Vertical distribution of planktic foraminifera through an Oxygen Minimum Zone:

how assemblages and test morphology reflect oxygen concentrations

Catherine V. Davis[1], Karen Wishner[2], Willem Renema[3,4] & Pincelli M. Hull[1,5]

[1]Department of Earth and Planetary Sciences, Yale University, New Haven CT 06511, USA

[2]Graduate School of Oceanography, University of Rhode Island, Narragansett, RI 02882, USA

[3]Department of Ecosystem & Landscape Dynamics, Institute for Biodiversity & Ecosystem Dynamics (IBED), University of Amsterdam, Amsterdam, the Netherlands

[4]Naturalis Biodiversity Center, Leiden, the Netherlands

[5]Peabody Museum of Natural History, Yale University, New Haven 06511, USA

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., 2018) of critical importance to future ocean

health. Despite this, there are limited geologic records with which to constrain long-term

Deleted: 2108

change in pelagic OMZ environments and, consequently, considerable uncertainty in projections of future OMZs (Stramma et al., 2012; Levin, 2017).

50   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

55   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

60   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.

65   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

70   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

75   species have been hypothesized to be 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

80   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.

Oxygen Minimum Zones are home to specialized groups of organisms capable of

tolerating low dissolved oxygen levels. A growing body of literature has focused on the

85   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

90   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
120   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

125   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
130   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
135   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
140   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 3/10ths and 1/125ths of material in a net was

examined, depending upon abundance of foraminifera, and all intact tests were isolated

145   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

150   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

155   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.

160   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

165   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

170   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

175   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

180   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

185   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

190 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

195 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 structure of the water column was

200 consistent across tows. A warm, oxygenated surface mixed layer overlaid an 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).

205 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

215   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 concentrations). The oxic group was the shallowest, with the deepest tow included in this category extending to only 150 m

220   water depth. These tows had the highest standing stock 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*

225   (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

230   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).

240   The transitional assemblages primarily represented depths between 100 and 250 m and had the lowest standing stock 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

245   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.*

250   *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

255   (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* (5.8%), and *O. universa* (5.1%). All other species comprised less than 2% of the

assemblage (Table 1). 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

265 cytoplasm.

3.4 Morphological Variation in *G. hexagonus*

3.4.1 Porosity

Porosity of the most recent chamber in *G. hexagonus* was highly variable among

270 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). We chose to focus porosity measurements on the most recent chamber as it was the chamber most likely to have formed under the conditions recorded at collection;

275 however as the foraminifera analyzed had not yet reproduced, it is not possible to know whether this chamber would also have been the terminal chamber, analogous to the final chamber in a fossil shell.

A comparison between porosity of the most recent chamber, measured by CT scan and light microscope, showed that CT measurements consistently demonstrated

280 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= 0.23(±0.05) x + 2.64(±1.49)). 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 a possible relationship between size, ontogeny, and porosity.

3.4.2 Size and Chamber Number

Size decreased with the log of oxygen (Spearman's ρ = -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 occurring at 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 ρ = -0.68; p-value < 0.001; Fig. 9).

3.4.3 Size-normalized Weight

Globorotaloides hexagonus tests weights averaged just 7.7 µg, ranging from 1 to 22 µg for tests 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

320 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).

325

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

330 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

335 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

340 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}

345   (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

350   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

355   individuals large enough (> 222 μm) to be sampled in our nets may have been present

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-

360   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
370   reflected premature mortality and/or the retention of some cytoplasm following
reproduction. On the other hand, *G. hexagonus* and *H. parapelagica* comprised 88.1% of
cytoplasm-bearing tests in OMZ nets, while being only found in low abundances in
surface assemblages. This suggests that these two species are truly endemic to deeper
hypoxic waters.

375   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
380   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 standing stock of planktic foraminifera (mean of 0.1 individual per m^{-3}

> **Deleted:** density

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
385   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,
390   food resources, predation pressure, 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.

395   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

400   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 oxygen-depleted habitats indicate that the species is adapted to live for long periods of time, likely its entire lifespan, within low oxygen conditions.

405   *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;

410   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

420   away from identifications of *G. hexagonus* in the modern Atlantic. However, additional evidence, such as molecular genetics, may be required to finally resolve this question. 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

425   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

430   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

435   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

440 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,

445 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

450 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

455 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

460 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

465   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

470   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

475   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.,

2015; Medina Faull et al., 2020).

> **Deleted:** 2105

Tests collected at lower oxygen levels also had lower size-normalized weights, a

property which negatively correlates with porosity. Size-normalized weight in planktic

480   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

(Dissolved Inorganic Carbon) 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

485   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

490   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 were less compact with more

chambers visible in the final whorl (Figure 10). The addition of more lobes via increased

chamber number have the effect of increasing the surface area/volume ratio for a given

495   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

500   area/volume ratios.

Although the increase in size at low oxygen levels appears enigmatic, there are

several potential reasons for this pattern. First, surface area increases with size, which

could be beneficial for increasing encounters with food. Larger sizes could also result

from delayed reproduction at lower oxygen levels. Alternatively, increased size (cell

505   volume) has been associated with greater capacity for denitrification 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

520 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

525 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

530 OMZ, and that a depauperate fauna occupies the upper oxycline. Two species, *G. hexagonus* and *H. parapelagica,* were found living 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

535 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

540 mid-water OMZ in which these foraminifera lived. As the species appears to be living

primarily 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.

545

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.

550

Competing Interests

The authors declare that they have no conflict of interest.

Acknowledgements

555 Many thanks to D. Outram for laboratory assistance, to R.C. Thunell (deceased) for invaluable support in the genesis of this project, and to R. Schiebel and an anonymous reviewer for their comments on the manuscript. This research was supported by NSF OCE 1851589 to Davis, NSF OCE 1459243 to Wishner, Seibel, and Roman, and a Sloan Research Fellowship to P.M.H.

