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Physiological and morphological scaling enables gigantism in pelagic protists

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Abstract

Planktonic foraminifera are pelagic protists frequently used to study paleoenvironmental change. Many planktonic foraminifera, like other taxa in Rhizaria, reach gigantic proportions relative to other pelagic protists (> 600 μm), placing them in a size class dominated by metazoans. Here, we combine new and existing respiration rate measurements, micro-CT scans, and test size measurements to investigate allometric scaling of metabolic rates, relative biomass density, and mixotrophy in contributing to the ability of planktonic foraminifera to reach large sizes. Respiration rate increases with foraminiferal biovolume with a slope of 0.51 ± 0.18. This allometric scaling slope is lower than those reported in other plankton. Further, the basal respiration rates for planktonic foraminifera exceed those of other organisms in their size class when probable biomass, rather than test volume, is considered. Using the allometric regression on a published database of modern planktonic foraminifera from the Atlantic Ocean, we estimate that gigantic individuals account for 15.3–26.1% of foraminiferal community respiration in temperate and tropical/subtropical latitudes, despite making up only 4.5–8.3% of individuals. We hypothesize that shallow scaling of test size with metabolism and of test size to actual biomass is the key factor allowing for gigantism in planktonic foraminifera. Having a large test and broadcasting rhizopodial networks increases the functional volume of the organism, allowing higher passive prey encounter rates to support the elevated metabolic rates in planktonic foraminifera. Mixotrophy may act as a mitigating factor for metabolic challenges at low latitudes, accounting for the presence of large populations of giant, predominately mixotrophic Rhizarians in these assemblages.

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Additional Supporting Information may be found in the online version of this article.

Author Contribution Statement: All authors contributed to the writing of this manuscript. JEB led project and drafted the original manuscript and figures. PMH advised on all aspects of the project and assisted with study design, analyses, and manuscript drafting. LEE cultured foraminifera and collected and processed respiration data for the 2017 field season. AEM collected and processed respiration data for the 2018 field season. Both LEE and AEM wrote methods for collecting and analyzing respirometry data. JEB and DEG cultured foraminifera during the 2018 field season. EGC assisted with and advised on the collection and reconstruction of micro-CT images. AYH advised on and assisted with foraminiferal size database analyses and error propagation. GF planned and advised on the culture of foraminifera for the 2017 field season.

Protists play a major role in pelagic ecosystems (De Vargas et al. 2015; Worden et al. 2015; Biard et al. 2016). Photosynthetic protist groups like diatoms, dinoflagellates, and haptophytes are important primary producers in many regions, while mixotrophic and heterotrophic clades like the Rhizaria (a group that includes foraminifera, siliceous Radiolarians, Acantharians, and Phaeodarians) can comprise most of the biomass in the microplankton to mesoplankton range throughout much of the ocean (De Vargas et al. 2015; Biard et al. 2016). Many protists have trophic strategies that fall between, or beyond, the classic primary producer vs. consumer dichotomy, including mixotrophy and saprotrophy (Worden et al. 2015). Protist species can also attain very large sizes for unicellular organisms, even in nutrient poor subtropical gyre environments (Biard

et al. 2016). Theoretical models have suggested that mixotrophy shifts the size distribution of pelagic food webs to larger size classes, and some of the largest protists in the pelagic realm are indeed mixotrophic (Biard et al. 2016; Ward and Follows 2016). Moreover, the effective size of pelagic protists in terms of the volume of space they occupy, and the size of their food/prey catchment is not just a factor of cell biomass or test (shell) size, but also the reach of cytoplasm. The rhizopodial and spine networks of Rhizaria can increase their effective volume by several orders of magnitude compared to the test alone (Gaskell et al. 2019). This means that "giant" pelagic protists are not only able to exist in a remarkably large size class for their clade, but also for their actual biomass (Michaels et al. 1995; Laget et al. 2022). How the trophic strategies of "giant" pelagic protists influence their ecosystems in comparison to other factors like physiological complexity and body size is, in part, a question of metabolism, for which there are relatively few constraints for pelagic protists.

Here we focus on planktonic foraminifera, a clade of Rhizaria with calcium carbonate shells ("tests"). Although not the most abundant clade of Rhizaria, planktonic foraminifera play an important role in the carbon cycle and have an excellent fossil record. It has been estimated that planktonic foraminifera contribute inorganic carbon exported to the deep sea in proportions ranging from 3.8% to as much as half (Schiebel and Hemleben 2000; Knect et al. 2023), with inorganic calcite being the primary long-term mechanism removing carbon from the ocean–atmosphere system (e.g., Berner 2004; Ridgwell and Zeebe 2005). Like many other Rhizaria, a number of planktonic foraminiferal species are mixotrophic, particularly in tropical to subtropical oceans. Planktonic foraminifera reach their largest sizes at these latitudes, with tests exceeding 1 mm in length in extreme cases. This pattern has been attributed to increased water column stratification in low latitudes resulting in greater capacity for niche differentiation with depth (Schmidt et al. 2004a,b; Al-Sabouni et al. 2007). However, large cell sizes in low latitudes could also be related to the fact that planktonic foraminiferal communities in tropical and subtropical waters are dominated by symbiont-bearing taxa such as *Globigerinoides sacculifer* and *Globigerinoides ruber*, while subpolar to polar communities are dominated by asymbiotic taxa such as *Neogloboquadrina pachyderma* (Al-Sabouni et al. 2007). We know less about the potential role of physiology or metabolism in the large cell-sizes reached by some Rhizarians. Limited metabolic rates for individual planktonic foraminifera have been reported, likely due to the difficulty of obtaining metabolic data from such small organisms (but *see* Jørgensen et al. 1985; Rink et al. 1998; Lombard et al. 2009; Davis et al. 2017). Previous work established reference values for the temperature dependence of respiration rates (Q_{10}), the relative rates and sensitivities of photosynthesis and respiration (Lombard et al. 2009), and effect of varying environmental pH on respiration rates (Davis et al. 2017). These existing studies of respiration have not included morphological measurements apart from test length, which is not directly proportional to test volume across all species (*see* Burke et al. 2020) or to cell mass (Michaels et al. 1995). This gap is an important one because metabolic rates, including respiration and photosynthesis, and total metabolic demand are expected to scale with the size of the organism. In other words, understanding how metabolic rates scale with organism size is central to testing the factors allowing for gigantism in the clade.

Allometric scaling refers to changes in traits with size or ontogeny. It is well known that metabolic rates scale with size in all organisms, often to a factor of ~ 0.67–0.75 (Gillooly et al. 2001; Brown et al. 2004; DeLong et al. 2010). This means that, generally, as organisms get larger, their total metabolism goes up but their mass-specific metabolic rate declines. Declining mass-specific metabolic rates with increased size are hypothesized to be the result of conservation of energy in larger organisms due to lower surface area to volume ratios or transport through fractal circulatory and respiratory systems (West et al. 1997, 1999). As such the expectation of declining mass-specific metabolic rates is most applicable to multicellular organisms. For unicellular organisms, which lack fractal circulatory systems and have fewer measurements with which to constrain such estimates, the scaling slope of metabolic rates with size is contentious (Tang and Peters 1995; Glazier 2005, 2009; Finkel et al. 2010) and is generally thought to be unity or higher (*see* DeLong et al. 2010). This would imply that mass-specific metabolic rates might not decline at all with increasing organismal size, making it relatively more expensive for unicellular organisms to maintain large sizes as compared to metazoans of comparable size. In addition, there is a strong relationship between organismal complexity and size (Knoll and Bambach 2000; Heim et al. 2017). The minimum organismal size is argued to be driven by size-constraints on complexity (i.e., a eukaryote has to be large enough to have a nucleus, and a metazoan large enough to have multiple cells, etc.) whereas the maximum organismal size is argued to be driven by physiological and/or metabolic constraints given that level of complexity. For instance, single cell organisms are limited to scales where diffusion is effective for gas and solute movement, past that scale, circulatory systems are needed to move gases and metabolites (summarized in Maurer and Marquet 2013). Thus, high metabolic scaling slopes should make it more difficult, and thus less likely, for protists to reach proportions seen in large Rhizarians.

However, there are reasons to suspect giant pelagic Rhizaria may have volume-specific metabolic scaling below one. Lombard et al. (2009) measured respiration rates and estimated biomass (from test length) of five planktonic foraminiferal specimens and found that the mass-specific scaling slope was 0.57 ± 0.18. Across Rhizaria, there is additional evidence that as organismal size increases the amount of organic matter relative to test volume declines (Michaels et al. 1995; Schiebel and Movellan 2012; Meilland et al. 2016; Stukel et al. 2018; Mansour et al. 2021; Laget et al. 2022). Declining organic density

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with increasing size would have the effect of reducing volume-specific metabolic rates even if mass-specific metabolic rates did not change. Hence, we hypothesize that giant protists evolved to thrive in size classes typical of multicellular organisms by having unusually low metabolic scaling, due to some combination of low mass-specific and/or low volume-specific respiration rates. While the relatively empty test volume and low density of Rhizaria, including foraminifera, has been noted before (e.g., Michaels et al. 1995; Stukel et al. 2018) and could drive relatively lower metabolic demands at a given functional size, this has yet to be quantitatively explored.

Here we measure oxygen consumption rates and test volumes in planktonic foraminifera. Our goal in generating these respiration rate measurements is to explore the scaling of respiration with biovolume in planktonic foraminifera in order to assess two possible mechanisms allowing pelagic protists to attain, and thrive at, large sizes: low allometric scaling of respiration rates and/or mixotrophy. To address these questions, our study has three main aims. The 1st aim is to establish the scaling of metabolic rates in planktonic foraminifera using new and published respiration rate measurements relative to estimates of test volume, biomass, and catchment volume. The 2nd aim is to compare these rates within Foraminifera and with other pelagic marine eukaryotes of a comparable size. Together aims one and two allow us to assess whether lower allometric scaling of respiration rate with size in planktonic foraminifera might account for their ability to attain large sizes more typical of metazoan plankton. To understand the relative importance of mixtrophy in allowing foraminifera to attain large sizes particularly at low latitudes, our 3rd aim explores the metabolic and trophic underpinnings of planktonic foraminiferal size patterns across the Atlantic Ocean. Specifically, we quantify the relative metabolic footprint of foraminiferal communities with regards to size, trophic ecology, and geography using our newly derived estimates of respiration rate scaling with size, existing estimates of the temperature dependence of respiration rates, and a published database of planktonic foraminifera test size by species.

