Vertical distribution of planktic foraminifera through an Oxygen Minimum Zone: how assemblages and test morphology reflect oxygen concentrations

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Abstract

Oxygen-depleted regions of the global ocean are rapidly expanding, with important implications for global biogeochemical cycles. However, our ability to make projections about the future of oxygen in the ocean is limited by a lack of empirical data with which to test and constrain the behavior of global climatic and oceanographic models. We use depth-stratified plankton tows to demonstrate that some species of planktic foraminifera are adapted to life in the heart of the pelagic Oxygen Minimum Zone (OMZ). In particular, we identify two species, *Globorotaloides hexagonus* and *Hastigerina parapelagica*, living within the Eastern Tropical North Pacific OMZ. The tests of the former are preserved in marine sediments and could be used to trace the extent and intensity of low-oxygen pelagic habitats in the fossil record. Additional morphometric analyses of *G. hexagonus* show that tests found in the lowest oxygen environments are larger, more porous, less dense, and have more chambers in the final whorl. The association of this species with the OMZ and the apparent plasticity of its test in response to ambient oxygenation invites the use of *G. hexagonus* tests in sediment cores as potential proxies for both the presence and intensity of overlying OMZs.

1. Introduction

Oxygenation in the oceans is temporally and spatially variable, and is controlled by physical factors like ventilation, as well as biotic factors such as photosynthesis and respiration. Oxygen Minimum Zones (OMZs), where dissolved oxygen can reach undetectable levels, are found in mid-waters (i.e., water depths of 100s to 1000s of meters) in some regions of the global ocean. They are often associated with Eastern Boundary Currents, and other upwelling regions, where surface productivity, and thus sub-surface respiration, is high and ventilation of intermediate waters is low. The presence and extent of dysoxic and anoxic waters and ecosystems have an outsized influence on global biogeochemical cycling (Gruber et al., 2008; DeVries et al., 2012; Breitburg et al., 2018), making the ongoing expansion and intensification of OMZs (Stramma et al., 2008; Keeling et al., 2009; Stramma et al., 2010; Levin, 2017; Schmidtko et al., 2017; Breitburg et al., 2108) of critical importance to future ocean health. Despite this, there are limited geologic records with which to constrain long-term change in pelagic OMZ environments and, consequently, considerable uncertainty in projections of future OMZs (Stramma et al., 2012; Levin, 2017).

Existing tools for detecting the presence and intensity of OMZs on geological time scales have severe limitations. Proxies for marine oxygenation currently fall into three broad categories: 1) those that are indicative of productivity, nutrient utilization, and preservation, such as carbon accumulation and stable isotopes of carbon and nitrogen; 2) benthic faunal assemblages; and 3) sedimentary indicators such as laminations or accumulation of redox-sensitive trace elements in sediments. Proxies of the first type are indirect indicators of OMZs and cannot deconvolve oxygenation and productivity. Although OMZs are generally associated with highly productive environments today, the formation of an OMZ reflects a combination of factors including source water oxygenation and local processes like nutrient cycling, primary productivity, and organic matter sinking and degradation rates. Proxies of the second and third types function only when a zone of low oxygen intersects the seafloor, which presents a significant geographic limitation. Thus, there is a real need for the development and application of new environmental and oxygenation proxies for OMZs in order to enhance the paleoceanographic toolkit for understanding long-term change in these critical environments.

The tests of planktic foraminifera form the basis of some of the most widely used paleoceanographic proxies for reconstructing past pelagic and near-surface environments (see Kucera, 2007; Katz et al., 2010 for reviews). Here we explore the potential of planktic foraminifera as proxies for the extent and intensity of OMZ environments. Several lines of evidence suggest that planktic foraminifera may occur in low oxygen environments. Laboratory experiments with the species *Orbulina universa* and *Globigerina bulloides* show that both can survive and calcify under low oxygen conditions (Kuroyanagi et al., 2013), despite living in the ocean mixed layer (e.g., Emiliani, 1954; Fairbanks et al., 1982; Field, 2004; Birch et al., 2013; Wejnert et al., 2013) where they are unlikely to experience sustained low oxygen. Moreover, multiple species have been hypothesized as low oxygen specialists: the rarely fossilized species, *Hastigerina digitata,* has been observed *in situ* within low oxygen waters (Hull et al., 2011), *Globorotaloides hexagonus* has been collected in plankton tows associated with low oxygen water masses (Ortiz et al., 1995; Birch et al., 2013), and numerous digitate foraminifers are associated with low oxygen waters in the fossil record (Coxall et al., 2007). However, without a systematic understanding of species distributions relative to the OMZ, foraminifera-based oxygen proxies can be interpreted only as reflecting a general “sub-surface” environment.

OMZs are home to specialized groups of organisms capable of tolerating extraordinarily low dissolved oxygen levels. A growing body of literature has focused on the distributions of larger zooplankton (e.g., Wishner et al., 1995; Wishner et al., 1998; Escribano et al., 2009; Wishner et al., 2013; Maas, et al., 2014; Wishner et al., 2018; 2020a), microbial (e.g., Duret et al., 2015; Podlaska et al., 2012; Medina Faull et al. 2020), and viral (Cassman, et al., 2012) populations that live and cycle nutrients within the OMZ, but no equivalent study has targeted planktic foraminifera. However, benthic foraminifera are widely understood to be among the extremophiles that thrive in the OMZ through special adaptations (Levin, 2003; Bernhard and Bowser, 2008; Glock et al., 2012, 2018, 2019; LeKieffre et al., 2017; Gooday, et al. 2020). Benthic foraminiferal adaptations include nitrate respiration (Risgaard-Petersen et al., 2006; Hogsland et al., 2008; Pina-Ochoa et al., 2010; Bernhard et al., 2011, 2012a, 2012b; Woehle et al., 2018, Orsi et al., 2020), dormancy (Bernhard & Alve, 1996; Ross & Hallock, 2016; LeKieffre et al., 2017), and morphologies consistent with facilitating increased gas exchange (Bernhard, 1986; Perez-Cruz & Machain-Castillo, 1990; Glock et al., 2011, 2012; Kuhnt et al., 2013, 2014; Rathburn et al., 2018). There they are important contributors to benthic food webs (e.g., Nomaki et al., 2008; Enge et al., 2014), and are used as indicators of low-oxygen environments (e.g., Kaiho, 1994; Bernhard et al., 1997; Cannariato et al., 1999; Jorissen et al., 2007; Ohkushi et al., 2013).

The goals of this study are to describe and quantify the abundance of living planktic foraminifera above and within a modern OMZ, to test:

1) whether modern planktic foraminifera are present within the OMZ;
2) whether specific species are preferentially or exclusively living within the OMZ; and
3) whether morphological traits of OMZ-dwelling foraminifera reflect oxygenation levels in the environments from which they are recovered

1.1. The Eastern Tropical North Pacific Oxygen Minimum Zone

The Eastern Tropical Pacific is home to the world's largest OMZ, fueled by a combination of high coastal and equatorial productivity and poorly ventilated sub-thermocline waters (Paulmier and Ruiz-Pino, 2009; Fiedler and Talley, 2006). The OMZ in the Eastern Tropical North Pacific (ETNP) is associated with both a deep particle maximum and a secondary nitrite maximum, indicative of reduction of nitrate to nitrite within the OMZ (Garfield et al., 1983; Buchwald, et al., 2015; Medina Faull et al., 2020).

The region sampled here is located west of the Baja peninsula and removed from the regions of greatest surface productivity, towards the northern reaches of the low oxygen tongue of the ETNP OMZ (Fig. 1; Supplemental Fig. 1).

2. Methods

2.1 Plankton Tow Collections

Day and night vertically stratified and horizontal MOCNESS (Multiple Opening/Closing Net and Environmental Sensing System) tows were taken onboard the *R/V Sikuliaq.* An updated MOCNESS system, 1 m^2 in diameter, with 222 µm mesh nets and a Sea-Bird SBE911 CTD with updated software in place of the original sensors was used (see Wishner et al., 2018). All tows were carried out within relatively close proximity to one another (21° N, 117° W) between January 26th and February 7th 2017 (Wishner et al, 2018, 2020a, 2020b). This study utilized a total of 8 tows, with each tow including the deployment of eight to nine nets to sample a defined depth interval. We use six depth-stratified vertical profiles (#716, #718, #720, #721, #722, #725) that sampled portions of the 0 – 1000 m water column, and two horizontal tows that sampled the OMZ at ~425 m depth (#724, #726) (Wishner et al. 2018, 2020a, 2020b). Vertical strata sampled by each net were 25 m to 200 m thick, depending on the tow and depth (see Supplemental Table 1 or Wishner et al. 2019, 2020b for net strata depths and volume filtered for each net in). In horizontal tows, each net sampled a distance of about 1 km (Wishner et al. 2018). Environmental data were collected with the MOCNESS CTD sensors simultaneous with plankton collections. For oxygen, a Sea-Bird SBE43 sensor was used. All plankton samples were stored in sodium borate-buffered seawater and formalin at sea. Isolation of foraminifera from samples occurred in 2017-2019 at the University of Rhode Island. Between 3/10^{ths} and 1/125^{ths} of material in a net was examined, depending upon abundance of foraminifera, and all intact tests were isolated from the split.