560

Tables

Species	% of Oxic Assemblage	% of Transitional Assemblage	% of OMZ Assemblage	% of Empty Shells
T. sacculifer	74.6	22.1	3.6	55.4
G. ruber	5.4	0.6	0.3	6.4
H. pelagica	5.0	3.9	1.4	11.7
G. siphonifera	4.0	9.6	1.0	6.0
O. universa	3.5	5.5	0.1	5.1
G. hexagonus	3.1	40.7	86.1	5.8
G. bulloides	1.9	0.0	0.1	1.0
H. parapelagica	0.3	0.8	2.0	0.0
G. menardii	0.9	5.0	0.8	1.7
G. conglomerata	1.0	6.4	0.1	0.2
P. obliquiloculata	0.2	0.7	0.7	0.4
G. tumida	0.2	0.0	<0.1	0.4
G. glutinata	0.0	0.0	3.2	0.9
H. digitata	0.0	0.0	0.0	1.9
G. conglobatus	0.0	2.4	0.4	1.1
S. dehiscens	0.0	1.6	0.3	0.2
C. nitida	0.0	0.7	0.0	0.1
G. calida	0.0	0.0	<0.1	0.2
G. falconensis	0.0	0.0	0.0	0.1
N. dutertrei	0.0	0.0	0.0	0.2

Table 1. The relative abundance of planktic foraminifera within oxygen defined

assemblages: the 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}).

580   **Figures**

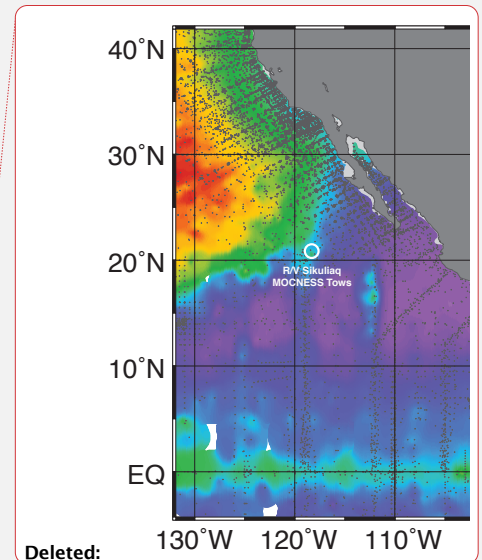
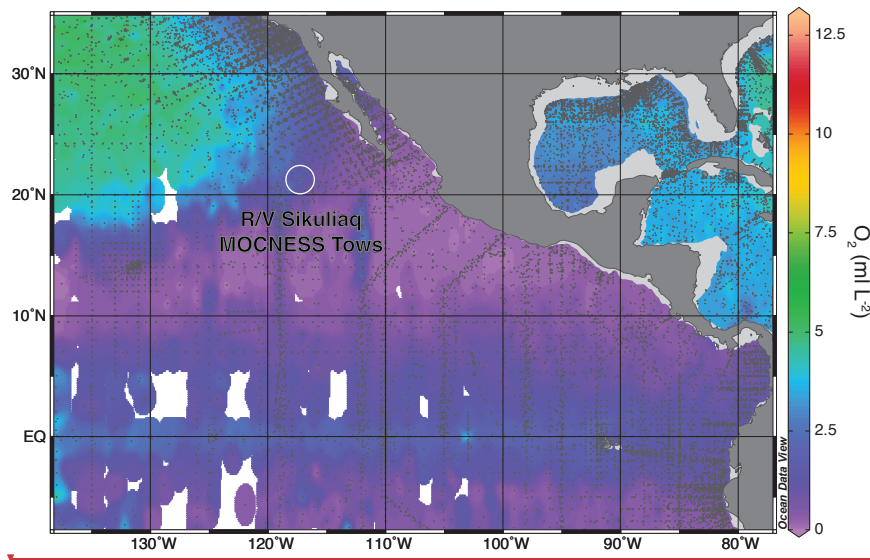



Fig. 1. Location of MOCNESS tows (white circle) taken onboard the *R/V Sikuliaq* plotted