Methods

To assess the scaling of respiration rates in foraminifera with size (Aim 1), we collected new respiration rate data and combined these measurements with those from the literature. We considered the scaling of respiration rates within foraminifera and across other groups of similarly size organisms (Aim 2) using multiple different frameworks with regards to size (i.e., test size or the effective size with extended pseudopodia), mass (i.e., multiple volume to biomass conversion factors), and temperature sensitivity. This allows us to keep comparisons methodologically consistent across studies and to explore the differing ecological implications of mass and volume. Published estimates of size by species throughout the Atlantic Ocean, were then used to consider the relative important of allometric scaling of respiration vs. mixotrophy in driving gigantism (Aim 3).

Specimen collection and culture

Oxygen consumption and size was measured in 21 individuals from 5 species: *G. ruber*, *Pulleniatina obliquiloculata*, *Globorotalia menardii*, *Hastigerina pelagica*, and *Orbulina universa*. All these species been shown to have symbiotic relationships with photosynthetic organisms except *H. pelagica* (Takagi et al. 2019), although the intensity of the association and photosynthetic activity varies. Specimens were obtained from the upper 30 m of the water column approximately 10 km off the coast of St. Georges, Bermuda in October 2017 and September 2018 (detailed in Table 1; Supporting Information Table S1). Specimens were towed from the surface (< 30 m) during the day using a Reeve net with a mesh size of 120 μm. Towed material was immediately transported back to the Bermuda Institute of Ocean Sciences where foraminiferal specimens were separated from the other plankton and placed in 0.2-μm mesh filtered seawater. Isolated specimens were kept at a constant temperature of 21°C, 24°C, or 26°C (± 1°C) in high light conditions (photosynthetically active radiation ~ 120) overnight, and then on a 12-h light/dark cycle (*see* Supporting Information Table S1). Specimens were measured and photographed using a microscope-mounted digital camera at the time they entered culture treatments. Specimens in culture for more than 1 d were fed a single *Artemia* nauplius every other day, at which points they were photographed and measured.

Respiration rate measurements and data processing

Acclimated specimens that showed signs of recovery (i.e., streaming symbionts or rhizopods present and spines regenerated, after 1–3 d in culture) were starved for a minimum of 8 h prior to respiration measurements. For respiration measurements, an individual specimen was rinsed in fresh 0.2 μm filtered seawater and transferred into a ~ 1-mL respiration chamber—a glass vial with a ground-glass stopper and containing an optically sensitive oxygen sensor (OXFOIL; PyroScience). Every 4th respiration chamber was filled solely with identically treated water to control for bacterial respiration. All respiration chambers were kept in darkness at a constant temperature of 21, 24, or 26°C and connected to a FireSting optical oxygen meter (PyroScience) to monitor the oxygen concentrations in the vial. Oxygen measurements were recorded every 30 s to every minute for up to 24 h. The 1st hour of respiration rate measurements were eliminated to avoid acclimation artifacts. Respiration rates were determined from the rate of oxygen concentration (μmol O_2 L^{-1}) decline relative to the volumes of each chamber (μmol O_2 ind^{-1} d^{-1}), after correcting for bacterial respirations rates in the control. Respiration rates thus reflect the respiration of the foraminifera, inclusive of its symbionts and other associated organisms (i.e., the holobiont). Respirations rates recorded during

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Table 1. Proportion of each latitudinal sample category as well as the proportion of the estimated total sample biovolume (μm^3) and respiratory output ($\mu mol\ h^{-1}$) to fall into the size fractions above and below 300 μm.

Biome	Percentage mixotrophic (%)	Percentage of sample > 300 μm (%)	Percentage of Total biovolume > 300 μm (%)	Percentage of total oxygen consumption > 300 μm (%)
Tropical/subtropical	93	54.2	56.5	77.7
Subtropical/temperate	58.9	49.4	51.4	70.5
Transitional/subpolar	22.8	38.4	39.9	54.9
Polar	1.8	10.1	10.5	15.3

occasional fluctuations in temperatures greater than 0.3°C were excluded from our calculations of organismal respiration rate. Additionally, if there was an observed change in metabolic rate over time, suggestive of declining animal health, the respiration dataset was truncated. Consequently, the duration of the experiments was on average 13.7 ± 1.01 h (standard error).

Some methods varied between the 2017 and 2018 culture seasons. During the 2017 season only, the culture water was treated with 25 mmol L^{-1} each of streptomycin and ampicillin to kill bacteria and all respiration chambers were kept on a shaker plate to ensure mixing of water. During the 2018 season, the volume of the respiration chambers was not noted, and an average volume was assumed, introducing an error of up to 0.20 mL in chamber volume. This omission could have created an error of as much as ± 15% in the respiration rate measurements. This uncertainty has been propagated into the values for the affected measurements.

Respiration rates were normalized to a common temperature of 24°C using a Q_{10} value of 3.18 from Lombard et al. (2009; determined from measurements of *G. ruber, O. universa*, and *Globigerinella siphonifera*) and biomass was estimated using the volume to mass conversion factors from Michaels et al. (1995) for analyses of mass-specific respiration rates (respiration in Watts g^{-1}). Oxygen consumption values originally reported in $\mu mol\ O_2\ h^{-1}$ were converted to Watts ($J\ s^{-1}$) assuming 0.224 mL per $\mu mol\ O_2$ and 21 $J\ mL^{-1}$, and volumes were converted to mass in grams using the conversion factors from Michaels et al. of 0.049 pg μm^{-1} for all species except *O. universa*, which had a conversion factor of 0.018 pg μm^{-1}. To assess the potential error that could be introduced by using the Q_{10} value of 3.18 from Lombard et al. (2009), we also converted the measurements using $Q_{10} = 2$ and incorporated the resulting discrepancy into the total uncertainty for each respiration rate measurement. This uncertainty was combined with the uncertainty introduced by the unknown measurement chamber volumes (noted above) by taking the root sum squared of the maximum uncertainty values for each parameter.

Tomographic imaging and model processing

All specimens with the exception of B21 and C18 were imaged at the Advanced Photon Source at Argonne National Labs, Beamline 2A-B (Supporting Information Table S1). Specimens were mounted inside capillary tubes and scanned individually at 10× magnification with a voxel size of 0.60 μm. Specimens B21 and C18 were imaged and reconstructed at the University of Southampton on 510 Versa X-ray Microscope (Zeiss Xradia California, USA) at a resolution of 1.6 $\mu m\ pixel^{-1}$. Volumes were reconstructed to generate 900 two-dimensional .tif images and visualized in VG StudioMax v. 3.0 (Volume Graphics). Major and minor axis length, volume, and surface area of the calcite tests of each individual were measured in VG Studio Max 3.0. Internal cavity/cell volumes were estimated by making a watertight polygonal mesh of the digitized test, exporting the mesh as a stereolithography (STL) file and performing a screened Poisson surface reconstruction of the external surface of the test in Meshlab ("wrap mesh") (Kazhdan and Hoppe 2013). The wrap mesh was then saved as an STL file and imported into VG StudioMax, converted to a solid volume, and measured ("wrap volume"). The volume of the digitized calcite test was subtracted from the wrap volume to obtain the volume of the internal cavity ("biovolume") (as in Burke et al. 2020). Size was measured as volume (μm^3) and respiration rates in $\mu mol\ O_2$ consumed per hour.

The tests of planktonic foraminifera are not always completely full of cytoplasm. Because the fullness of the final chambers was not estimated, we have reported biovolumes as 75% of the measured internal test cavity volume and incorporated uncertainty of ± 25% of the total test cavity volume to represent tests with final chambers between 50% and 100% full (Hannah et al. 1994).

Incorporation of data from published sources

We combined our new measurements with planktonic foraminiferal oxygen consumption data from Lombard et al. (2009), which included respiration data from Jørgensen et al. (1985) and Rink et al. (1998). Measurements were taken for these specimens at temperatures ranging from 15.3°C to 29.6°C and were normalized to 24°C using a Q_{10} value of 3.18 from Lombard et al. (2009). Biovolumes were estimated based on the test lengths reported in Lombard et al. (2009) using predictive equations for cell volume based on length from Burke et al. (2020) updated with additional specimens (*see*

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below; Supporting Information Fig. S1) for all species except *O. universa*, whose volume was predicted using the volume of a sphere with a diameter equal to the test length. We also compared planktonic foraminiferal respiration rates with those of other pelagic marine eukaryotes (including diatoms, coccolithphores, and many species of arthropod) sampled from the compilation of Hatton et al. (2019) and adjusted the estimates of size and respiration rate to match their methods (*see* Supporting Information Table S4 for data). Specifically, planktonic foraminiferal respiration rates were normalized in two different ways. In order to conform to the same assumptions used by Hatton et al. (2019) for many unicellular organisms in the compilation, we scaled planktonic foraminiferal respiration measurements to a temperature of 20°C using a Q_{10} of 2 and recalculated biomass assuming a 1 g mL^{-1} mass-to-volume conversion factor. For comparison, we also compare our respiration measurements to Hatton et al. (2019) at a temperature of 20°C using the planktonic foraminiferal scaling factors (i.e., Q_{10} of 3.18 from Lombard et al. 2009 and biomass estimates after Michaels et al. 1995). Planktonic foraminiferal respiration rates were compared to published benthic foraminifera rates from Geslin et al. (2011), normalized to a common temperature of 24°C using an Arrhenius temperature (T_A) for respiration of 10,293K from Lombard et al. (2009; table 2) to duplicate the analytical methodology of the benthic study.