Foraminifera were identified to the species level by light microscope at the University of South Carolina and Yale University. Some tests (9% of the total observed) were either damaged or, more rarely, appeared to be juvenile forms, such that no species-level identification could be assigned. Due to excellent tissue preservation, the presence or absence of foraminiferal cytoplasm was identifiable, and foraminifera were classified as either "live," based on the presence of cytoplasm, or "dead" in the absence of cytoplasm (Fig. 2). Although, preservation was excellent in most tows, some dissolution was observed in 3 shallow (< 100 m) nets. These have been excluded from further analyses, to prevent skewing assemblages towards more dissolution-resistant taxa. We note that these 3 nets were exceptionally high in organic matter and that organic matter degradation was the likely cause of dissolution despite buffering and a relatively short storage interval. The organic matter concentration and preservation concerns in these 3 nets do not apply to the other nets considered in this study.

2.2 Counting and Statistics

Total counts of foraminifera were adjusted for both the tow split analyzed as well as the total water volume filtered and are presented as individuals m^{-3} or as relative abundance. Diversity was calculated using the 'diversity' function and Shannon index in the R ‘vegan’ package (Oksanen, et al., 2013). All other statistics were carried out in the base package in R (R Core Team, 2017).

2.3 Morphological Analyses

All individuals of the species *G. hexagonus* were weighed on a Mettler Toledo ultramicrobalance (± 1 μg) in the Yale Analytical and Stable Isotope Center and imaged on a Leica DM6000 light microscope at Yale University. Measurements were made in ImageJ by identifying a flat section of the F (final/ultimate) or F-1 (penultimate) chamber minimally affected by glare and measuring the total area of the section and the total area of section excluding pores. All other morphometric measurements were made using the AutoMorph software (Hsiang et al., 2016).

Porosity is reported as the percentage of test surface area comprised of pores. Size-normalized weight was assessed using the area density method described by Marshall et al. (2013), with the weight of each test normalized to its 2-dimensional surface area. The compactness of tests was assessed as the ratio of the 2-dimensional surface area to the area of a circle (the most compact possible geometry) of the same perimeter. The aspect ratio was defined as the ratio between the height (longest dimension) and width (perpendicular to the longest dimension) as measured in the AutoMorph software (Hsiang et al., 2016). Test size was ascertained by length, surface area, and test perimeter. As surface area and test perimeter were used in deriving compactness and size-normalized weights, respectively, and all parameters are interrelated, we refer to the longest test dimension when referring to size.

Micro CT-scans were generated at the Naturalis Biodiversity Center using a Zeiss Xradia 520 Versa micro-CT scanner aiming at a voxel size of 0.627 µm; realized resolution varied from 0.4-0.7 µm. Scans were made at 90 kV using 20X optical magnification, and were reconstructed using the Zeiss software. Micro CT scans were processed and analyzed in VG Studio, with volumes assessed by creating a mesh wrap in the MeshLab software (Cignoni et al., 2008) as described in Burke et al. (2020).

3. Results

3.1 Hydrological Data from Tows

Plankton tows sampled depths between 0 and 1000 m, across dissolved oxygen levels between 0.03 and 4.93 ml L^{-1} and temperatures ranging from 4.5 to 22.9° C. Although small-scale oxygen features and their depth relative to the oxycline and OMZ varied somewhat (Wishner et al., 2018, 2020b), the overall hydrographic structure of the water column was consistent across tows. A warm, oxygenated surface mixed layer overlaid an extremely oxygen depleted OMZ, with gradual cooling at increasing depth below the thermocline. The upper oxycline (the zone of rapidly decreasing oxygen) was located between 150 and 250 m water depth, with its upper boundary at the thermocline (Fig. 3-5). Categorization of oxygen levels follows the discussion of Hofmann et al. (2011) and Moffitt et al. (2015). We defined environments with $[O_2] > 2.45$ ml L^{-1} (109 µM) as oxic, between 2.45 ml L^{-1} and 1.4 ml L^{-1} (63 µM) as transitional ("mild hypoxia" in previous literature), and < 1.4 ml L^{-1} as OMZ conditions ("hypoxia" and below). Previous authors have distinguished between intermediate (0.5-1.4 ml L^{-1}) and severe hypoxia (< 0.5 ml L^{-}

^{1}; 22 μM), but we have collapsed these to 'hypoxia' as foraminiferal assemblages did not differ between the two categories (see Supplemental Table 1).

3.2 Live Foraminiferal Assemblages

Assemblages of live foraminifera, described using the definitions of oxygen outlined above, can be divided into three categories: those living in oxic conditions (minimum [O_2] within a net > 2.45 ml L^{-1}), OMZ conditions (maximum [O_2] within a net < 1.4 ml L^{-1}), and transitional (nets sampling between these two extremes). The oxic group was the shallowest, with the deepest tow included in this category extending to only 150 m water depth. These tows had the densest population of foraminifera with 3.4 individuals m^{-3} and the greatest diversity with a mean Shannon index value of 1.3 (ranging from 1.2 to 1.5 across 5 nets). In this relatively shallow, oxic environment, the assemblage was dominated by *Trilobatus sacculifer* (74.6%) followed by *Globigerinoides ruber* (5.4%), *Hastigerina pelagica* (5.0%), *Globigerinella siphonifera* (4.0%), *Orbulina universa* (3.5%), *Globorotaloides hexagonus* (3.1%), and *Globigerina bulloides* (1.9%). The species *Hastigerina parapelagica*, *Globorotalia menardii*, *Globoquadrina conglomerata, Pulleniatina obliquiloculata*, and *Globorotalia tumida* were all found in low abundance (<1%) (Table 1; Fig. 6).

Foraminifera from the OMZ assemblage were found in nets collected below 250 m water depth, and occurred at much lower densities of 0.2 individuals m^{-3}. This assemblage was heavily dominated by *G. hexagonus* (86.1%), followed by *G. sacculifer* (3.6%), *H. parapelagica* (2.0%), *H. pelagica* (1.4%), and *G. menardii* (0.8%). The species *G. ruber*, *O. universa*, *G. siphonifera, G. glutinata, G. conglobatus, P.*

obliquiloculata, and *G. bulloides* were found in low abundance (<1%) (Table 1; Fig. 6). The OMZ assemblages were also the least diverse, with a mean Shannon index value of 0.9 (ranging from 0.8 to 1.0 in 54 nets).

The transitional assemblages primarily represented depths between 100 and 250 m and had the lowest density of foraminifera with 0.1 individuals m^{-3}. There was one net that sampled 800 to 1000 m and would also fall into this oxygen categorization, but was excluded from analyses as it contained only a few *G. ruber* (< 0.01 individuals m^{-3}) which were likely dead, and cannot be readily compared to the upper oxycline habitat of other transitional samples. The transitional assemblage was nearly as diverse as the oxic assemblage with a Shannon index of 1.2 (ranging from 1.1 to 1.2 across 4 nets). It was composed of *G. hexagonus* (40.7%), *G. sacculifer* (22.1%), *G. siphonifera* (9.6%), *G. conglomerata* (6.4%), *O. universa* (5.5%), *Globorotalia menardii* (5.0%), *H. pelagica* (3.9%), *G. conglobatus* (2.4%), and *S. dehiscens* (1.6%). A few other species, *H. parapelagica*, *C. nitida*, *G. ruber*, and *P. obliquiloculata*, were found in abundances < 1% (Table 1; Fig. 6).

3.3 Empty Test Foraminiferal Assemblages

Empty test assemblages mirrored living assemblages, with high species diversity (Shannon index > 1) at depths up to 400 m, after which diversity declined to Shannon index values between 0.5 and 1. An average of 0.2 empty tests m^{-3} were recovered for all tows. The majority of the empty test assemblage was made up of *G. sacculifer* (55.4%), followed by *H. pelagica* (11.7%), *G. ruber* (6.4%), *G. siphonifera* (6.0%), *G. hexagonus* (5.9%), and *O. universa* (5.1%). All other species comprised less than 2% of the assemblage. While every species occurring with cytoplasm was also found without cytoplasm, two species, *Hastigerina digitata* and *Neogloboquadrina dutertrei,* were identified in low abundances without cytoplasm, but were not observed with cytoplasm.