against 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

585   Ocean Data Viewer.

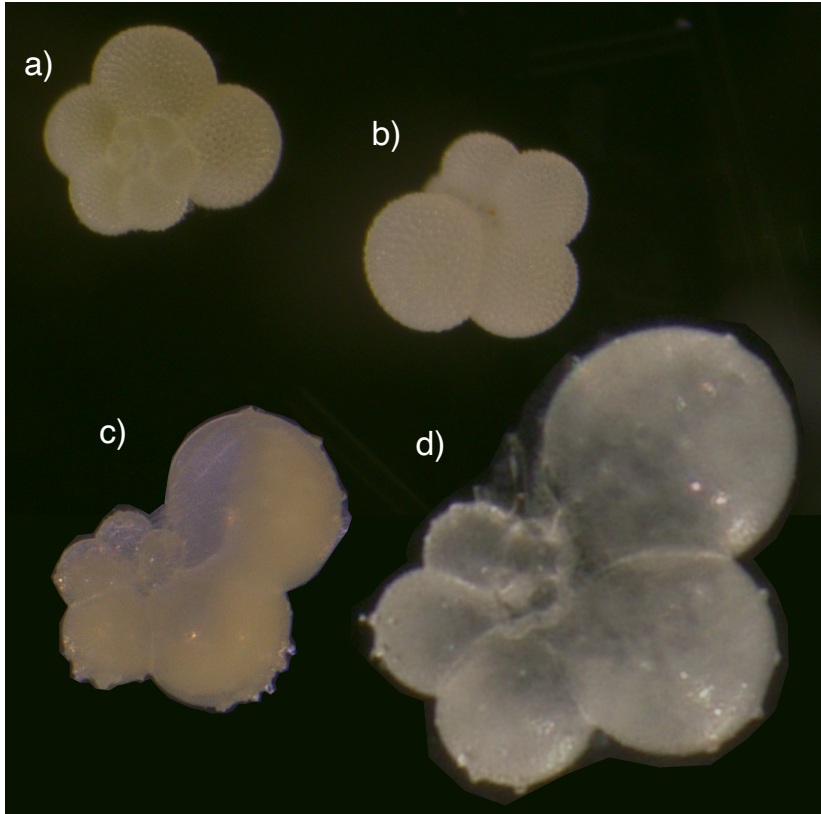



Fig. 2. A side-by-side comparison from the same tow of (a) a dorsal view of a live

590   (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*

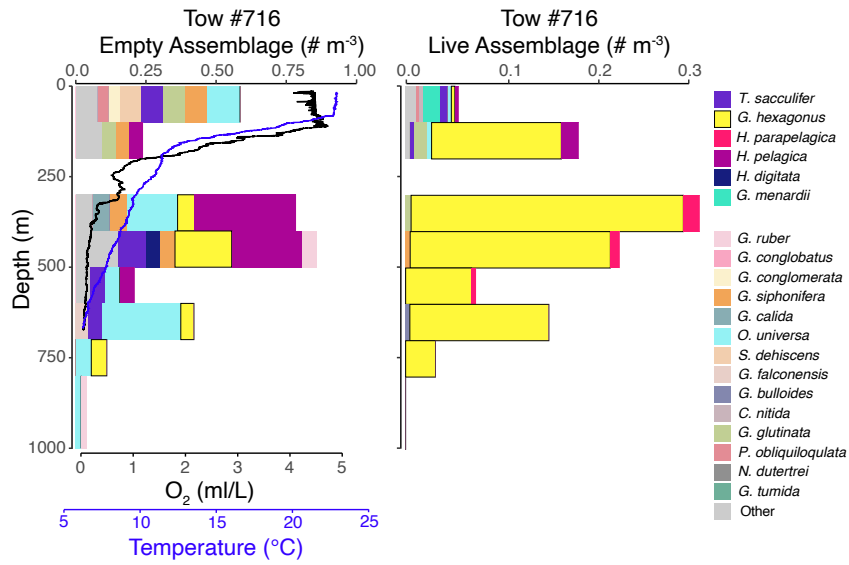



Fig. 3. Vertical profiles of the empty test assemblage, dissolved oxygen and temperature (left) and live foraminiferal assemblage (right) from tow #716 (0-1000 m). Each color represents a different species (see legend), with brighter colors for the six most salient species across nets and depths. Note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

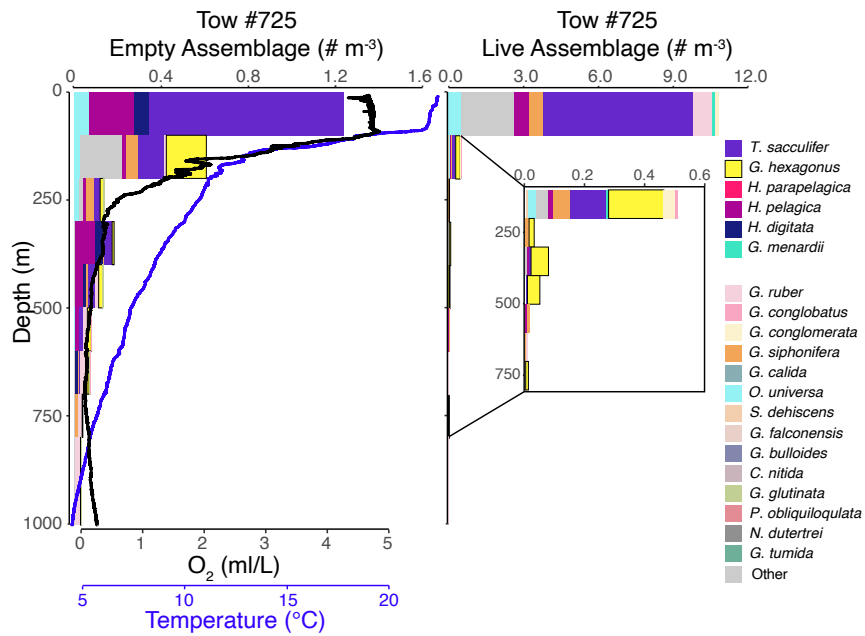



Fig. 4. Vertical profiles of the empty test assemblage, dissolved oxygen and temperature (left) and live foraminiferal assemblage (right) from tow #725 (0-1000 m). Each color represents a different species (see legend). Abundance axes vary, with the inset showing an enlargement of abundance data in that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