Respiration rates in modern foraminiferal assemblages

Planktonic foraminifera respiration was estimated for 22,481 individuals in the > 150um sieve size fraction from 31 Atlantic Ocean core top sites (i.e., sediment samples of time-integrated depth assemblages) with published test length data (Elder et al. 2018), using the newly derived allometric relationships from this study. Test volume was estimated from reported test maximum diameter lengths using updated length to volume regressions after Burke et al. (2020) and species identifications from Hsiang et al. (2019). Specifically, the 21 specimens measured in this study were combined with those from Burke et al. (2020) to derive new length to volume regressions (Supporting Information Fig. S1). Specimen volume was estimated from major axis length using

$$\text{Volume}\left(\mu m^{1/3}\right) = 0.62\,(\text{Major Axis}\,(\mu m)) - 8.94$$

with the exception of the relatively discoidal species *G. menardii*, *Globorotalia hirsuta*, *Globorotalia scitula*, and *Globorotalia tumida*, which were estimated as

$$\text{Volume}\left(\mu m^{1/3}\right) = 0.31\,(\text{Major Axis}\,(\mu m)) + 52.08$$

Data from three of the original 34 sites quantified in Elder et al. (2018) were excluded due to low numbers of species identified at those sites (fewer than 200 specimens). Metabolic rates were calculated from volume using the equations presented herein and assuming a temperature sensitivity of a $Q_{10} = 3.18$ (from Lombard et al. 2009). Sea surface temperature data for the collection localities (10 m depth) was obtained from the World Ocean Atlas 2013 database (Locarnini et al. 2013) from the nearest degree of latitude/longitude. Presence or absence of active algal symbionts was specified for each species after Takagi et al. (2019) where possible and microtax.org isotope paleobiology distinctions in other cases (Young et al. 2017).

Results

Aim 1: Oxygen consumption rates of 21 specimens of planktonic foraminifera from *G. ruber*, *O. universa*, *P. obliquiloculata*, *H. pelagica*, and *G. menardii* range from 0.32 to 05.6 nmol O_2 h^{-1}. Once normalized to a midpoint temperature of 24°C, oxygen consumption rates ranged from 2×10^{-4} to 4.9×10^{-3} μmol O_2 h^{-1} (Fig. 1).

Our data, combined with previously published planktonic foraminiferal data generated and compiled in Lombard et al. (2009) and new taxa-specific volume estimates, were used to assess the relationship between oxygen consumption rates and test volume. We find respiration rate to be significantly and positively correlated with estimated biovolume in planktonic foraminifera using linear regressions (Fig. 1; $p < 0.001$), with a slope of 0.51 ± 0.18 (95% confidence interval) and an $R^2 = 0.49$. When catchment volume (the total volume occupied by the living organisms with its rhizopodial network extended) is estimated using factors from Gaskell et al. (2019), no significant scaling slope is present.

Aim 2: The linear relationship of respiration rates with biovolumes in planktonic and benthic foraminifera have significantly different intercepts (i.e., significantly different according to ANCOVA, $p < 0.001$; benthic intercept = -12.18 ± 1.6; planktonic intercept = -8.38 ± 1.24), but not slopes (benthic slope = 0.89 ± 0.22; planktonic slope = 0.51 ± 0.18; ANCOVA, $p = 0.08$; Fig. 2) due to the wide confidence bounds on both regressions. In comparison to other plankton, planktonic foraminifera have a significantly smaller increase in respiration rate with mass (planktonic foraminiferal slope = 0.51 ± 0.18, all marine plankton slope = 0.83 ± 0.02, 10^{-7} to 10^{-3} g size-class marine plankton = 0.95 ± 0.08; ANCOVA, $p < 0.001$; Fig. 3). When planktonic foraminiferal biomass is estimated using the 1 : 1 volume to biomass conversions that are employed for unicellular organisms in the plankton compilation (Hatton et al. 2019; Fig. 3a, solid black points) the respiration rates of planktonic foraminifera are comparable to the other species in their size class. However, when planktonic foraminifera-specific biomass conversion factors—which likely more closely approach the true biomass of planktonic foraminifera—are used, the respiration rates of planktonic foraminifera are higher than the others in their size class (Fig. 3).

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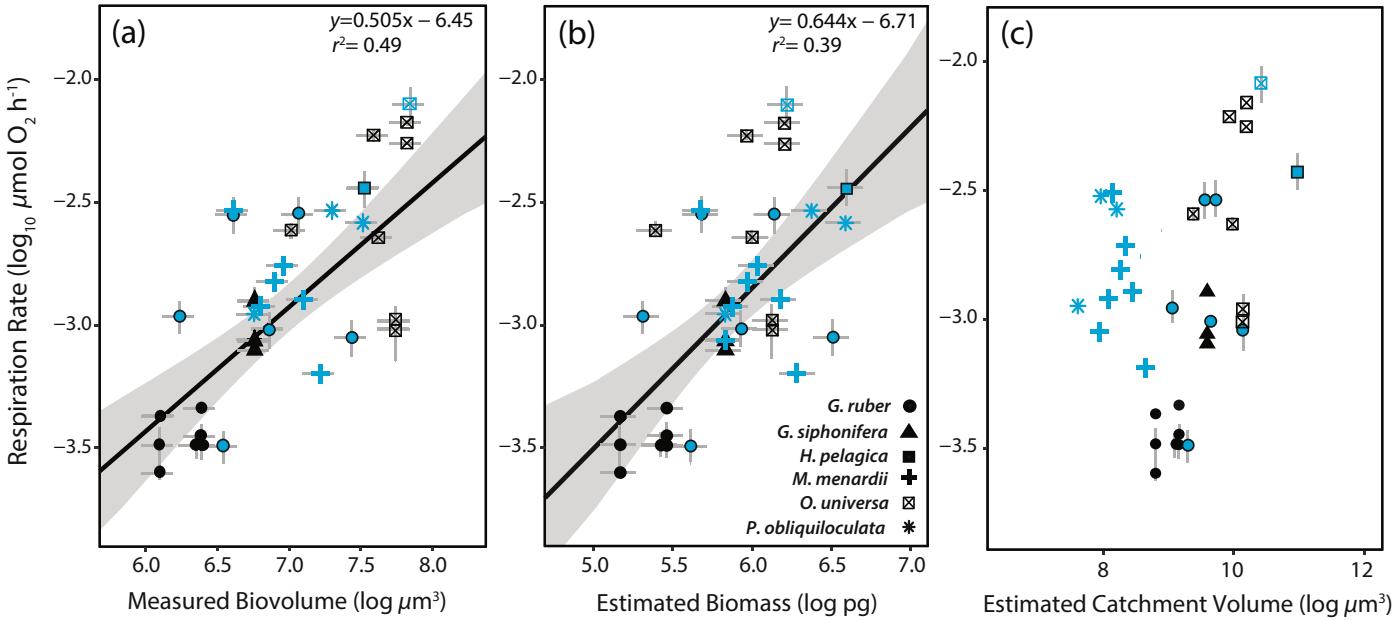

Fig. 1. Scaling of individual planktonic foraminifera respiration rates as a function of (**a**) major axis length, (**b**) estimated biomass, and (**c**) estimated catchment volume, for new (blue symbols) and previously published data (i.e., Lombard et al. 2009; black symbols). Error bars on the x-axis represent uncertainty as to the fullness of the final chamber. *Y*-axis error bars are the root sum squared of the uncertainty introduced during respiration rate measurements and temperature normalization. Linear regressions are significant at a $p < 0.001$ in (**a**, **b**), and gray-shaded regions represent the 95% confidence bounds of the regression; (**c**) does not have a regression line because the two variables are not significantly correlated.

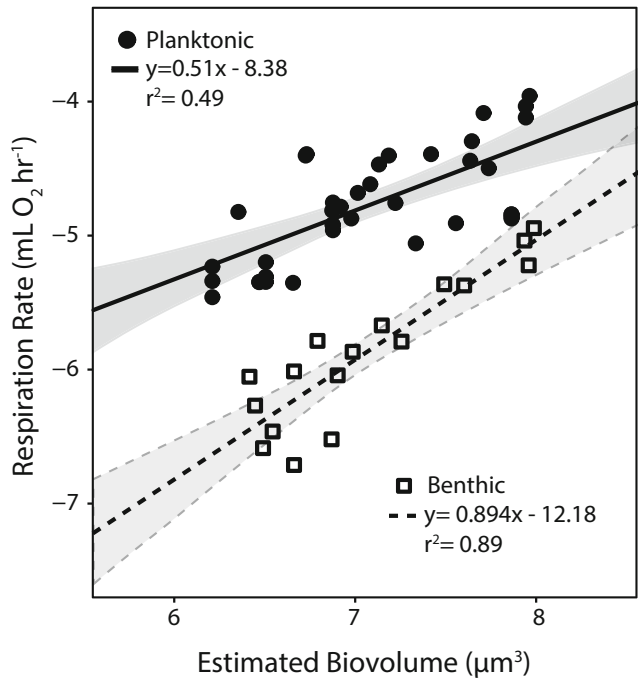

Fig. 2. Scaling of planktonic foraminifera (circles) and benthic foraminifera (squares, from Geslin et al. 2011) respiration rates as a function of estimated biovolume. Linear regressions are significant at a $p < 0.001$, and gray-shaded regions represent the 95% confidence bounds of the regression.

Aim 3: We found that our estimate of average planktonic foraminiferal assemblage respiration rate varies inversely with latitude (i.e., high at low latitudes, low at high latitudes; Fig. 4a). We lumped sample localities into four geographic groups based on similarities in assemblage respiration rate (Fig. 4c; tropical/subtropical, temperate, transitional/subpolar, polar), with all four geographic groups differing significantly in respiration rate according to a one-way ANOVA followed by Tukey's HSD test for multiple comparisons (Supporting Information Table S7). Although average size (major axis length and estimated biovolume) is similar across latitudes, low-latitude sites are strongly positively skewed, with proportionally more individuals in the largest classes (Fig. 5a,b, Table 1). More specifically, the dominant size class in terms of number of individuals and total biomass is the 150–300 μm class across all latitudes (Fig. 5d,e), but the proportion of individuals in the > 300 μm size class differs by latitudinal group (Table 1). For example, less than 1% of the polar sample is larger than 300 μm, whereas 30% of the tropical sample is over 300 μm (Fig. 5d,e). The combined effect of this positive size skew and environmental temperatures is an inverse relationship between latitude and assemblage respiration rate (Fig. 5c), with specimens larger than 300 μm accounting for over 50% of the total respiration in the tropical group (Fig. 5f). In the tropical group, the 300–450 μm sieve size fraction is dominant in terms of estimated total oxygen consumption, in contrast to the 150–300 μm size fraction at other latitudes (Fig. 5f).