3.4 Morphological Variation in *G. hexagonus*

3.4.1 Porosity

Porosity of the final chamber in *G. hexagonus* was highly variable among individuals and among tows, ranging from 1.7% to 19.4% of the surface area measured by light microscope. Porosity decreased as oxygen increased, with the clearest relationship between the log of porosity and log of dissolved oxygen ($R^2 = 0.38$, p-value < 0.001). A comparison between porosity of the final chamber, measured by CT scan and light microscope, showed that CT measurements consistently demonstrated higher porosities (Fig. 7). This methodology allowed for non-destructive imaging of the inner test unobscured by later calcite growth, the ability to manipulate test orientation to reduce artifacts of test curvature, as well as higher resolution, and should be considered a more accurate measure of test porosity. A direct comparison of the two methods carried out on a subset of tests ($n = 31$) showed that the results from the two approaches are correlated ($R^2 = 0.37$, p-value < 0.001; Fig. 7), indicating that the less labor-intensive use of light-microscope measurements captures some of the same trend as the CT-based approach ($y= 0.23x + 2.64$). While the two methods are comparable in capturing a similar trend, the approaches are distinct enough that measurements by one method (light microscopy) are not sufficient to predict porosity as measured by another (CT scan). Final chamber porosity increased linearly with the size across individuals ($R^2 = 0.33$, p-value < 0.001), and with ontogeny within individuals (Fig. 8), demonstrating an interaction between size, ontogeny, and porosity.

3.4.2 Size and Chamber Number

Size decreased with the log of oxygen (Spearman's $\rho = -0.64$; p-value < 0.001). The largest change in size, as well as the largest change in size-normalized weight and chamber number, was a step change corresponding to oxygen levels between 0.1 and 0.2 ml L^{-1} (Fig. 9). The number of chambers visible in the final whorl ranged between 4 and 7 (net means between 4.8 and 6.1) and the largest change in mean chamber number also occurred between 0.1 and 0.2 ml L^{-1} O_2, with tests having a greater number of chambers in the final whorl in low oxygen tows (correlation of chamber number to log of average oxygen: Spearman's $\rho = -0.68$; p-value < 0.001; Fig. 9).

3.4.3 Size-normalized Weight

Globorotaloides hexagonus tests were light for their size, with individual test weights averaging just 7.7 μg, and ranging from 1 to 22 μg for tests sized between 297 and 631 μm in length. Size-normalized weight increased with oxygenation, especially below 0.2 ml L^{-1} O_2 (correlation of size-normalized weight to the log of oxygen: Spearman's $\rho = 0.52$; p-value < 0.001; Fig. 9). Size-normalized weight and porosity were correlated ($R^2 = 0.34$; p-value < 0.001), as were calcite volume and final chamber porosity measured in CT-scanned foraminifera ($R^2 = 0.18$; p-value < 0.001; Supplemental Fig. 2). Size-normalized weight is also dependent upon size (Henehan et al., 2017), although in our study the variance in size-normalized weight explained by size was low ($R^2 = 0.10$ p-value < 0.001).

3.4.4 Compactness and Aspect Ratio

We further tested the utility of test compactness and aspect ratios as potentially diagnostic of the morphological gradient observed. Although test compactness increased linearly with oxygenation ($R^2 = 0.03$ p-value $= 0.04$) and aspect ratio decreased linearly with the log of oxygen ($R^2 = 0.09$ p-value < 0.001), oxygenation accounted for very little of the variance in either parameter and they were not considered further.

4. Discussion

4.1 Distinct OMZ Community of Planktic Foraminifera

Live foraminifera obtained from vertical profiles with depth-stratified nets in the ETNP form three distinct pelagic assemblages associated with differing oxygen levels. The OMZ community, living at the lowest oxygen level, was typified by the presence and high relative abundance of the foraminifer *G. hexagonus*.

The shallow, oxic assemblage (< 150 m) of planktic foraminifera was relatively diverse and included species typical of the Pacific subtropical gyre (Eguchi et al., 1999; Kuroyanagi et al., 2002), with affinities for warmer sea surface temperatures and oligotrophic conditions. However, there was substantial variation between the three tows for which surface assemblages were available (#716, #721, and #725), with abundances in the upper 100 m varying from < 0.1 individuals m^{-3} (tow #716) to 3.0 individuals m^{-3} (tow #721) and 11.0 individuals m^{-3} (tow #725) (Fig. 3-5). In the latter two tows the majority of the assemblage was comprised of *T. sacculifer*, whereas in Tow #716, *G. menardii* was the most abundant species. A slightly shallower thermocline (compare Fig. 3 to Fig. 4 and 5) and deep chlorophyll maximum may be partially responsible for differing abundances. However, there may also be a lunar-associated reproductive response affecting abundance patterns. Tow #716 was taken during a waning moon, but tows #721 and #725 were taken during a waxing moon (USNO, accessed 10/10/2019). *Trilobatus sacculifer* reproduces on a lunar cycle, with the largest sizes reached just prior to reproduction during the full moon (Bijma et al., 1990; Erez et al., 1991; Kawahata et al., 2002; Lin et al., 2010; Jonkers et al., 2015; Venancio et al., 2016). As a result, more large individuals (> 222 μm) of this species were likely to be present in our nets just prior to a full moon (tows #721 and #725).

The OMZ assemblage was dominated by the species *G. hexagonus*, followed by *T. sacculifer* and *H. parapelagica*. Use of presence/absence of cytoplasm as an indicator for living foraminifera results in an overestimation of live individuals, as empty or post-reproductive individuals may retain some cytoplasm while live individuals cannot be devoid of cytoplasm. Thus, despite the presence of *T. sacculifer* in several OMZ samples, it is unlikely that this species, which has photosymbionts and a relatively shallow, photic zone habitat (Fairbanks et al., 1982; Ravelo & Fairbanks, 1992; Schiebel et al., 2004; Regenberg, et al., 2009; Birch et al., 2013; Rebotim et al., 2017), was resident in the deep OMZ. It is more likely that cytoplasm-bearing tests of *T. sacculifer* found below the photic zone are a consequence of their very high abundance in the surface ocean and reflected premature mortality and/or the retention of cytoplasm following reproduction. On the other hand, *G. hexagonus* and *H. parapelagica* comprised 88.1% of cytoplasm-bearing tests in OMZ nets, while only found in low abundances in surface assemblages. This suggests that these two species are truly endemic to deeper hypoxic waters.

The transitional assemblage was a mix between the well-oxygenated surface assemblage, with abundant *T. sacculifer*, and the deeper OMZ assemblage, composed primarily of *G. hexagonus*. This mix of species was almost certainly an artifact of the depth (and oxygen) range integrated within a single net (50-100 m thick strata) through the steep oxycline. However, the transitional assemblage also had two unique characteristics. The first was the presence of deeper-dwelling taxa, such as *G. conglomerata* and *G. menardii*, which were rare in most other nets. The second was the exceptionally low density of planktic foraminifera (mean of 0.1 individual per m^{-3} across 4 tows; Fig. 3-5). The low density of foraminifera in the oxycline is an interesting contrast to the vertical distributions of many metazoan species that often peak in abundance in the upper oxycline and decline in the core of the OMZ (Maas et al. 2014, Wishner et al., 1995, 2013, 2020b). Based on the mixed assemblage and low densities, we hypothesize that planktic foraminifera are largely absent from the upper oxycline, with populations restricted to either the oxygenated photic zone habitat above or the OMZ below. Whether this distributional pattern is related to physiological constraints, food resources, physical oceanographic mechanisms, or other environmental parameters is unknown and future sampling at higher vertical resolution through the oxycline is required to test these hypotheses.

4.2 *Globorotaloides hexagonus* as an OMZ Indicator Species

Globorotaloides hexagonus was consistently found within our low oxygen nets, though individuals were sparsely distributed (mean density of 0.2 individual m^{-3}), with peak abundances between 300-500 m depth in the core of the OMZ (Fig. 3-5; Supplemental Fig. 3-5). There was no evidence of diel vertical migration when comparing distributions in tows taken during the day (#718, #722, #724, #725, #726) and night (#716, #720, #721), in agreement with the lack of diel vertical migration observed in shallow-dwelling species (Meilland et al., 2019). Absence of large-scale migrations and a preference for extremely oxygen-depleted habitats indicate that the species is adapted to live for long periods of time, likely its entire lifespan, within extremely low oxygen conditions.