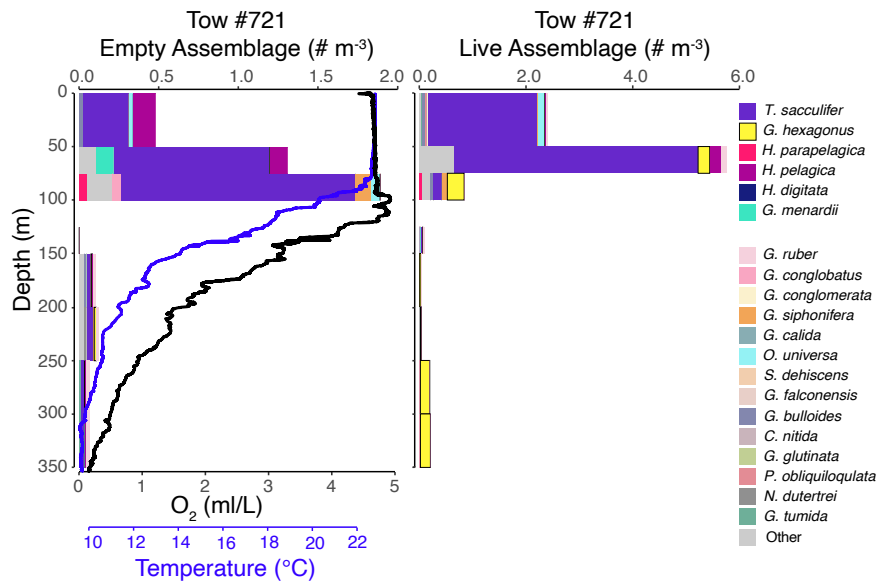



Fig. 5. Vertical profiles of the empty test assemblage, dissolved oxygen and temperature (left) and live foraminiferal assemblage (right) from tow #721 (0-350 m). Each color represents a different species (see legend). Abundance axes vary between panels.

Oxic Assemblage

Transitional Assemblage

OMZ Assemblage

Legend:
- *T. sacculifer*
- *G. hexagonus*
- *H. parapelagica*
- *H. pelagica*
- *H. digitata*
- *G. menardii*
- *G. ruber*
- *G. conglobatus*
- *G. conglomerata*
- *G. siphonifera*
- *G. calida*
- *O. universa*
- *S. dehiscens*
- *G. falconensis*
- *G. bulloides*
- *C. nitida*
- *G. glutinata*
- *P. obliquiloqulata*
- *N. dutertrei*
- *G. tumida*

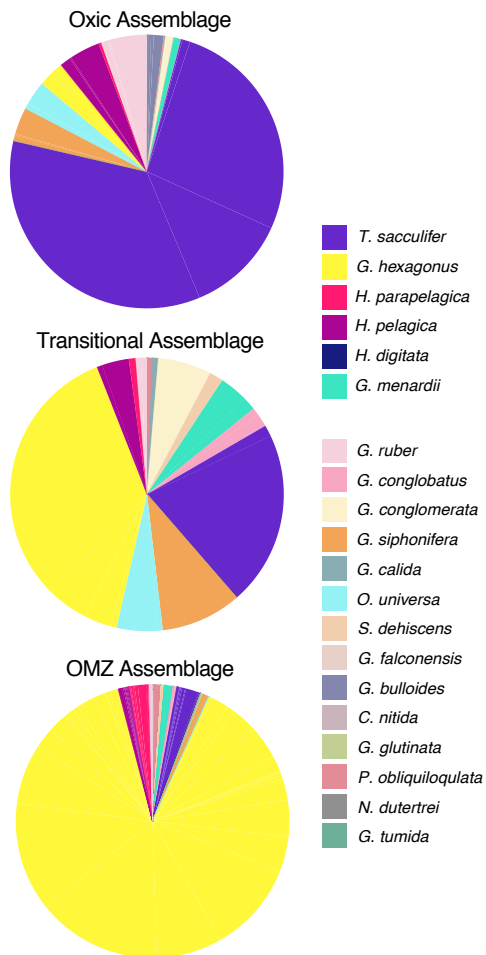



Fig. 6. Pie plots of the live foraminiferal assemblages recovered from oxic nets (minimum dissolved oxygen > 2.45 ml L^{-1}; top), transitional nets (middle) and OMZ nets (maximum dissolved oxygen < 1.4 ml L^{-1}; bottom). Each color represents a different species (see legend).

610

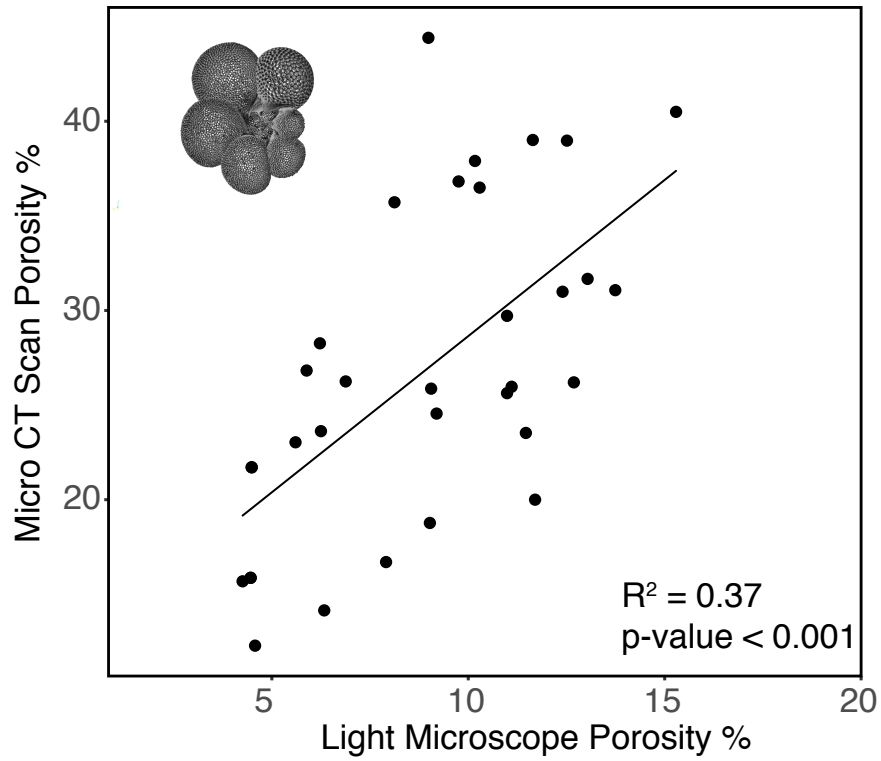



Figure 7. Relationship between *G. hexagonus* final chamber porosity measured by light microscope or CT-scan ($R^2 = 0.45$, p-value < 0.001). A representative image reconstructed from CT-scanning is inset in the upper left corner.