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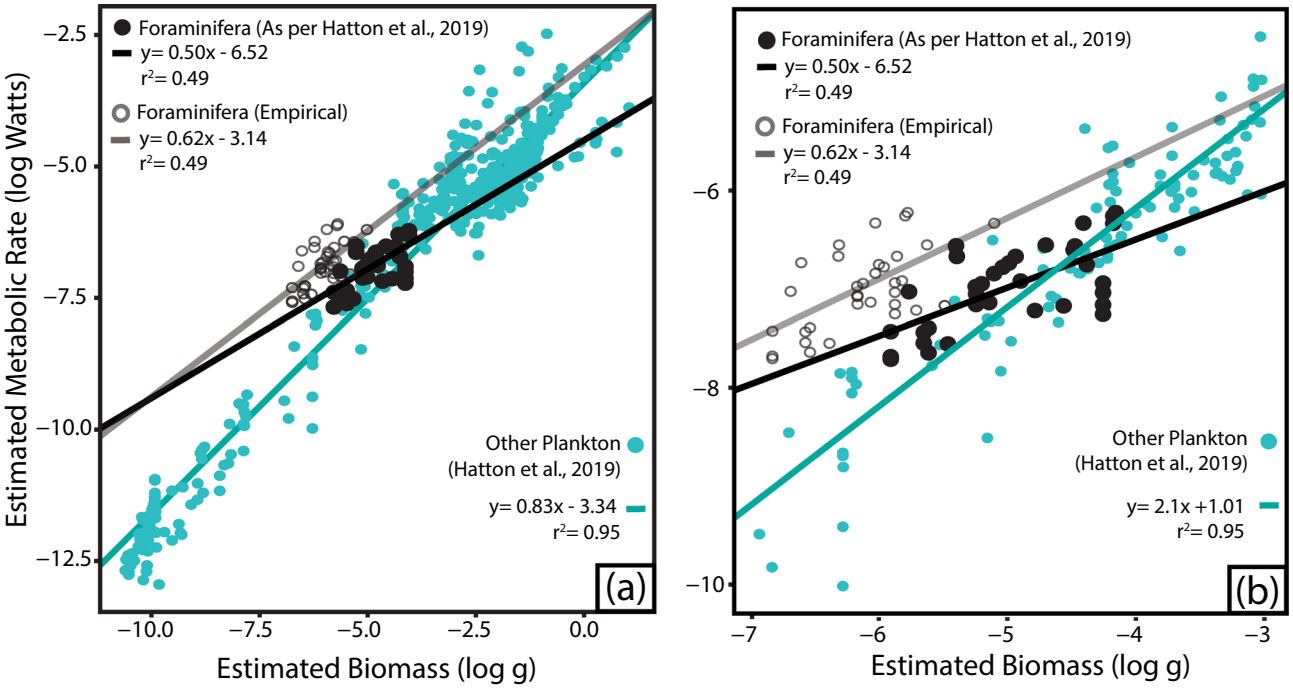

Fig. 3. Scaling of planktonic foraminiferal (black circles) respiration rates as a function of estimated biomass as compared to (**a**) all marine plankton (blue circles) and (**b**) marine plankton in the size range of planktonic foraminifera, from Hatton et al. (2019). In open circles, planktonic foraminiferal biomass is estimated using factors from Michaels et al. (1995) and respiration rates adjusted for temperature using Q_{10} from Lombard et al. (2009). All regressions are significant ($p < 0.01$).

Mixotrophic species dominated tropical/subtropical assemblages, comprising over 93% of individuals (Fig. 4b; Table 1), a proportion that declined with latitude (mixotrophic proportion in temperate samples = 59%, transitional/subpolar samples = 22%, polar samples = 1.8%). Although mixotrophic taxa have significantly larger maximum sizes (major axis and biovolume) and respiration rates within all latitudinal groups (Fig. 6, ANOVA with Tukey's HSD test for multiple comparisons, Supporting Information Table S7), both mixotrophic and heterotrophic taxa exhibit an inverse latitudinal gradient between size (median, 75th percentile, 95th percentile) and respiration rate. Furthermore, within the tropical/subtropical group, mixotrophic taxa are not significantly larger on average than heterotrophic taxa (ANOVA, $p = 0.098$), although in all other latitudinal groups mixotrophic taxa are significantly larger on average ($p < 0.05$; Supporting Information Table S6).

Discussion

Scaling of respiration rate in foraminifera

Across eight species of planktonic foraminifera, respiration rate scales with test biovolume with a slope of 0.51 ± 0.18 (Fig. 1a). In compilations of unicellular organisms including protists and bacteria, allometric scaling factors have ranged between 0.60 and 1.00 (Tang and Peters 1995; Glazier 2009). Our findings thus place planktonic foraminifera well below most cross-taxa metabolic scaling estimates. When catchment volume is considered, planktonic foraminifera are more remarkable still. Like many Rhizaria, planktonic foraminifera do not live within the confines of their test walls, and can increase their effective volume by up to several orders of magnitude by pseudopodial streaming (Gaskell et al. 2019). When we estimate catchment volume instead of test volume, the relationship between biovolume and respiration rate becomes nonsignificant (Fig. 1c), indicating a remarkable insensitivity of total oxygen utilization to organismal size.

We did not observe consistent differences amongst species hosting different types of photosymbionts or hosting symbionts in different locations on their tests (dinoflagellate, spine-hosted: *G. ruber*, *O. universa*; pelagophyte, spine-hosted: *G. siphonifera*; chrysophyte, internal: *P. obliquiloculata, Menardella menardii*; Schiebel and Hemleben 2017; Takagi et al. 2019). The only asymbiotic individual measured here, *H. pelagica*, has respiration rates consistent with the other taxa. Eight additional measurements of *Globigerina bulloides* (Davis et al. 2017; Davis pers. comm.), a nominally asymbiotic species (Takagi et al. 2019, although *see* Bird et al. 2017), did not significantly change our regressions (with *G. bulloides*: slope = 0.51 ± 0.40; Supporting Information Fig. S3). However, the *G. bullloides* respiration rates are generally higher than other specimens in same size range, and do not exhibit intraspecific allometric scaling (Supporting Information

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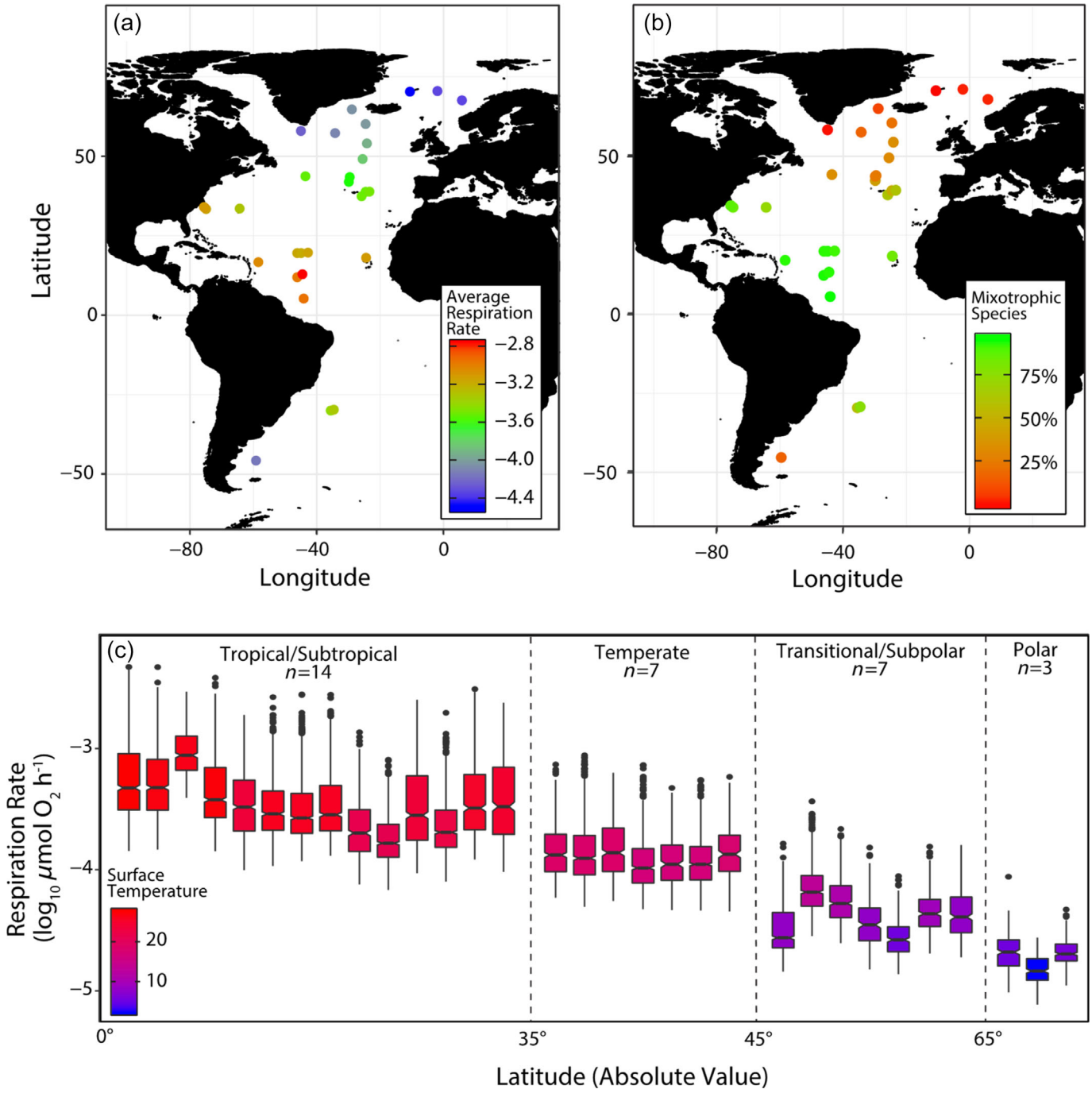

Fig. 4. Geography of (**a**) average assemblage respiration rates and (**b**) proportion of photosymbiont bearing taxa (i.e., mixotrophic), as calculated from a published core top Atlantic dataset (Elder et al. 2018; Hsiang et al. 2019) with photosymbiont bearing taxa identified primarily after Takagi et al. (2019) (*see* "Methods" section). (**c**) The determinants of gigantism in planktonic foraminifera were considered by dividing the data into four latitudinal bands (breakpoints at the absolute latitudes 35°, 45°, and 65°) on the basis of similarity in average respiration rate.