Globorotaloides hexagonus has previously been associated with deep, low oxygen water masses across the Indo-Pacific, including the Eastern North Pacific (Sautter & Thunell, 1991; Ortiz et al., 1996; Davis et al., 2016), Equatorial Pacific (Fairbanks et al., 1982; Rippert et al., 2016; Max et al., 2017; Rippert et al., 2017), the Peru-Chile margin (Marchant et al., 1998), and the Indian Ocean (Rao et al., 1989; Schiebel et al., 2004; Birch et al., 2013). The species is sometimes assumed to be extinct in the Atlantic, with recent identifications of *G. hexagonus* in Atlantic sediments explicitly used to date sediments as pre-Holocene or ascribed to taxonomic error (e.g., Kucera et al., 2005; Siccha & Kucera, 2017). However, the assumption of a basin-wide extinction appears poorly supported, and *G. hexagonus* tests were isolated from deep (500 – 3200 m) Atlantic sediment traps as recently as 2009-2013 (Smart et al., 2018). We hypothesize that *G. hexagonus* occupies low-oxygen mid-waters globally (i.e., in the Atlantic as well as the Indo-Pacific), but that its deep habitat and low abundance have biased observations away from identifications of *G. hexagonus* in the modern Atlantic. Altogether, the geographic distribution, presence of cytoplasm-bearing *G. hexagonus* in OMZ tows, and scarcity of *G. hexagonus* above the oxycline, strongly suggest that *G. hexagonus* lives preferentially, or even exclusively, within the OMZ. This species can be considered an indicator of an OMZ habitat and may be useful as an OMZ marker in sedimentary records.

We also found a second, less abundant, species, *H. parapelagica*, in association with low oxygen waters. This same morphology was previously observed *in situ* in low oxygen waters by Hull et al. (2011), and more recently by Gaskell et al. (2019), referred to as "*Hastigerina* spp." by the former and "*Hastigerina pelagica*" by the latter. Given the depth distribution and morphological variation observed here for *H. parapelagica,* we suspect that it is synonymous with the globally distributed "*Hastigerina pelagica*" genotype IIa, described by Weiner et al. (2012) and use the name *Hastigerina parapelagica* (Saito et al., 1976) as the senior synonym of *Hastigerina pelagica* genotype IIa (Weiner et al. 2012).

4.3 Morphological Variation in *G. hexagonus* Reflects Water Column Oxygenation

Globorotaloides hexagonus shares several morphological traits with low-oxygen associated benthic foraminifera including a flattened whorl maximizing its surface area/volume ratio at a given size and large pores (e.g., Bernhard, 1986). Both characters could serve to increase gas exchange and fulfill metabolic requirements in an oxygen-limited environment (Leutenegger & Hansen, 1979; Corliss, 1985). Unlike some digitate planktic foraminifera previously associated with deep and oxygen depleted environments

(Hull et al., 2011; Coxall et al., 2007; Gaskell et al., 2019), *G. hexagonus* is non-spinose, which may suggest that it is herbivorous or bacterivorous as described for other non-spinose foraminifera (Schiebel & Hemleben 2017; Bird et al., 2018), rather than dependent on live zooplankton as prey.

The tests of *G. hexagonus* in deeper, less oxygenated waters appeared more porous, larger, and less compact than those from shallower, more oxygenated environments. These observations, and the presence of *G. hexagonus* across a wide range of depths and oxygenation levels, led us to quantify the environmental correlates of morphological variation in porosity, size-normalized weight, size, chamber number and shape as potential proxies in paleo-environmental reconstructions. A high test porosity and high pore density have been widely associated with low oxygen environments in benthic foraminifera (Bernhard, 1986; Perez-Cruz & Machain-Castillo, 1990; Glock et al., 2011, 2012; Kuhnt et al., 2013, 2014; Rathburn et al., 2018) and in cultured planktic foraminifera (Kuroyanagi et al., 2013). These characteristics may play an important role in facilitating gas exchange (Leutenegger & Hansen, 1979; Corliss, 1985), and may represent a balance between the need for gas exchange and structural constraints (Richirt et al., 2019). However, increased porosity has also been associated with other parameters: increasing temperature (Bijma et al., 1990; Burke et al., 2018), decreasing nitrate availability (Glock et al.; 2011, 2018), and increasing test size (Burke et al., 2018). In the OMZ samples where *G. hexagonus* was found, porosity increased with both decreasing oxygen concentration and increasing test size, with the lowest oxygen conditions hosting the largest and most porous tests (Fig. 9). In contrast to this trend, porosity decreases through ontogeny in *G. hexagonus* with the most recent chamber being less porous than earlier chambers (Fig. 8). While the presence of a relationship between porosity of *G. hexagonus* and oxygenation is clear in our data set, any future efforts to quantify this relationship should target a population of exclusively post-reproductive individuals, using both light microscopy and CT imaging in addition to Scanning Electron Microscopy of the inner test walls. Neither temperature nor nitrate availability (used by some benthic foraminifera as an alternative terminal proton acceptor in very low oxygen environments; Risgaard-Petersen et al., 2006; Hogsland et al., 2008; Pina-Ochoa et al., 2010; Bernhard et al., 2011, 2012a, 2012b; Woehle et al., 2018), are likely to drive the observed variation in porosity as temperature was nearly constant (7.7-8.5 °C) across samples and nitrate availability increases with depth in the region (Podlaska et al., 2012; Buchwald et al., 2105; Medina Faull et al., 2020).

Tests collected at lower oxygen levels also had lower size-normalized weights, a property which negatively correlates with porosity. Size-normalized weight in planktic foraminifera has frequently been associated with changes in carbonate chemistry (i.e., Bijma et al., 2002; Russell et al., 2004; Marshall et al., 2013). As oxygen and DIC depth profiles in the ocean are inversely related, the OMZ is also a region of exceptionally high DIC (Paulmier et al., 2008, 2011). While no carbonate chemistry measurements are available in conjunction with our tows, calcite saturation state at equivalent latitudes in the Eastern Tropical South Pacific OMZ approaches 1, below which calcite dissolution is favored (Bates, 2018). Both an increase in porosity, as well as a decrease in size-normalized weight (whether due to porosity, a decrease in test thickness, or a combination of factors), is consistent with a reduction of overall calcification in low calcite saturation states associated with the OMZ, where precipitation and maintenance of a test may be more metabolically expensive.

Tests collected from the lowest oxygen conditions tended to be larger and less compact, with more chambers visible in the final whorl (Figure 10). Both decreased compactness and the addition of more lobes via increased chamber number have the effect of increasing the surface area/volume ratio at a given size, which could facilitate increased gas exchange via diffusion. However, the increase in size with decreased oxygen availability is such that larger *G. hexagonus* in low oxygen environments would still have lower surface/volume ratios than smaller individuals from more oxygenated environments (Supplemental Fig. 6). It may be that increased porosity in larger individuals is able to partially compensate for this decrease in surface area/volume ratios.

Although the increase in size at low oxygen levels appears enigmatic, there are several potential reasons that could account for this pattern. One benefit could be a larger surface area for interception of food. Alternatively, increased size (cell volume) has been associated with greater capacity for denitrification as in some benthic foraminifera (Glock et al., 2019). An inconsistent relationship between surface area/volume ratios and oxygenation has also been observed in several facultative anaerobic species of benthic foraminifera, with only two of the four species studied showing the expected decrease in size with decreasing oxygen levels (Keating-Bitonti and Payne, 2017). Whether *G. hexagonus* possesses physiological strategies that allow it to function as a facultative anaerobe cannot be determined at this point. However, the combination of increased size (potentially indicative of anaerobic strategies) and increased porosity and morphologies apparently optimized for increasing aerobic capacity in low oxygen environments, suggest a complex physiology. A decrease in porosity with ontogeny could even hint at a shift in physiology over the lifespan of an individual (Fig. 8). Further unraveling the environmental pressures driving test morphology in *G. hexagonus* will require a greater understanding of the species' ecology.

