparent shortly after collection, with color degrading overtime even when stored in a preservative. Conversely, dead individuals can be identified for most species by their thickened tests, associated with gametogenic crusting near the end of life (Hupp and Fehrenbacher, 2023). However, the distinction between a thickened test and a thin test, without colorful cytoplasm as an additional indicator of life, can be difficult to discern post sample preservation as most live specimens become bleached overtime. Therefore, the data from this and other studies may include dead individuals collected as they have fallen through the water column after death. The exclusion of deeper depth intervals may offset this issue, however, the decision to exclude these intervals may disregard individuals who truly live at deeper depths (e.g., *G. hexagonus*; Ortiz et al., 1996; Davis et al., 2021), demonstrating that either choice of removing or including these intervals could be rationalized given the focus of the study. Prompt processing of plankton tow samples is recommended so that live vs. dead specimens can be more easily identified (e.g., Hupp and Fehrenbacher, 2023).

Analysis of constrained depth habitats herein revealed that while broad ecological patterns such as the separation of spinose and non-spinose taxa are consistent with established understanding, significant variability exists both within and between species. Differences in ALD and VD across taxa, years, latitudes, and ocean basins demonstrate that depth habitats are dynamic rather than fixed for most taxa, influenced by environmental variables and biological processes. Specific taxa (e.g., *T. quinqueloba, N. pachyderma*) may even track physiochemical surfaces or constrained environmental conditions within the water column, whereas taxa such as *N. incompta* appear to have more constrained depth habitats that are not so easily influenced by environmental parameters. These findings highlight the need to carefully constrain regionally specific depth habitats when applying modern observations to paleoceanographic reconstructions, as even small shifts in vertical distribution can alter the environmental signals recorded in foraminiferal tests.

6. Conclusions

Depth-stratified plankton tows collected from throughout the Northern California Current were characterized to investigate spatiotemporal variability in planktic foraminiferal community composition and depth habitat in this transitional foraminiferal province that commonly hosts polar and subpolar taxa. Across the study area, community composition was driven primarily by temporal variability rather than latitude, indicating that interannual environmental fluctuations appeared

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to exert a strong influence on assemblage structure. Comparison of assemblages from this study to prior studies in the NCC show that decadal-scale environmental oscillations (i.e., PDO) or transient environmental change (MHWs) in part dictate if communities are dominated by subtropical taxa (i.e., during PDO warm phase or MHW) or polar and subpolar taxa (i.e., during PDO cool phase or non-MHW years).

Vertical patterns in community composition further revealed strong ecological partitioning within the water column. Spinose taxa were concentrated in the upper 25 m of the water column, whereas non-spinose taxa dominated deeper intervals, likely reflecting differences in buoyancy control, feeding strategies, symbiotic relationships, and environmental tolerances. These patterns were reinforced by depth habitat estimates, which showed that spinose taxa occupied shallower and more constrained habitats while non-spinose taxa inhabited deeper and more vertically expansive niches. Dominant polar and subpolar taxa in this study included *T. quinqueloba*, *N. pachyderma*, and *N. incompta*, the ALDs and VDs of which were 24 m ± 13 m, 49 m ± 27 m, and 47 m ± 27 m, respectively, when weighted by the number of individuals that contributed to each individual calculation. It is recommended that the unweighted depth habitat for *T. quinqueloba* (38 ± 23 m) be taken into consideration given the potential effects of synchronized reproduction on the weighted depth habitat estimate from this study. Notably, these depth habitats are shallower than estimates from other studies in varying foraminiferal provinces and ocean basins, potentially due to genotypic variation in these taxa across the global ocean (Darling et al., 2006; 2007; 2017). Patterns in diversity further underscore vertical structuring, as Shannon H. Index values and species richness exhibited stark decreases in diversity at the 50-100 m depth interval, reflective of highly variable environmental conditions in this depth range. In addition, the positive relationship between ALD and VD suggests that deeper-dwelling species integrate environmental signals over broader depth ranges, whereas surface-dwelling taxa record more localized conditions. Importantly, this study demonstrates that depth habitats are not fixed but vary across both spatial and temporal scales. In transitional foraminiferal regions, taxa with more stable depth habitats (e.g., *N. incompta*) may be preferential in paleoreconstructions compared to taxa with more variable depth habitats (e.g., *N. pachyderma, T. quinqueloba*).

Finally, the results of this study emphasize the importance of integrating modern ecological data with proxy development and calibration efforts. While assemblage-based, isotopic, and trace element proxies remain powerful tools for reconstructing past ocean conditions, their accuracy depends on a complete understanding of the ecological and environmental factors that influence foraminiferal distribution throughout the water column. Future work should focus on expanding depth-stratified sampling across broader spatiotemporal scales, integrating high-resolution environmental data with ALD, VD, and depth-stratified abundance data, and further constraining species-specific, morphotype-specific, and genotype-specific depth habitat variability. Such efforts will improve the calibration of foraminiferal proxies and enhance their reliability in reconstructing past ocean conditions, particularly in polar and subpolar regions that are most sensitive to climate change.

Data availability

Supplementary tables and figures can be found in the supplement linked to this publication. All data referenced herein can be found in Hupp et al. (2026) in the Zenodo Data Repository. Direct link for review:

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https://zenodo.org/records/20162754?preview=1&token=eyJhbGciOiJIUzUxMiJ9.eyJpZCI6ImZlODI5OWE3LWJlYTctNGFhNi1iMmM3LWRmNTE5ODA1ZWI4ZCIsImRhdGEiOnt9LCJyYW5kb20iOiI2NjgzZjZiMmM0N2ZkMDM2NWYwNDQ4MDIwNjQ3YTZkZiJ9.mul3wmx0momRxV9CLDVdtmA8X8ly2wtUrfkkPtVmldVX_WnwJrJXKNHiQ_PRMsmb-rWE_P9O7AvB-FIpIXOXcQ

Author contributions

CM contributed to the conceptualization, formal analysis, investigation, data curation, writing – Original Draft, writing – review & editing, and visualization. BH contributed to the conceptualization, methodology, investigation, resources, data curation, writing – original draft, writing – review & editing, visualization, supervision, project administration, and funding acquisition. JF contributed to the conceptualization, methodology, investigation, resources, writing – review & editing, and funding acquisition.

Competing interests

The authors declare no competing interests.

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