Fig. S3). Several confounding influences could be responsible for these differences, including the fact that these individuals were caught and cultured at 16°C, a much lower temperatures than most of the other specimens in this study, and that the respiration rates were measured using different methods. However, they could indicate that *G. bulloides*, a species that is frequently found in nutrient rich, cool/temperate environments, employs a different metabolic strategy altogether than the warm-water taxa featured in our analysis. Thus, although our data support using a single metabolic scaling relationship

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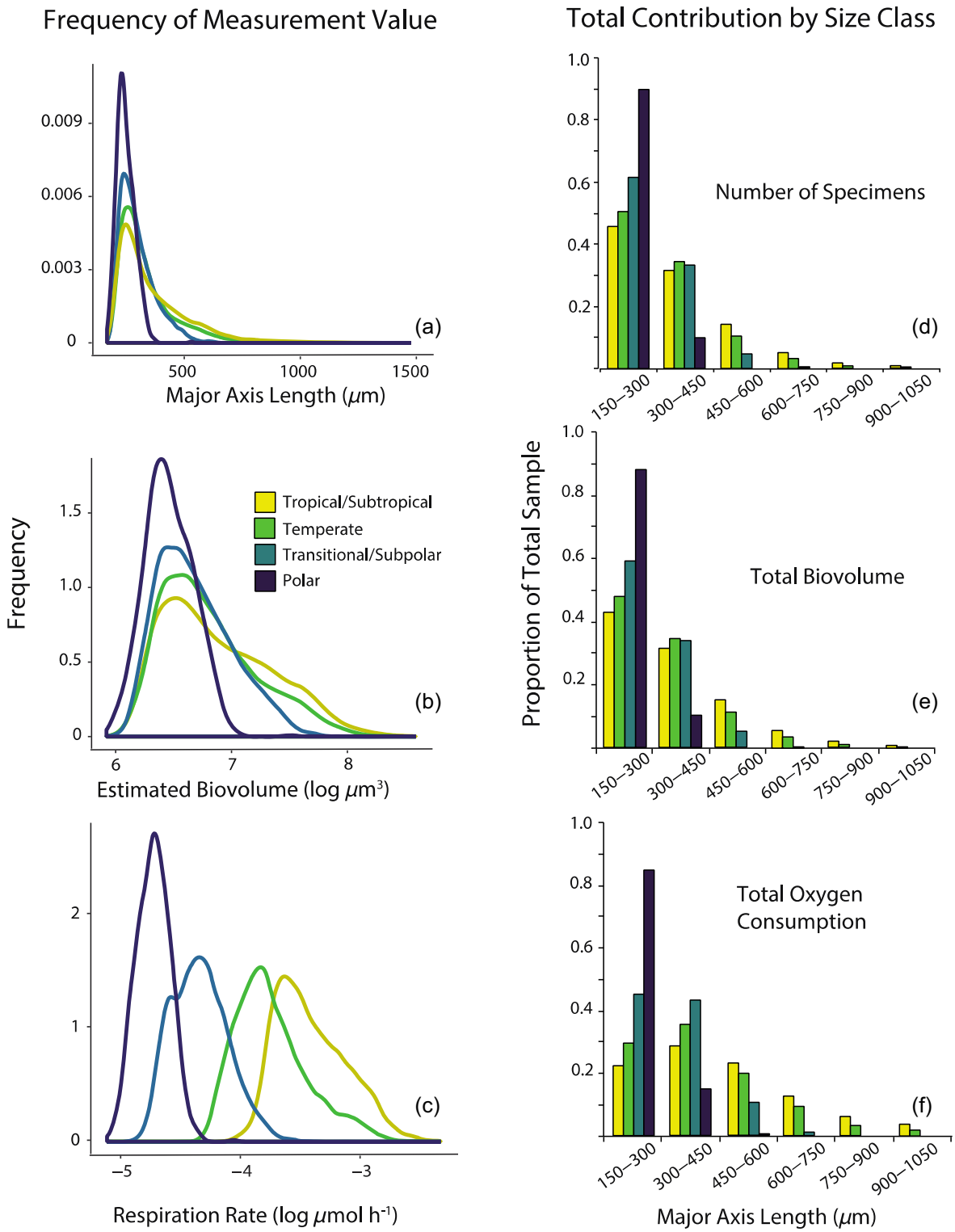

Fig. 5. The frequency and relative contribution of large vs. small individuals as a function of latitudinal groups. (**a**–**c**) Frequency distribution of (**a**) test length, (**b**) estimated biovolume, and (**c**) respiration rate, by latitudinal group. (**a**–**f**) Proportion of assemblage sample by size class by (**d**) number of specimens, (**e**) total estimated biovolume, and (**f**) total estimated oxygen consumption.

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across all planktonic foraminifera, more respiration rate measurements are needed to validate this hypothesis, particularly in asymbiotic and/or cold-water taxa.

Benthic foraminifera have similarly been hypothesized to have unusually low metabolic rates for their biovolume due to low biomass per cellular volume (cell density; Geslin et al. 2011). However, benthic foraminifera have a steeper metabolic scaling (slope $= 0.88 \pm 0.22$) than planktonic foraminifera that is comparable to other benthic organisms of a similar size (Geslin et al. 2011), and a much lower intercept ($b = -8.3 \pm 0.60$ for planktonics, $b = -12.2 \pm 0.80$ for benthics) (Fig. 2). Although metabolic scaling analyses for benthic foraminifera were conducted using different methods for estimating temperature sensitivity and biovolume (*see* Geslin et al. 2011 for details), when we recalculated metabolic scaling for planktonic foraminifera using the same methods we obtained a slope of 0.50 and intercept of −8.38. This indicates that the volume and rate adjustments are not responsible for the differences observed between planktonic and benthic foraminifera. In short, this implies that at the smallest cell sizes, planktonic foraminifera have much higher metabolic rates than comparable benthic foraminifera, and the magnitude of this difference decline through ontogeny.

Respiration rates in planktonic foraminifera vs. other plankton

Metabolic scaling in planktonic foraminifera is low compared to estimates of 0.60–1.8 for other unicellular organisms (Tang and Peters 1995; Glazier 2009; DeLong et al. 2010) and the controversial but frequently cited estimates of 0.67–0.75 across all organisms (Hemmingsen 1960; West et al. 1999, West et al. 1997; Dodds et al. 2001; Gillooly et al. 2001; Brown et al. 2004; Glazier 2005). A recently published compilation by Hatton et al. (2019) presented an updated dataset for over 7300 organisms ranging from bacteria to large mammals. Only about 2% of this dataset are protozoan measurements (which included marine, freshwater, and terrestrial protozoa), with no foraminifera or other Rhizaria. We extracted the data for all of the pelagic marine taxa (456 data points) from this compilation, plotted them with our planktonic foraminiferal data, and obtained a metabolic scaling factor of 0.83 ± 0.02 (Fig. 3). If we recalculate our data using cross-taxon assumptions from Hatton et al. (including $Q_{10} = 2$, a reference temperature of 20°C, and a biomass to volume conversion of 1 g mL^{-1}) we find that planktonic foraminifera still have lower allometric scaling for respiration than the rest of the compiled dataset (Fig. 3, black dots). Despite the lower allometric scaling, planktonic foraminiferal biomass-specific respiration rates are similar to other pelagic taxa (Fig. 3, black dots). However, planktonic foraminifera have much lower biomass to volume conversion than the 1 g mL^{-1} of many estimates compiled in Hatton et al. (0.014 g mL^{-1} for most planktonic foraminifera; Michaels et al. 1995), and when this conversion is used planktonic foraminifera stand out for having unusually high mass-specific metabolic rates (Fig. 3, open circles). In other words, depending on how biomass is estimated, the estimated respiration rates of planktonic foraminifera are either unremarkable or could be interpreted as being unusually high. The consistent biomass to volume scaling factor used by Hatton et al. (2019) is useful because it provides a consistent ruler given relatively sparse empirical constraints, but it may also obscure important biological differences that could change how we understand the rate scaling of metabolic rates. For Rhizaria specifically, but perhaps for single-celled eukaryotes more generally, low biomass density and variable volumes may be the physiological and ecological key to understanding how they outcompete similar sized metazoans.

When the size of the catchment is considered—and it should be, given that this is the size at which they interact with other organisms—planktonic foraminiferal metabolic rates are markedly low for their size class (Fig. 7). Perhaps by operating ecologically in a larger size class, planktonic foraminifera can consume relatively large prey (as has been observed here, and elsewhere, cultured specimens quickly dispose of juvenile *Artemia* spp. nauplii larger than themselves), allowing them to maintain fast metabolisms. Conversely, having low-density biomass might allow the attainment of "gigantic" catchment sizes and increased levels of prey encounter in planktonic foraminifera and other Rhizaria in metabolically challenging environments. In addition, in the larger size classes of planktonic foraminifera ($> 200\ \mu$m) biomass density declines as size increases (e.g., Meilland et al. 2016) as has been observed in siliceous Rhizarians (Laget et al. 2022). Together the combination of low allometric scaling of respiration, low cell density, and low allometric scaling of cell density make it energetically very cheap for planktonic foraminifera to reach gigantic protistan sizes of $> 600\ \mu$m, with respiration rates based on catchment volume suggesting no increase in net respiration with size across mid- to large-size classes (Fig. 7).