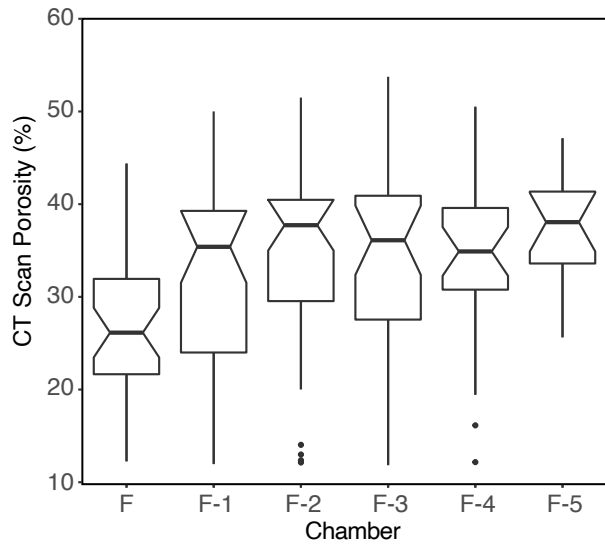



Fig. 8. Boxplots of *G. hexagonus* test porosity, determined by inside-out analyses of CT

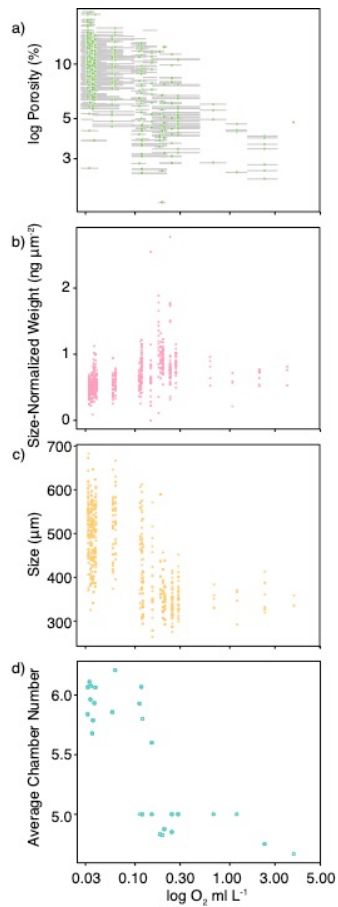
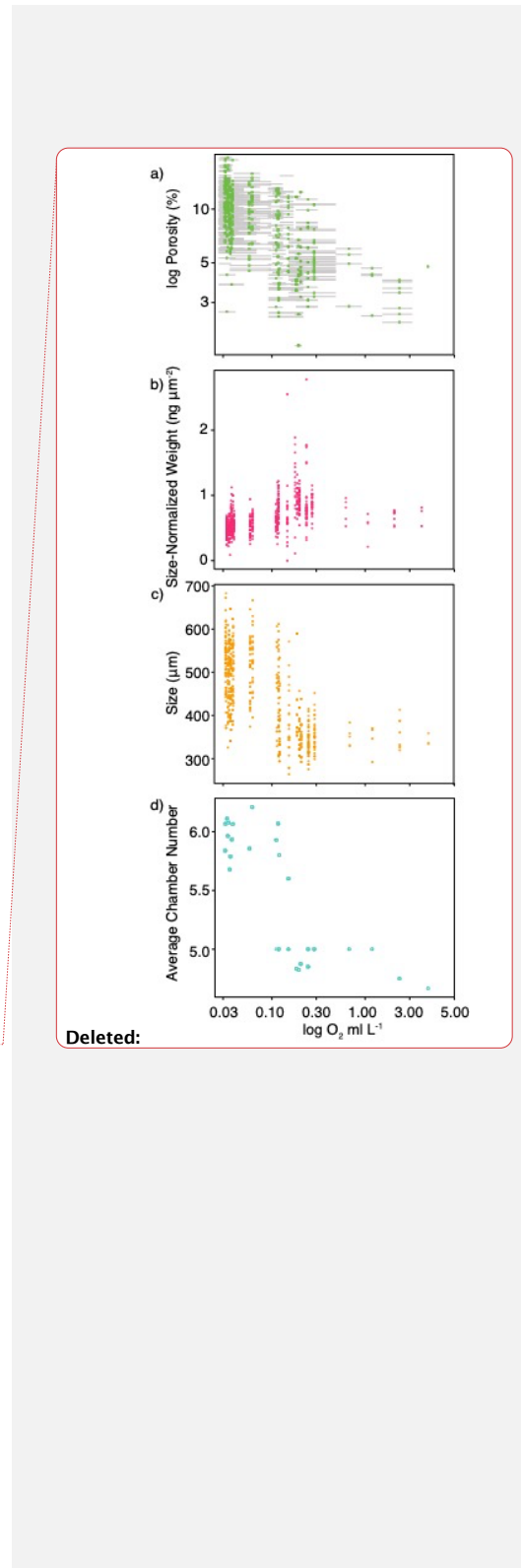
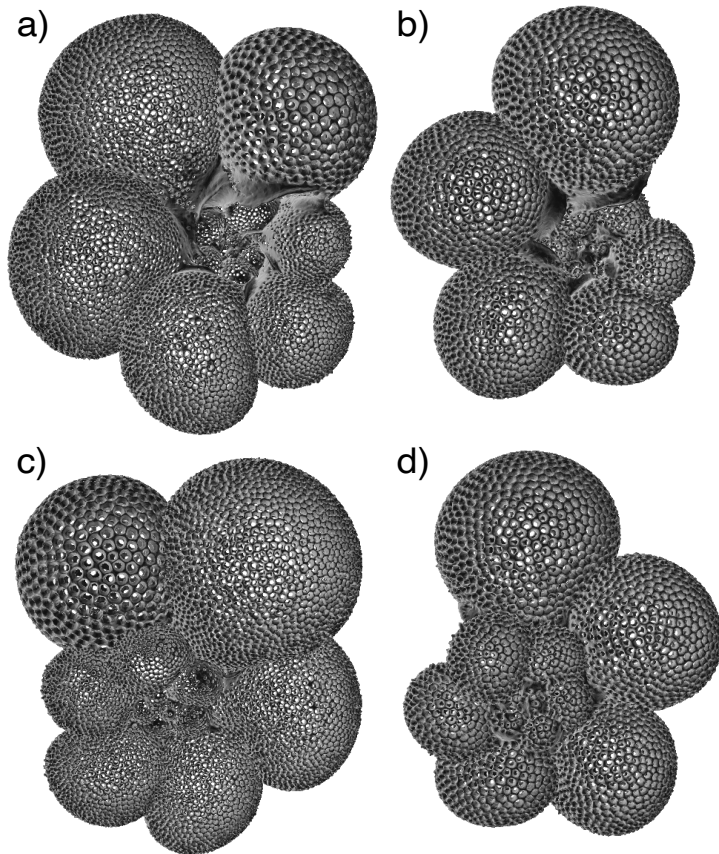
scan images, showing an increase in porosity in the most recently formed, F chamber.