5 Conclusions

Vertically-stratified plankton tows taken through the Eastern Tropical North Pacific show that distinct assemblages of planktic foraminifera live above and within the OMZ, and that a depauperate fauna occupies the upper oxycline. Two species, *G. hexagonus* and *H. parapelagica,* were found preferentially or exclusively within the OMZ. Several aspects of test morphology in *G. hexagonus* varied in response to ambient oxygen levels. Some morphological features may be associated with facilitating gas exchange (i.e., porosity, chamber arrangement) or decreasing expenditure on calcification (size-normalized weight, porosity) under the low oxygen and/or carbonate saturation state conditions of the OMZ. The function of other morphological trends, like size, remain enigmatic. Abundance patterns and the co-variation of specific morphological features with oxygenation levels in *G. hexagonus* tests could be used to reconstruct changes in OMZ environments, providing an additional proxy record of the mid-water OMZ in which these foraminifera lived. As the species appears to be living primarily or exclusively in the OMZ, recovery of *G. hexagonus* tests from sediments would be a strong indication of low-oxygen mid-waters. Moreover, large tests with high porosity, low size-normalized weight and more chambers in the final whorl could be interpreted as having calcified closer to the core of the OMZ than their smaller, less porous conspecifics.

Data Availability

All data associated with this article is available in the supplement or has been previously published and archived on the BCO-DMO database found at http://lod.bco-dmo.org/id/dataset/755088.

Competing Interests

The authors declare that they have no conflict of interest.

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Tables

Species	% of Oxic Assemblage	% of Transitional Assemblage	% of OMZ Assemblage
T. sacculifer	74.6	22.1	3.6
G. ruber	5.4	0.6	0.3
H. pelagica	5.0	3.9	1.4
G. siphonifera	4.0	9.6	1.0
O. universa	3.5	5.5	0.1
G. hexagonus	3.1	40.7	86.1
G. bulloides	1.9	0.0	0.1
H. parapelagica	0.3	0.8	2.0
G. menardii	0.9	5.0	0.8
G. conglomerata	1.0	6.4	0.1
P. obliquiloculata	0.2	0.7	0.7
G. tumida	0.2	0.0	<0.1
G. glutinata	0.0	0.0	3.2
H. digitata	0.0	0.0	0.0
G. conglobatus	0.0	2.4	0.4
S. dehiscens	0.0	1.6	0.3
C. nitida	0.0	0.7	0.0
G. calida	0.0	0.0	<0.1
G. falconensis	0.0	0.0	0.0
N. dutertrei	0.0	0.0	0.0

Table 1. The relative abundance of planktic foraminifera within oxygen defined assemblages: an oxic assemblage (minimum O_2 within a net $O_2 > 2.45$ ml L^{-1}), transitional assemblage, and OMZ assemblage (maximum O_2 within a net < 1.4 ml L^{-1}).

Figures

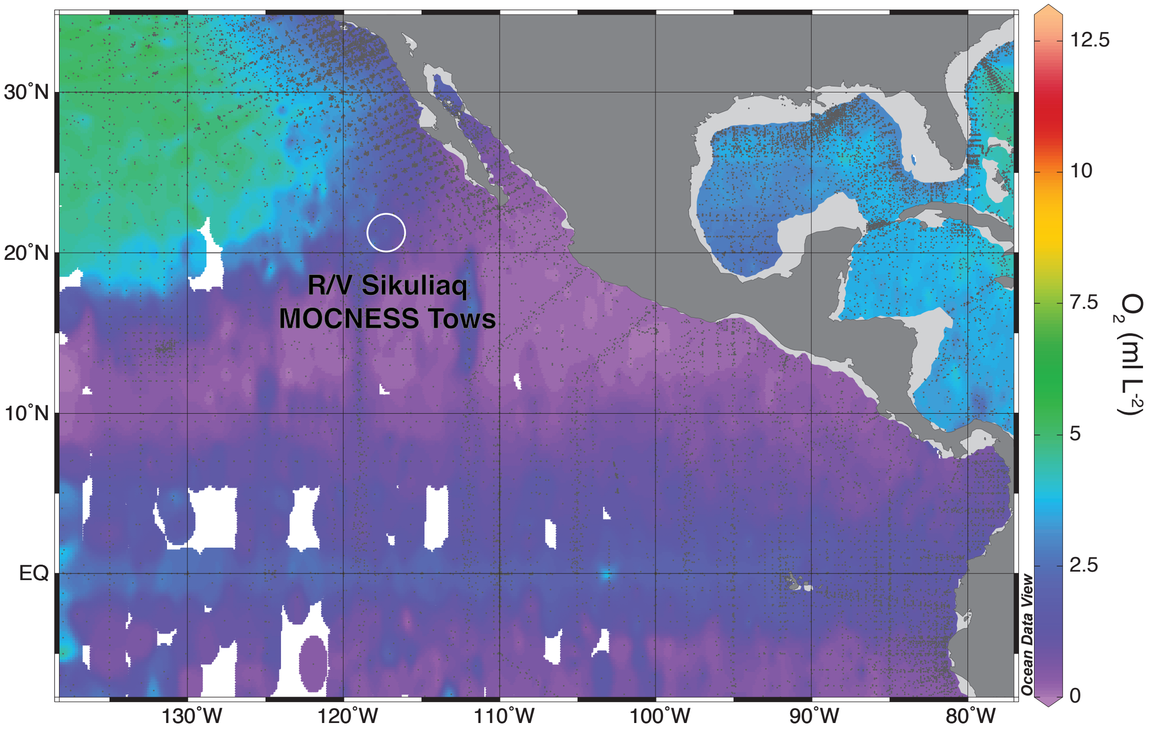


Fig. 1. Location of MOCNESS tows (white circle) taken onboard the *R/V Sikuliaq* shown on a map of dissolved oxygen measured at 200 m below the sea surface. Oxygen data are aggregated from the World Ocean Atlas (Garcia et al., 2018) and plotted using Ocean Data Viewer.

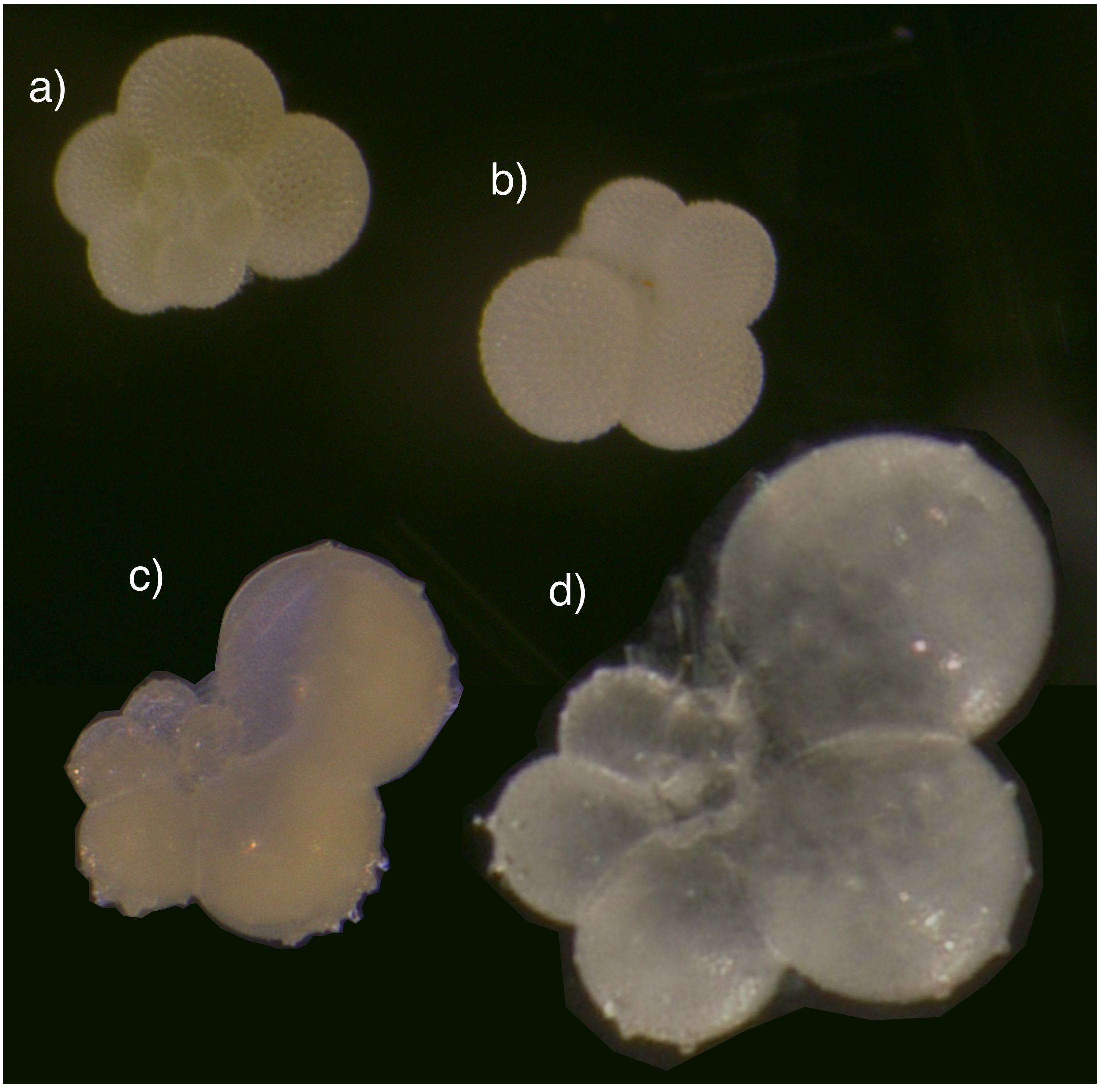


Fig. 2. A side-by-side comparison from the same tow of (a) a dorsal view of a live (cytoplasm containing) *G. hexagonus* and (b) a ventral view of the empty test of *G. hexagonus*, as well as (c) a live and (d) empty *H. parapelagica*