To test the allometric scaling slope presented here, additional metabolic data from juvenile, diminutive (adult specimens smaller than 125 μm in test length), and cold-dwelling species are needed. Particularly, our data suggests that the smallest foraminifera have very high size-specific respiration rates, matching their relatively dense organic biomass (Meilland et al. 2016). If true, this could indicate that planktonic foraminifera may employ a relatively risky life history strategy of "living fast" and growing rapidly throughout early ontogeny. Such speedy growth, enabled by high metabolic rates early in life, could be used, for example, to allow planktonic foraminifera to exploit spatially and temporally patchy resources—a particularly important strategy in relatively food-depauperate or seasonal regions. Alternatively, the high basal mass-specific respiration may reflect the high energetic costs of being a Rhizaria, with relatively large and dynamic

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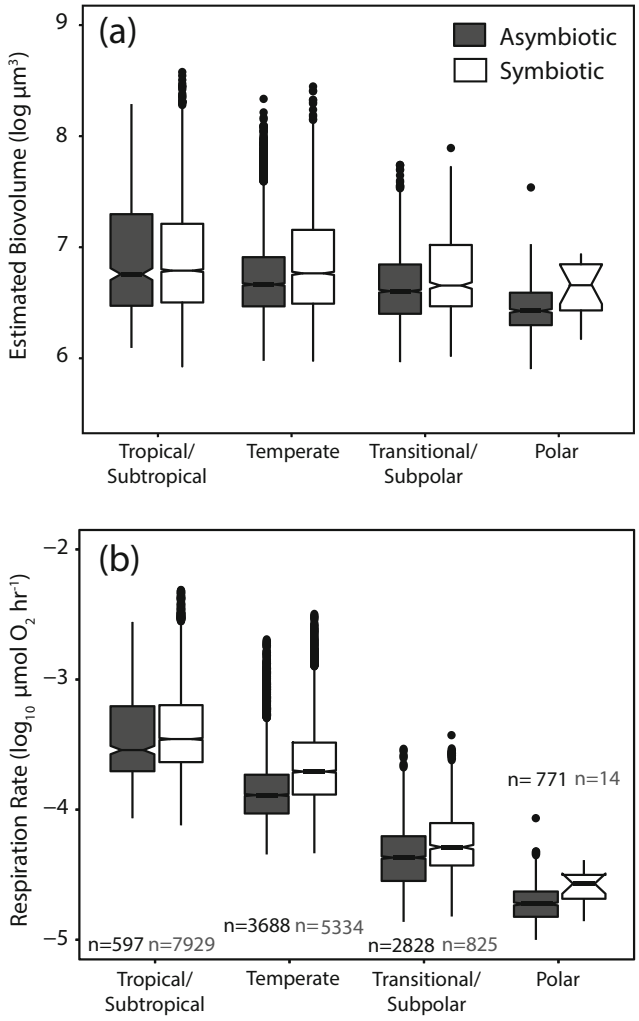

Fig. 6. Distributions of biovolume estimates (top) and respiration rate estimates (bottom) within each latitudinal group subdivided by presence (white) or absence (gray) of symbionts in the species identified.

genomes (e.g., Goetz et al. 2022) and considerable cellular resources dedicated to cytoplasmic streaming and organization (e.g., Travis et al. 1983).

Biogeography of planktonic foraminiferal respiration and mixotrophy

We estimate a pronounced, inverse latitudinal gradient in planktonic foraminiferal community respiration rates (Figs. 5c, 6c) that reflects the combined effect of increasing size and increasing temperatures at low latitudes, with large sized individuals accounting for a greater proportion of community respiration at low latitudes (Fig. 5f). Planktonic foraminiferal assemblages are dominated by small size classes in terms of species diversity and number of individuals (Al-Sabouni et al. 2007). Lower latitude assemblages exhibit greater diversity, greater proportions of large individuals, and greater maximum sizes than high latitude assemblages (Schmidt et al. 2004a,b; Al-Sabouni et al. 2007). We confirmed these size trends across the 22,482 specimens from 31 sites from the Atlantic Ocean (Elder et al. 2018; Hsiang et al. 2019), with median body size decreased modestly with latitude, ranging from 311.8 μm in the tropics to 241.7 μm in the polar region (Fig. 6a). By combining size and respiration rates, we find that specimens larger than 600 μm account for 15.3–26.1% of total estimated community oxygen consumption in the temperate to tropical/subtropical latitudes while comprising only 4.5–8.3% of individuals respectively. In polar latitudes, there were no individuals larger than 600 μm. This pattern is counterintuitive because it suggests that in the warmest, most oligotrophic parts of the global ocean, planktonic foraminifera communities are using the most energy.

Existing theories do not provide an interpretive framework for understanding the existence of relatively large bodied, energetically expensive life history strategies at low latitudes. There are two primary hypotheses for the increase in Rhizarian cell size toward low latitudes: water column stratification (hypothesized for planktonic foraminifera; Schmidt et al. 2004a,b; Al-Sabouni et al. 2007; Schmidt et al. 2006) and mixotrophy (hypothesized for siliceous Rhizarians; Biard et al. 2016). While water column stratification and niche partitioning provide a reasonable explanation for high diversity in low latitudes (Schmidt et al. 2006), it fails to explain why individuals would, on average, be larger and have higher total metabolic demands. Indeed, mechanistic models of plankton communities predict that mixotrophs, like heterotrophs, should reach their largest sizes in the coldest and/or most productive regions of the ocean (Ward et al. 2013; Ward and Follows 2016).

In contrast, we do find a dramatic increase in the proportion of mixotrophic planktonic foraminifera in lower latitudes (Fig. 6; Table 1), with mixotrophs comprising > 90% of assemblages in the tropical group but less than 2% of individuals in the polar group. We also find mixotrophic lineages to be bigger and have greater metabolic demands on average in lower latitudes (Figs. 5, 6). However, we also find that heterotrophic lineages reach gigantic proportions (> 600 μm) at low latitudes as well and are also characterized by the same inverse latitudinal size and metabolic gradients as occur in mixotrophic lineages (Fig. 6). Thus, although warm, oligotrophic waters with scarce food availability and deeper light penetration may lead to the greater dominance of mixotrophic planktonic foraminifera at low latitudes (Fig. 6), this alone cannot explain the presence of relatively large cell sizes and the inverse-latitudinal size gradient because strict heterotrophs exhibit the same trends.

Revised hypothesis for the existence and importance of gigantic Rhizarians in low latitudes

We propose that low allometric scaling of energetic needs is the key factor that leads to the inverse latitudinal gradient in Rhizarian size, but mixotrophy acts to boost the advantages

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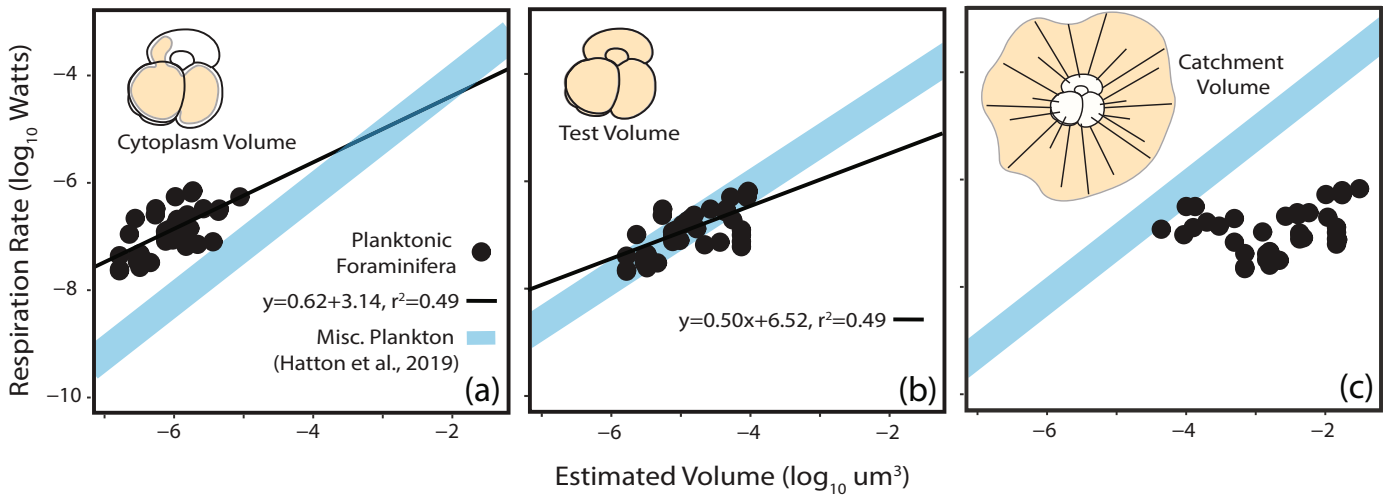

Fig. 7. Comparison of the planktonic foraminiferal allometric scaling relationship to other planktonic eukaryotes when size is estimated based on cytoplasm volume, test volume, or the size of the entire catchment including the spines and rhizopodial network.

of Rhizarians in oligotrophic environments thereby accounting for their relative success (i.e., high relative abundance). We briefly recap the factors underpinning this two-part hypothesis.

1. Metabolic underpinning of gigantism in oligotrophic environments

Pelagic Rhizarians are able to succeed in relatively large size classes (> 600 μm) because they "live large" relative to their energetic demands, thereby reaping the benefits of large size for predation and photosynthesis without accruing the metabolic costs. Here we provide evidence of low (to no) increase in oxygen utilization with increasing catchment volume (Figs. 1, 7), likely due to the combination of low organic density (e.g., Michaels et al. 1995), low allometric scaling of organic density (e.g., Meilland et al. 2016; Laget et al. 2022), low allometric scaling of respiration (this study), spines effect on catchment volume (estimates from Gaskell et al. 2019), and shape (this study). The final factor we investigated using surface area : volume (SA : V) ratios and found that upper-quartile SA : V ratios are highest in the tropics (Supporting Information Fig. S4). Planktonic foraminifera achieve this through having relatively compressed or digitate forms (like *G. menardii* or *H. pelagica*) in low latitudes, as the smaller high latitude tests have inherently higher SA : V (i.e., surface area scales with radius^2, volume with radius^3).

Low allometric scaling may allow for gigantic proportions, but alone does not explain why large test sizes are favored in lower latitudes. For this, we propose that large catchment areas are under stronger selection in relatively food-depauperate regions. When food resources are scarce, the biomineralized taxa across Rhizaria can maintain the same effective catchment volume (for capture of prey and exposing symbionts to photosynthetically active radiation) while shrinking their internal cytoplasmic volume, as has been observed (i.e., Meilland et al. 2016). This strategy may not have the same advantages in more nutrient rich areas where food encounter rates are higher. Ecologically, pelagic Rhizarians employ additional low-energy strategies including sit-and-wait predation (e.g, Hull et al. 2011) and no-diel vertical migration (Manno and Pavlov 2013; Meilland et al.; 2019) and may minimize their predation risk through relatively high handling times (i.e., biomechanically robust tests; e.g., Burke and Hull 2017). Altogether, planktonic foraminifera keep their metabolic costs low for their effective catchment size class, perhaps to their competitive advantage against zooplankton in the most food-limited regions of the ocean.