620

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.

625

630 **Fig. 10**. Examples of *G. hexagonus* tests from tow #716 imaged by micro CT-scanning, showing a) a more porous 6-chambered individual recovered deeper in the OMZ and b) a less porous 5-chambered individuals captured shallower in the OMZ. 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.

635

References

645   Bates, N. R.: Seawater carbonate chemistry distributions across the Eastern South

        Pacific Ocean sampled as part of the GEOTRACES project and changes in marine

        carbonate chemistry over the past 20 years, Front. Mar. Sci., 3, 398, 2018.

        Bernhard, J. M.: Characteristic assemblages and Morphologies of benthic

        foraminifera from anoxic, organic-rich deposits: Jurassic through Holocene, *J.*

650   Foramin. Res., 16, 207-215, 1986.

        Bernhard, J. M. & Alve, E.: Survival, ATP pool, and ultrastructural characterization of

        benthic foraminifera from Drammensfjord (Norwar): response to anoxia, Mar.

        Micropaleontol., 28 (1), 5-17.

        Bernhard J. M., Sen Gupta B. K., ND Borne P. F.: Benthic foraminiferal proxy to

655   estimate dysoxic bottom-water oxygen concentrations; Santa Barbara Basin, US

        Pacific continental margin, J. Foramin. Res., 27, 301-310, 1997.

        Bernhard J. M. and Bowser S. S.: Peroxisome proliferation in Foraminifera

        inhabiting the chemocline: an adaptation to reactive oxygen species exposure?, *J.*

        Eukaryot. Microbiol., 55, 135-144, 2008.

660   Bernhard, J. M., Edgcomb, V. P., Casciotti, K. L., McIlvin, M. R. and Beaudoin, D. J.:

        Dentrification likely catalyzed by endobionts in an allogromiid foraminifer, ISME

        J., 6, 951-960, 2011.

        Bernhard, J. M., Edgcomb, V. P., Casciotti, K. L., McIlvin, M. R., and Beaudoin, D. J.:

        Denitrification likely catalyzed by endobionts in an allogromiid foraminifer.

665   ISME J., 6, 951-960, doi:10.1038/ismej.2011.171, 2012.

        Bernhard, J. M., Casciotti, K. L., McIlvin, M. R., Beaudoin, D. J., Visscher, P. T., and

Edgcomb, V. P.: Potential importance of physiologically diverse benthic foraminifera in sedimentary nitrate storage and respiration, J. Geophys. Res. Biogeosci., 117, doi:10.1029/2012JG001949, 2012.

670   Bijma, J., Faber, W. W., and Hemleben, C.: Lunar and semi-lunar reproductive cycles in some spinose planktonic foraminifers, J. Foramin. Res., 20: 117-127, 1990.

Bijma, J., Faber, W. W., and Hemleben, C: Temperature and salinity limits for growth and survival of some planktonic foraminfiers in laboratory cultures, J.

675   Foramin. Res., 20, 95-116, 1990.

Bijma, J., Honisch, B., and Zeebe, R. E.: Impact of the ocean carbonate chemistry on living foraminiferal shell weght: Comment on "Carbonate ion concentration in glacia-age deep waters of the Caribbean Sea" by W. S. Broecker and E. Clark, Geochem. Geophys. Geosyst., 3, 1-7, 2002.

680   Birch H., Coxall H. K., Pearson P. N., Kroon D., and O'Regan M.: Planktonic foraminifera stable isotopes and water column structure: Disentangling ecological signals, Mar. Micropaleontol. 101, 127-145, 2013.

Bird, C., Darling, K. F., Russell, A. D., Fehrenbacher, J. S., Davis, C. V., Free, A., & Ngwenya, B. T. (2018). 16S rRNA gene metabarcoding and TEM reveals

685   different ecological strategies within the genus Neogloboquadrina (planktonic foraminifer). *PloS one*, *13*(1), e0191653.