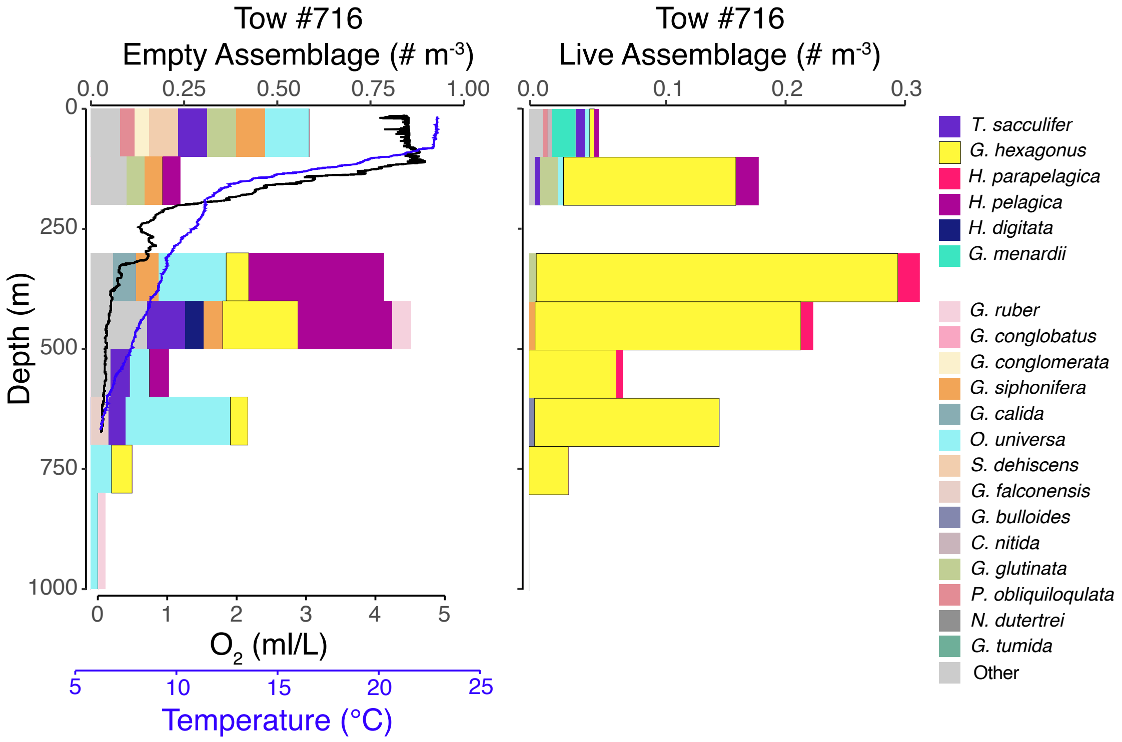


Fig. 3. Vertical profiles of the empty test assemblage, dissolved oxygen and temperature (left) and live foraminiferal assemblage (right) from tow #716 (0-1000 m). Each color represents a different species (see legend), with brighter colors for the six most salient species across nets and depths. Note that the abundance axes vary between panels.

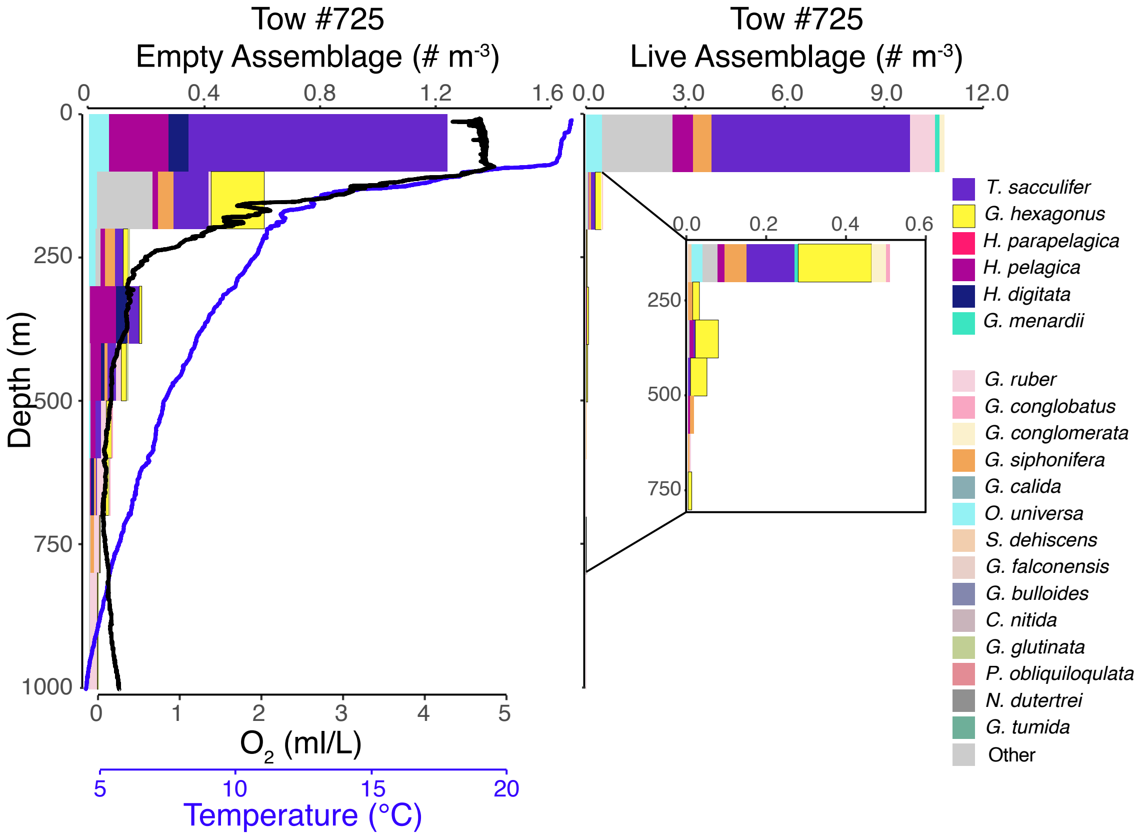


Fig. 4. Vertical profiles of the empty test assemblage, dissolved oxygen and temperature (left) and live foraminiferal assemblage (right) from tow #725 (0-1000 m). Each color represents a different species (see legend). Abundance axes vary, with the inset showing an enlargement of abundance data in that part of the water column.