2. Mixotrophy amplifies the Rhizarian advantage in resource-limited environments

We propose that mixotrophy acts to amplify the metabolic advantages of gigantic Rhizarians over zooplankton in a similar size class by providing an alternative food source when prey are scarce. Mixotrophic planktonic foraminifera are not only the most abundant component of foraminiferal assemblages in low latitudes, they also have relatively consistent and high abundances throughout the year—with greater seasonality in the abundance of mixotrophs near the cold-ends of their range (Jonkers and Kučera 2015). This relatively tight coupling of abundance to temperature, regardless of primary productivity, has been interpreted as arising from the presence and importance of symbionts—thereby reducing the importance of primary productivity on their energy budgets (Jonkers and Kučera 2015). Indeed, across photosymbiont-bearing planktonic Rhizarians (e.g., Acantharia, Radiolaria, and

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Foraminifera), Caron et al. (1995) found primary production rates (per volume seawater) within the host exceeded those locally by more than four orders of magnitude and contributed up to ~80% of the carbon to the host–symbiont complex (Anderson et al. 1983; Caron et al. 1995). The patterns we find of gigantism, low metabolic scaling, and high total community energetic demand in low latitude, heterotrophic planktonic foraminifera refute hypotheses for gigantism that rely on mixotrophy alone. However, we also present clear evidence that mixotrophic taxa are by far the most abundant component of planktonic foraminifera assemblages at these latitudes. Thus, we posit a two-pronged hypothesis to account for the patterns observed in pelagic Rhizarians combining low allometric scaling of respiration with mixotrophy.

Although integrating our linear relationships with the Elder et al. (2018) and Hsiang et al. (2019) datasets has enabled us to broadly evaluate the potential differences in total community metabolism, there are limitations to this initial analysis. First, only surface environmental conditions were used; differences in depth habitat amongst species (and individuals) have not been considered. In highly stratified low latitude waters, the difference in habitat temperature between a *G. ruber* living in the top 20 m and a *Globorotalia truncatulinoides* living 200 m below the surface could have a dramatic effect on the inferred metabolic rate. For example, a specimen 250 μm in length living at one of the Tropical/Subtropical localities from the Elder et al. (2018) and Hsiang et al. (2019) datasets (19.567°N, 44.95°W) living in the upper 10 m of the water column where the average temperature is 25.76°C would have an estimated respiration rate of 0.46 nmol h^{-1}. The same specimen living at 200 m at an average temperature of 13.99°C would have an estimated respiration rate of 0.12 nmol h^{-1}. However, because the assemblages in the tropical and subtropical latitudinal bands are dominated by surface dwelling species (e.g., *G. ruber* and *G. sacculifer* alone comprise 67% of the tropical/subtropical latitudinal group), the observed patterns are likely to remain even with the addition of more species-specific depth habitat data. Similarly, seasonal variation in temperature was not considered in these estimates, although Jonkers and Kučera et al. (2017) concluded that, for most species that dominate Atlantic assemblages like those explored here, temperatures at the time of peak test production vary modestly (± 2.5°C) from annual average surface temperatures. Further, all specimens in the dataset were passed through a 150-μm sieve, largely eliminating all specimens from the community smaller than that size. The excluded size fraction would likely shift the community size and metabolic structure toward smaller size classes, as a large portion of planktonic foraminiferal diversity falls into that category (Al-Sabouni et al. 2007). Even so, the relative distribution and influence of large size classes across latitudes would remain the same. In addition, because volume-to-biomass conversions for planktonic foraminifera are relatively limited (e.g., Michaels et al. 1995; Meilland et al. 2016), the question of whether tropical foraminifera have lower densities remains to be fully tested. Regardless, the fact that all currently available measurements of planktonic foraminifera indicate a low metabolic scaling, and that these observations are supported by the biomineralized test construction and low-density biomass of Rhizarians, suggest that our core conclusions are likely to hold as new data become available.

Conclusion

As one of the only components of marine plankton to leave a robust fossil record, planktonic Rhizarians such as foraminifera are highly valuable archives of past environments. However, their utility is tied to our understanding of their biology, physiology, and ecology. Here, we present the 1st set of paired direct measurements of respiration rates and test volumes to quantify the relationship between size and metabolic rates in planktonic foraminifera (Aim 1), as compared to benthic foraminifera and other pelagic marine eukaryotes (Aim 2). This new approach has allowed us to present a new hypothesis for how they attain their largest sizes in warm, often oligotrophic environments. Our results show that respiration rate increases with test biovolume by a relatively shallow slope of 0.51 in planktonic foraminifera. The shallow scaling of metabolic rate with size, in combination with the previously observed low-density biomass and the increase in prevalence of symbiotic taxa toward the tropics, suggests a two-prong set of mechanisms that may have enabled planktonic foraminifera (and indeed, Rhizaria) to thrive at large sizes in oligotrophic environments by maximizing their effective size while maintaining a modest cell size (Aim 3). This causes planktonic foraminifera to outpace their biomass size class metabolically with less nutritional demands than those in the size class they interact with ecologically (determined by the size of their test and pseudopod/spine network). Foraminiferal size has been known to fluctuate throughout their fossil record in conjunction with extinction events and changes in global climates (Chaisson 2003; Kaiho et al. 2006; Wade and Olsson 2009; Brombacher et al. 2017). Using the predictive equations presented here to examine foraminiferal size trends through the lens of metabolism could provide an opportunity to further explore their macroevolutionary history and future in the changing oceans.

Data availability statement

The data used for this manuscript is available on Zenodo at the following link: https://zenodo.org/records/12801293?preview=1&token=eyJhbGciOiJIUzUxMiJ9.eyJpZCI6ImY1NWQyNDhmLTUzZGQtNGQ1Mi05ODM1LTcxMjQ1OGVjYzE3MSIsImRhdGEiOnt9LCJyYW5kb20iOiIwN2QyZTkwMzcxZWQyNTk1ZWFmNmQwZWI3NDU0ZjlmOSJ9.LTiQ7FAl6HWslnZr4oCpdWKofIDMfMNAABQdvJvL2wEMruWaIcMoAo-a6-g1qZvA_yYDX-j2jkbQHiHHeCH0Qg.

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References

Al-Sabouni, N., M. Kucera, and D. N. Schmidt. 2007. Vertical niche separation control of diversity and size disparity in planktonic foraminifera. Mar. Micropaleontol. **63**: 75–90.

Anderson, O. R., N. R. Swanberg, and P. Bennett. 1983. Assimilation of symbiont-derived photsynthates in some solitary and colonial radiolaria. Mar. Biol. **77**: 265–269.

Berner, R. A. 2004. The phanerozoic carbon cycle: CO_2 and O_2. Oxford Univ. Press.

Biard, T., and others. 2016. In situ imaging reveals the biomass of giant protists in the global ocean. Nature **532**: 504–507.

Bird, C., and others. 2017. Cyanobacterial endobionts within a major marine planktonic calcifier (*Globigerina bulloides*, Foraminifera) revealed by 16S rRNA metabarcoding. Biogeosciences **14**: 901–920.

Brombacher, A., P. A. Wilson, and T. H. Ezard. 2017. Calibration of the repeatability of foraminiferal test size and shape measures with recommendations for future use. Mar. Micropaleontol. **133**: 21–27.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. Ecology **85**: 1771–1789.

Burke, J. E., and P. M. Hull. 2017. Effect of gross morphology on modern planktonic foraminiferal test strength under compression. J. Micropalaeontol. **36**: 174–182. doi:10.1144/jmpaleo2016-007

Burke, J. E., W. Renema, R. Schiebel, and P. M. Hull. 2020. Three-dimensional analysis of inter-and intraspecific variation in ontogenetic growth trajectories of planktonic foraminifera. Mar. Micropaleontol. **155**: 101794.

Caron, D. A., A. F. Michaels, N. R. Swanberg, and F. A. Howse. 1995. Primary productivity by symbiont-bearing planktonic sarcodines (Acantharia, Radiolaria, Foraminifera) in surface waters near Bermuda. J. Plankton Res. **17**: 103–129. doi:10.1093/plankt/17.1.103

Chaisson, W. 2003. Vicarious living: Pliocene menardellids between an isthmus and an ice sheet. Geology **31**: 1085–1088.

Davis, C. V., E. B. Rivest, T. M. Hill, B. Gaylord, A. D. Russell, and E. Sanford. 2017. Ocean acidification compromises a planktic calcifier with implications for global carbon cycling. Sci. Rep. **7**: 2225.

De Vargas, C., and others. 2015. Eukaryotic plankton diversity in the sunlit ocean. Science **348**: 1261605.

DeLong, J. P., J. G. Okie, M. E. Moses, R. M. Sibly, and J. H. Brown. 2010. Shifts in metabolic scaling, production, and efficiency across major evolutionary transitions of life. Proc. Natl. Acad. Sci. USA **107**: 12941–12945.

Dodds, P. S., D. H. Rothman, and J. S. Weitz. 2001. Re-examination of the "3/4-law" of metabolism. J. Theor. Biol. **209**: 9–27.

Elder, L. E., A. Y. Hsiang, K. Nelson, L. C. Strotz, S. S. Kahanamoku, and P. M. Hull. 2018. Sixty-one thousand recent planktonic foraminifera from the Atlantic Ocean. Sci. Data **5**: 180109.

Finkel, Z. V., J. Beardall, K. J. Flynn, A. Quigg, A. V. Rees, and J. A. Raven. 2010. Phytoplankton in a changing world: Cell size and elemental stoichiometry. J. Plankton Res. **32**: 119–137. doi:10.1093/plankt/fbp098

Gaskell, D. E., M. D. Ohman, and P. M. Hull. 2019. Zooglider-based measurements of planktonic foraminifera in the California Current System. J. Foraminifer. Res. **49**: 390–404.

Geslin, E., N. Risgaard-Petersen, F. Lombard, E. Metzger, D. Langlet, and F. Jorissen. 2011. Oxygen respiration rates of benthic foraminifera as measured with oxygen microsensors. J. Exp. Mar. Biol. Ecol. **396**: 108–114.

Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov. 2001. Effects of size and temperature on metabolic rate. Science **293**: 2248–2251.