Breitburg D., Levin, L. A., Oschlies, A., Gregoire, M., Chavez, F. P., Conley, D. J., Garcon, V., Gilbert, D., Gutierrez, D., Isensee, K., Jacinto, G. S., Limburg, K. E., Montes, I., Naqvi, S. W. A., Pitcher, G. C., Rabalais, N. N., Roman, M. R., Rose,

690   K. A., Seibel, B. A., Telszewski, M., Yasuhara, M., and Zhang, J.: Declining

oxygen in the global ocean and coastal waters, Science, 359, 2018.

Buchwald, C., Santoro, A. E., Stanley, R. H. R., and Casciotti, K. L.: Nitrogen

cycling in the secondary nitrite maximum of the eastern tropical North Pacific off

Coasta Rica, Global Biogeochem. Cy., 29, doi:10.1002/2015GB005198, 2015.

695   Burke J. E., Renema, W., Henehan, M. J., Elder, L. E., Davis, C. V., Maas, A. E., Foster,

G. L., Schiebel, R., and Hull, P. M.: Factors influencing test porosity in

planktonic foraminifera, Biogeosciences, 15, 6607-6619, 2018.

Burke, J. E., Renema, W., Schiebel, R., and Hull, P. M.: Three-dimensional analysis of

inter-and intraspecific variation in ontogenetic growth trajectories of planktonic

700   foraminifera, Mar. Micropaleontol., 155, 101794, 2020.

Cannariato K. G., Kennett J. P., and Behl R. J.: Biotic response to late Quaternary rapid

climate switches in Santa Barbara Basin: Ecological and evolutionary

implications, Geology, 27, 63-66, 1999.

Cassman, N., Prieto-Davo, A., Walsh, K., Silva, G. G. Z., Angly, F., Akhter, S., Barott,

705   K., Busch, J., McDole, T., Haggerty, J.M., Willner, D., Alarcon, G., Ulloa, O.,

DeLong, E. F., Dutilh, B. E., Rohwer, F., and Dinsdale, E. A.: Oxygen minimum

zones harbor novel viral communities with low diversity, Environ. Microbiol., 14,

3043-3065, 2012.

Cignoni, P., Callieri, M., Corsini, M., Dellepiane, M., Ganovelli, F., and Ranzuglia, G.:

710   MeshLab: an open-source mesh processing tool, Sixth Eurographics Italian

Chapter Conference, 129-136, 2008.

Corliss, B. H.: Microhabitats of benthic foraminifera within deep-sea sediments, Nature,

314, 435-439, 1985.

Coxall H. K., Pearson P. N., Wilson P. A., and Sexton P. F.: Iterative evolution of

715   digitate planktonic foraminifera, Paleobiology, 33, 495-516, 2007.

Davis C. V., Hill T. M., Russell A. D., Gaylord B., and Jahncke J.: Seasonality in

         planktic foraminifera of the central California coastal upwelling region,

         Biogeosciences, 13, 5139, 2016.

DeVries T., Deutsch C., Primeau F., Chang B., and Devol A.: Global rates of

720   water-column denitrification derived from nitrogen gas measurements, Nature

         Geosci., 5, 547, 2012.

Duret, M. T., Pachiadaki, M. G., Stewart, F. J., Sarode, N., Christaki, U., Mochy, S.,

         Srivastava, A., and Edgcomb, V. P.: Size-fractionated diversity of eukaryotic

         microbial communities in the Eastern Tropical North Pacific oxygen minimum

725   zone, FEMS Microbiol. Ecol., 91, doi: 10.1093/femsec/fiv037, 2017.

Eguchi, N. O., Kawahata, H., and Asahiko, T.: Seasonal Response of Planktonic

         Foraminifera to surface ocean conditions: Sediment trap results from the Central

         North Pacific Ocean, J. Oceanogr., 55, 681-691, 1999.

Emiliani, C.: Depth habitats of some species of pelagic foraminifera as indicated by

730   oxygen isotopic ratios, Am. J. Sci., 252, 149-158, 1954.

Enge, A. J., Witte, U., Kucera, M., and Heinz, P.: Uptake of phytodetritus by benthic

         foraminifera under oxygen depletion at the Indian margin (Arabian Sea),

         Biogeosciences, 11, 2017-2026, 2014.

Erez, J., Almogi-Labin, A., and Avraham, S.: On the life history of planktonic

735   foraminifera: Lunar reproduction cycle in *Globigerinoides sacculifer* (Brady),

        Paleoceanography, 6, 295-306, 1991.

        Escribano, R., Hidalgo, P., and Krautz, C.: Zooplankton associated with the oxygen

        minimum zone system in the northern upwelling region of Chile during March

        2000, Deep-Sea Res. Pt. II, 56, 1083-1094, 2009.

740   Fairbanks, R. G., Sverdlove, M., Free, R., Wiebe, P. H., and Be, A. W. H.: Vertical

        distribution and isotopic fractionation of living planktonic foraminifera from the

        Panama Basin, Nature, 298, 841-844, 1982.

        Field, D. B.: Variability in vertical distributions of planktonic foraminifera in the

        California Current: Relationships to vertical ocean structure, Paleoceanography,

745   19, PA2014, doi:10/1029/2003PA000970, 2004.

        Fiedler P. C. and Talley L. D.: Hydrography of the eastern tropical Pacific: A

        Review, Prog. Oceanogr. 69, 143-180, 2006.

        Garcia, H. E., K. Weathers, C. R. Paver, I. Smolyar, T. P. Boyer, R. A. Locarnini, M. M.

        Zweng, A. V. Mishonov, O. K. Baranova, D. Seidov, and Reagan, J. R. : World

750   Ocean Atlas 2018, Volume 3: Dissolved Oxygen, Apparent Oxygen Utilization,

        and Oxygen Saturation. A. Mishonov Technical Ed.; NOAA Atlas NESDIS 83,

        2018.