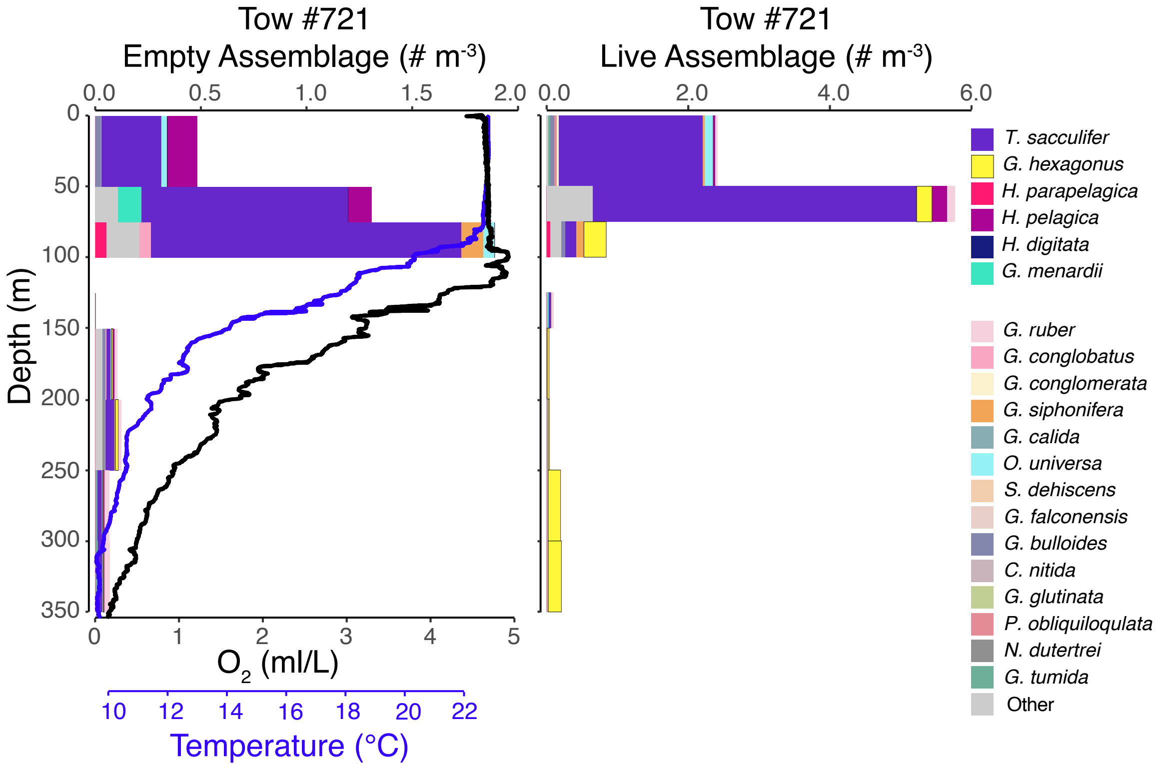


Fig. 5. Vertical profiles of the empty test assemblage, dissolved oxygen and temperature (left) and live foraminiferal assemblage (right) from tow #721 (0-350 m). Each color represents a different species (see legend). Abundance axes vary between panels.

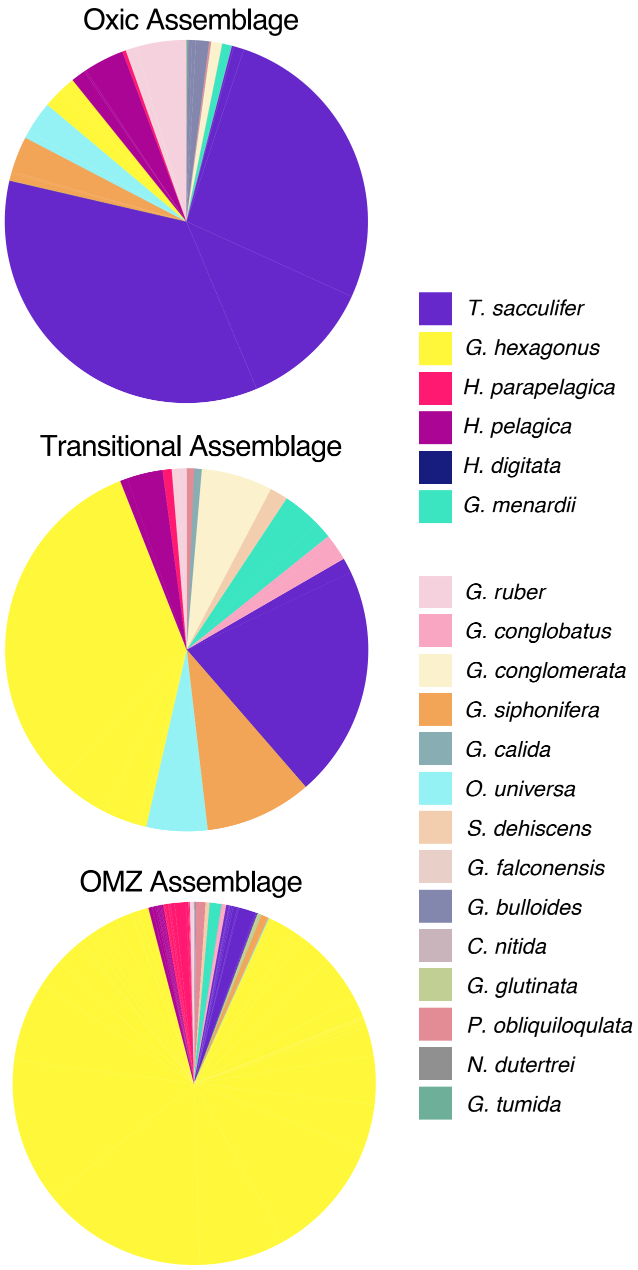
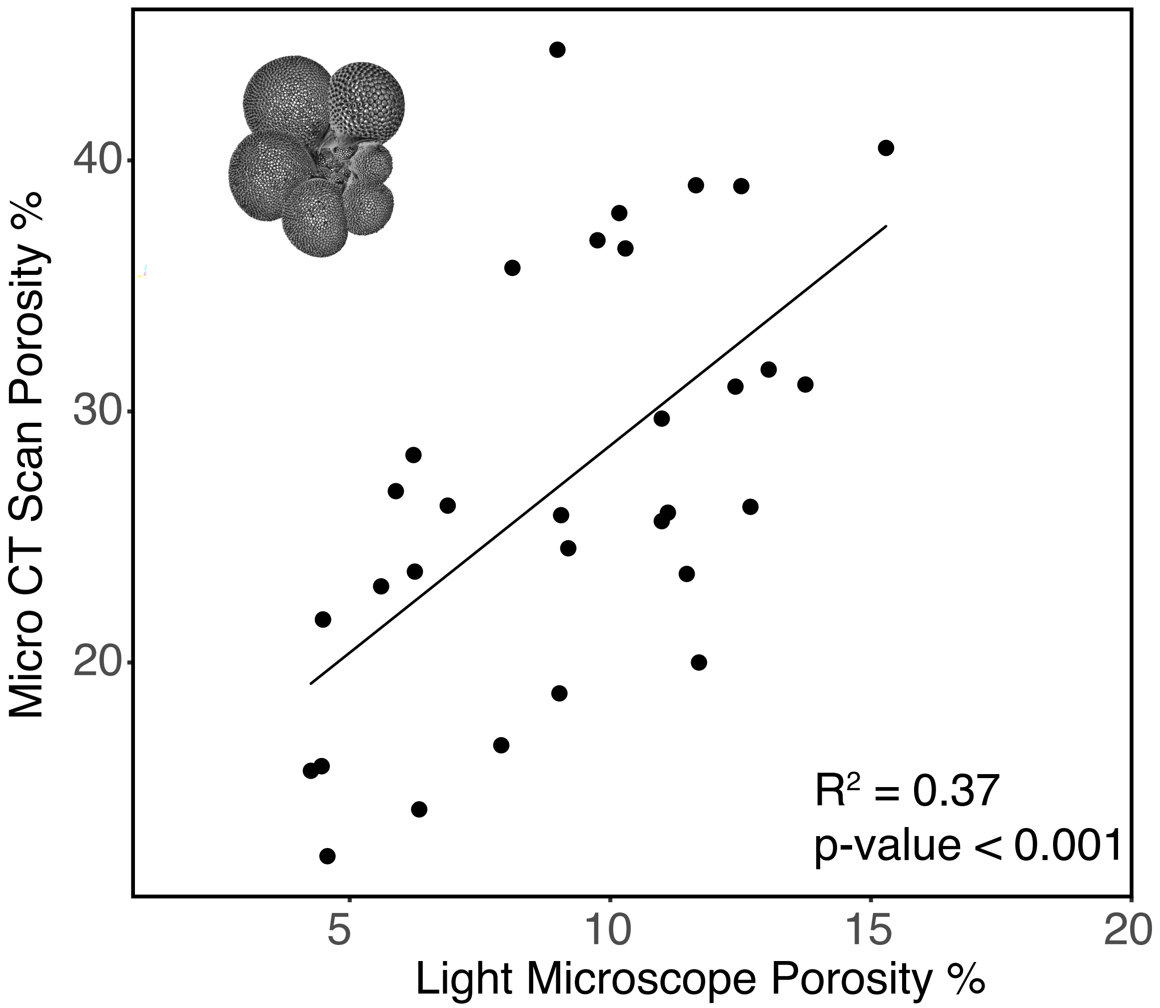


Fig. 6. Pie plots of the live foraminiferal assemblages recovered from oxic nets (minimum dissolved oxygen > 2.45 ml L^{-1}; top), transitional nets (middle) and OMZ nets (maximum dissolved oxygen < 1.4 ml L^{-1}; bottom). Each color represents a different species (see legend).