Glazier, D. S. 2005. Beyond the "3/4-power law": Variation in the intra-and interspecific scaling of metabolic rate in animals. Biol. Rev. **80**: 611–662.

Glazier, D. S. 2009. Metabolic level and size scaling of rates of respiration and growth in unicellular organisms. Funct. Ecol. **23**: 963–968.

Goetz, E. J., M. Greco, H. B. Rappaport, A. K. M. Weiner, L. M. Walker, S. Bowser, S. Goldstein, and L. A. Katz. 2022. Foraminifera as a model of the extensive variability in genome dynamics among eukaryotes. Bioessays **44**: e2100267. doi:10.1002/bies.202100267

Hannah, F., A. Rogerson, and J. Laybourn-Parry. 1994. Respiration rates and biovolumes of common benthic foraminifera (protozoa). J. Mar. Biol. Assoc. UK **74**: 301–312.

Hatton, I. A., A. P. Dobson, D. Storch, E. D. Galbraith, and M. Loreau. 2019. Linking scaling laws across eukaryotes. Proc. Nat. Acad. Sci. USA **116**: 201900492.

Heim, N. A., and others. 2017. Hierarchical complexity and the size limits of life. Proc. R. Soc. B Biol. Sci. **284**: 20171039.

Hemmingsen, A. M. 1960. Energy metabolism as related to body size and respiratory surface, and its evolution. Rep. Steno Mem. Hosp. **13**: 1–110.

Hsiang, A. Y., and others. 2019. Endless Forams: >34,000 modern planktonic foraminiferal images for taxonomic training and automated species recognition using convolutional neural networks. Paleoceanog. Paleoclimatol. **34**: 1157–1177.

Hull, P. M., K. J. Osborn, R. D. Norris, and B. H. Robison. 2011. Seasonality and depth distribution of a mesopelagic foraminifer, *Hastigerinella digitata*, in Monterey Bay, California. Limnol. Oceanogr. **56**: 562–576. doi:10.4319/lo.2011.56.2.0562

Jonkers, L., and M. Kučera. 2015. Global analysis of seasonality in the shell flux of extant planktonic Foraminifera. Biogeosciences **12**: 2207–2226. doi:10.5194/bg-12-2207-2015

Jonkers, L., and M. Kučera. 2017. Quantifying the effect of seasonal and vertical habitat tracking on planktonic foraminifera proxies. Clim. Past **13**: 573–586.

19395590, 2025, 2, Downloaded from https://aslopubs.onlinelibrary.wiley.com/doi/10.1002/lno.12770 by Department Of Geological Sciences, Wiley Online Library on [24/02/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Jørgensen, B. B., J. Erez, P. Revsbech, and Y. Cohen. 1985. Symbiotic photosynthesis in a planktonic foraminiferan, *Globigerinoides sacculifer* (Brady), studied with microelectrodes 1. Limnol. Oceanogr. **30**: 1253–1267.

Kaiho, K., K. Takeda, M. R. Petrizzo, and J. C. Zachos. 2006. Anomalous shifts in tropical Pacific planktonic and benthic foraminiferal test size during the Paleocene–Eocene thermal maximum. Palaeogeog. Palaeoclimatol. Palaeoecol. **237**: 456–464.

Kazhdan, M., and H. Hoppe. 2013. Screened poisson surface reconstruction. ACM Trans. Graph. **32**: 29.

Knect, N. S., and others. 2023. The impact of zooplankton calcifiers on the marine carbon cycle. Global Biogeochem. Cycles **37**: e2022GB007685. doi:10.1029/2022GB007685

Knoll, A. H., and R. K. Bambach. 2000. Directionality in the history of life: Diffusion from the left wall or repeated scaling of the right? Paleobiology **26**: 1–14.

Laget, M., N. Llopis-Monferrer, J.-F. Maguer, A. Leynaert, and T. Biard. 2022. Elemental content allometries and silicon uptake rates of planktonic Rhizaria: Insights into their ecology and role in biogeochemical cycles. Limnol. Oceanogr. **68**: 439–454. doi:10.1002/lno.12284

Locarnini, R. A., and others. 2013. World Ocean atlas 2013, volume 1: Temperature, p. 73. *In* NOAA Atlas NESDIS. US Department of Commerce National Oceanic and Atmospheric Association.

Lombard, F., J. Erez, E. Michel, and L. Labeyrie. 2009. Temperature effect on respiration and photosynthesis of the symbiont-bearing planktonic foraminifera *Globigerinoides ruber*, *Orbulina universa*, and *Globigerinella siphonifera*. Limnol. Oceanogr. **54**: 210–218.

Manno, C., and A. K. Pavlov. 2013. Living planktonic foraminifera in the Fram Strait (Arctic): Absense of diel vertical migration during the midnight sun. Hydrobiologia **721**: 1–11. doi:10.1007/s10750-013-1669-4

Mansour, J. S., A. Norlin, N. L. Monferrer, S. L'Helguen, and F. Not. 2021. Carbon and nitrogen content to biovolume relationships for marine protist of the Rhizaria lineage (Radiolaria and Phaeodaria). Limnol. Oceanogr. **66**: 1703–1717. doi:10.1002/lno.11714

Maurer, B. A., and P. A. Marquet. 2013. Processes responsible for patterns in body mass distributions, p. 168–186. *In* Smith, F. A. and S. K. Lyons [eds.]. Animal body size: linking pattern and process across space, time, and taxonomic group. University of Chicago Press, 280 pp.

Meilland, J., H. Howa, C. Lo Monaco, and R. Schiebel. 2016. Individual planktic foraminifera protein biomass affected by trophic conditions in the Southern Indian Ocean [30° S-60° S]. Mar. Micropaleontol. **124**: 63–74.

Meilland, J., and others. 2019. Highly replicated sampling reveals no diurnal vertical migration but stable species-specific vertical habitats in planktonic foraminifera. J. Plankton Res. **41**: 127–141. doi:10.1093/plankt/fbz002

Michaels, A. F., D. A. Caron, N. R. Swanberg, F. A. Howse, and C. M. Michaels. 1995. Planktonic sarcodines (Acantharia, Radiolaria, Foraminifera) in surface waters near Bermuda: Abundance, biomass and vertical flux. J. Plankton Res. **17**: 131–163.

Ridgwell, A., and R. E. Zeebe. 2005. The role of the global carbonate cycle in the regulation and evolution of the Earth system. Earth Planet. Sci. Lett. **234**: 299–315.

Rink, S., M. Kühl, J. Bijma, and H. Spero. 1998. Microsensor studies of photosynthesis and respiration in the symbiotic foraminifer *Orbulina universa*. Mar. Biol. **131**: 583–595.

Schiebel, R., and C. Hemleben. 2000. Interannual variability of planktic foraminiferal populations and test flux in the eastern North Atlantic Ocean (JGOFS). Deep-Sea Res. II Top. Stud. Oceanogr. **47**: 1809–1852.

Schiebel, R., and C. Hemleben. 2017. Planktic foraminifers in the modern ocean. Springer.

Schiebel, R., and A. Movellan. 2012. First-order estimate of the planktic foraminifer biomass in the modern ocean. Earth Syst. Sci. Data **4**: 75–89.

Schmidt, D. N., D. Lazarus, J. R. Young, and M. Kucera. 2006. Biogeography and evolution of body size in marine plankton. Earth Sci. Rev. **78**: 239–266. doi:10.1016/j.earscirev.2006.05.004

Schmidt, D. N., S. Renaud, J. Bollmann, R. Schiebel, and H. R. Thierstein. 2004*a*. Size distribution of Holocene planktic foraminifer assemblages: Biogeography, ecology and adaptation. Mar. Micropaleontol. **50**: 319–338.

Schmidt, D. N., H. R. Thierstein, J. Bollmann, and R. Schiebel. 2004*b*. Abiotic forcing of plankton evolution in the Cenozoic. Science **303**: 207–210.

Stukel, M. R., T. Biard, J. Krause, and M. D. Ohman. 2018. Large Phaeodaria in the twilight zone: Their role in the carbon cycle. Limnol. Oceanogr. **63**: 2579–2594.

Takagi, H., and others. 2019. Characterizing photosymbiosis in modern planktonic foraminifera. Biogeosciences **16**: 3377–3396.

Tang, E. P., and R. H. Peters. 1995. The allometry of algal respiration. J. Plankton Res. **17**: 303–315.

Travis, J. L., J. F. Kenealy, and R. D. Allen. 1983. Studies on the motility of the foraminifera. II. The dynamic microtubular cytoskeleton of the reticulopodial network of *Allogromia laticollaris*. J. Cell Biol. **97**: 1668–1676. doi:10.1083/jcb.97.6.1668

Wade, B. S., and R. K. Olsson. 2009. Investigation of pre-extinction dwarfing in Cenozoic planktonic foraminifera. Palaeogeogr. Palaeoclimatol. Palaeoecol. **284**: 39–46.

Ward, B. A., S. Dutkiewicz, and M. J. Follow. 2013. Modelling spatial and temporal patterns in size-structured marine plankton communities: Top-down and bottom-up controls. J. Plankton Res. **36**: 31–47. doi:10.1093/plankt/fbt097

Ward, B. A., and M. J. Follows. 2016. Marine mixotrophy increases trophic transfer efficiency, mean organism size, and vertical carbon flux. Proc. Natl. Acad. Sci. USA **113**: 2958–2963.

19395590, 2025, 2, Downloaded from https://aslopubs.onlinelibrary.wiley.com/doi/10.1002/lno.12770 by Department Of Geological Sciences, Wiley Online Library on [24/02/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

West, G. B., J. H. Brown, and B. J. Enquist. 1997. A general model for the origin of allometric scaling laws in biology. Science **276**: 122–126.

West, G. B., J. H. Brown, and B. J. Enquist. 1999. The fourth dimension of life: Fractal geometry and allometric scaling of organisms. Science **284**: 1677–1679.

Worden, A. Z., M. J. Follows, S. J. Giovannoni, S. Wilken, A. E. Zimmerman, and P. J. Keeling. 2015. Rethinking the marine carbon cycle: Factoring in the multifarious lifestyles of microbes. Science **347**: 1257594.

Young, J. R., B. S. Wade, and B. T. Huber. 2017. pforams@mikrotax website.

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Conflict of Interest

None declared.

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