565 **Figure 7.** Relationship between *G. hexagonus* final chamber porosity measured by light microscope or CT-scan ($R^2 = 0.45$, p-value < 0.001). A representative image reconstructed from CT-scanning is inset in the upper left corner.

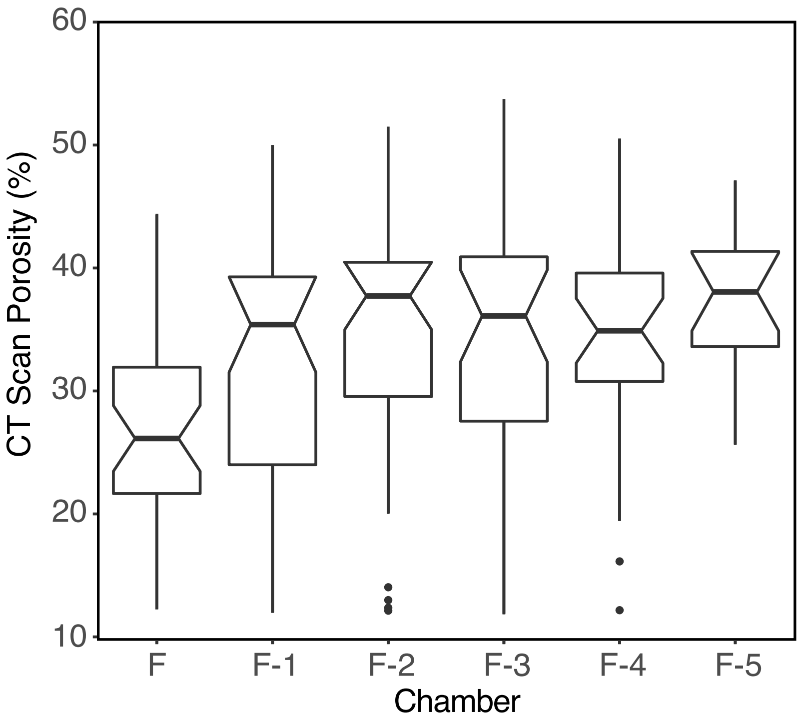


Fig. 8. Boxplots of *G. hexagonus* test porosity, determined by inside-out analyses of CT scan images, showing an increase in porosity in the most recently formed, F chamber.

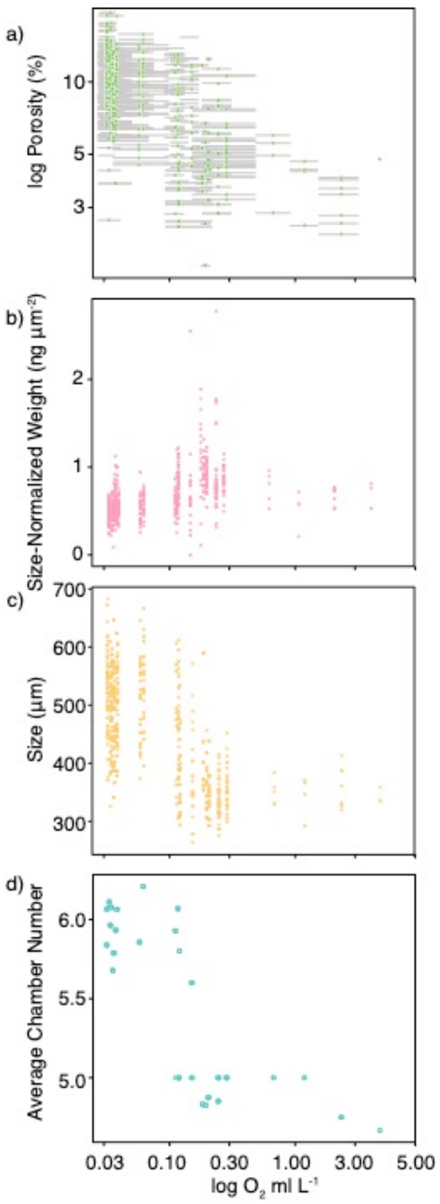


Fig. 9. Morphological traits of *G. hexagonus* tests plotted against the average dissolved oxygen (log scale) measured in the nets in which they were collected. The depicted characteristics are a) log of porosity, b) size-normalized weight (using the area-density method), c) size as measured by the longest dimension, and d) the average number of chambers in the final whorl in a tow. Horizontal gray bars in a) show the range of oxygen measured for each net.

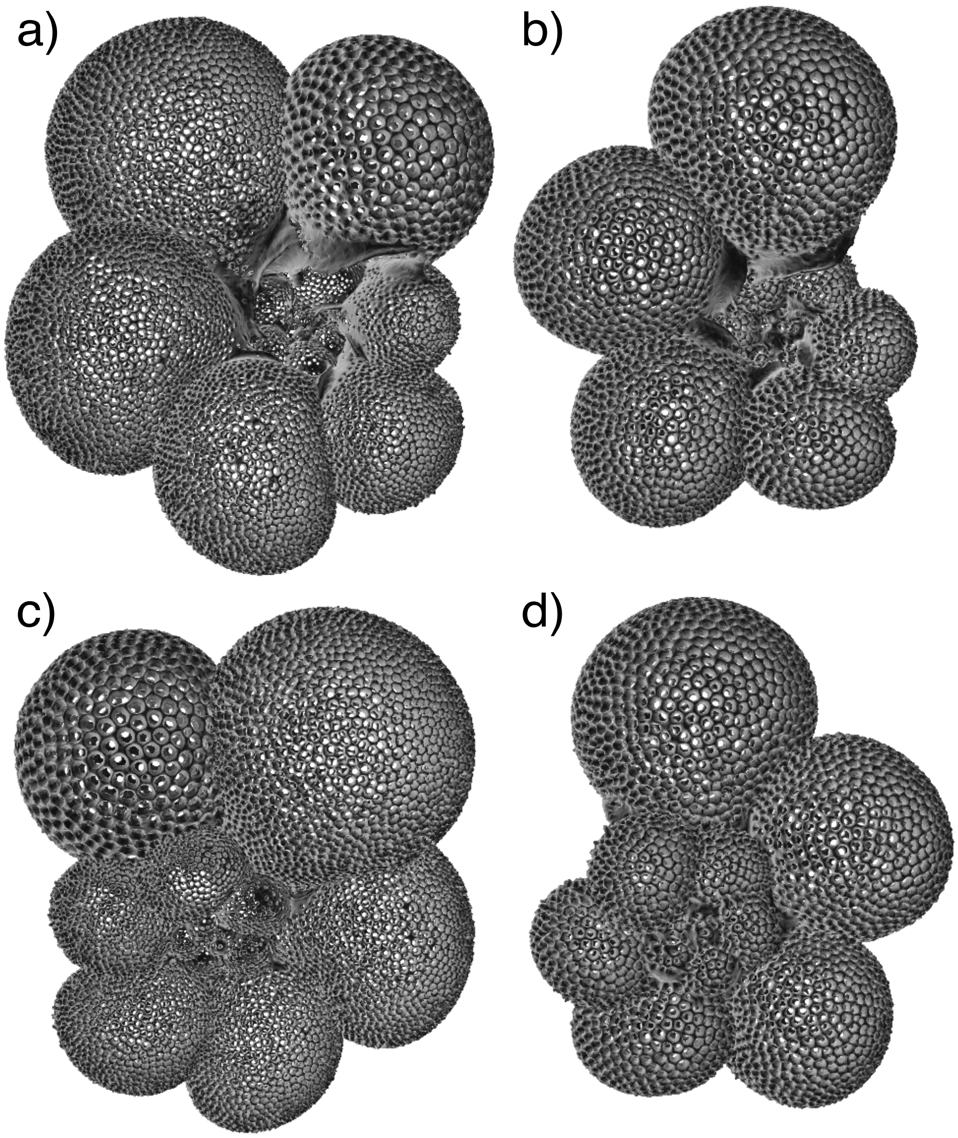


Fig. 10. Examples of *G. hexagonus* tests from tow #716 imaged by micro CT-scanning, with both a more porous deeper 6-chambered individual (a) and a less porous shallower 5-chambered individuals (b). Dorsal views of the same to specimens are shown in (c) and (d) and both represent typical rather than extreme examples along the continuum of morphological diversity observed.

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