        Garfield, P. C., Packard, T. T., Friederich, G. E., and Codispoti, L. A.: A subsurface

        particle maximum layer and enhanced microbial activity in the secondary nitrate

755   maximum of the northeastern tropical Pacific Ocean, J. Mar. Res., 41, 747-768,

        1983.

        Gaskell, D. E., Ohman, M. D., and Hull, P. M.: Zooglider-based measurements of

planktonic foraminifera in the California Current system, J. Foramin. Res., 49,
390-404, 2019

760   Glock, N., Eisenhauer, A., Milker, Y., Liebetrau, V., Schonfeld, J., Mallon, J., Sommer,
S. and Hensen, C.: Environmental influences on the pore density of *Bolivina
spissa* (Cushman), J. Foramin. Res., 41, 22-32, 2011.

Glock N., Schönfeld J., and Mallon J.: The Functionality of Pores in Benthic
Foraminifera in View of Bottom Water Oxygenation: A Review. *Anoxia,* Cellular
765   Origin, Life in Extreme Habitats and Astrobiology, eds Altenbach A. V.,
Bernhard J. M., and Seckbach J. (Springer Netherlands), Vol 21, 537-552, 2012.

Glock, N., Erdem, Z., Wallmann, K., Somes, C. J., Liebetrau, V., Schonfeld, J., Gorb, S.,
and Eisenhauer, A.: Coupling of oceanic carbon and nitrogen facilitates spatially
resolved quantitative reconstruction of nitrate inventories, Nat. Commun., 9,
770   1217, 2018.

Glock, N., Roy, A. S., Romero, D., Wein, T., Weissenbach, J., Revsbech, N. P.,
Hogslund, S., Clemens, D., Sommer, S and Dagan, T: Metabolic preference of
nitrate over oxygen as an electron acceptor in foraminifera from the Peruvian
oxygen minimum zone, Proc. Natl. Acad. Sci., 116, 2860-2865, 2019.

775   Gooday, A. J., Bernhard, J. M., Levin, L. A., and Suhr, S. B.: Foraminifera in the Arabian
Sea oxygen minimum zone and other oxygen-deficient settings: taxonomic
composition, diversity, and relation to metazoan faunas, Deep-Sea Res. Pt II, 47,
25-54, 2000.

Gooday, A. J., Schoenle, A., Dolan, J. R., and Arndt, H.: Protist diversity and function in
780   the dark ocean – Challenging the paradigms of deep-sea ecology with special

emphasis on foraminiferans and naked protists. Eur. J. Protistol., 75: 125721.

Gruber N.: The marine nitrogen cycle: overview and challenges. *Nitrogen in the marine environment* 2:1-50, 2008.

Henehan, M. J., Evans, D., Shankle, M., Burke, J. E., Foster, G. L., Anagnostou, E.,

785   Chalk, T. B., Stewart, J. A., Alt, C. H. S., Durrant, J. and Hull, P. M.: Size-dependant response of foraminiferal calcification to seawater carbonate chemistry, Biogeosciences, 14: 3287-3308, 2017.

Hofmann, A. F., Peltzer, E. T., Walz, P. M., and Brewer, P. G.: Hypoxia by degrees: Establishing definitions for a changing ocean, Deep-Sea Res. Pt 1, 58, 1212-1226,

790   2011.

Hogslund, S., Revsbech, N. P., Cedhagen, T., Nielsen, L. P., and Gallardo, V. A.: Denitrification, nitrate turnover, and aerobic respiration by benthic foraminiferans in the oxygen minimum zone off Chile, J. Exp. Mar. Biol. Ecol., 39, 85-91, 2008.

Hsiang, A. Y., Nelson, K., Elder, L. E., Sibert, E. C., Kahanamoku, S. S., Burke, J. E.,

795   Kelly, A., Liu, Y., and Hull, P. M.: *Automorph*: Accelerating morphometrics with automated 2D and 3D image processing and shape extraction, Methods Ecol. Evol., 9, 605-612, 2018.

Hull P. M., Osborn K. J., Norris R. D., and Robison, B. H.: Seasonality and depth distribution of a mesopelagic foraminifer, *Hastigerinella digitata*, in Monterey

800   Bay, California, Limnol. Oceanogr. 56, 562-576, 2011.

Jorissen F. J., Fontanier C., and Thomas, E.: Chapter seven paleoceanographical proxies based on deep-sea benthic foraminiferal assemblage characteristics. Developments in Marine Geology, 1, 263-325, 2007.

Jonkers, L., Reynolds, C. E., Richey, J., and Hall, I. R.: Lunar periodicity in the

805   shell flux of planktonic foraminfiera in the Gulf of Mexico, Biogeosciences, 12,

30161-3070, 2015.

Kaiho K.: Benthic foraminiferal dissolved-oxygen index and dissolved-oxygen levels in

the modern ocean, Geology, 22, 719-722, 1994.

Katz, M. E., Cramer, B. S., Franzese, A., Hönisch, B., Miller, K. G., Rosenthal, Y., and

810   Wright, J. D.: Traditional and emerging geochemical proxies in foraminifera, J.

Foramin. Res., 40, 165-192, 2010.

Kawahata, H., Nichimura, A., and Gagan, M. K.: Seasonal change in foraminiferal

production in the western equatorial Pacific warm pool: evidence from sediment

trap experiments, Deep-Sea Res. Pt II, 49: 2783-2800, 2002.

815 Keating-Bitonti, C. R., and Payne, J. L.: Ecophenotypic responses of benthic f

foraminifera to oxygen availability along an oxygen gradient in the California

Borderland, Mar. Ecol., 38, e12430, 2017.

Keeling R. F., Körtzinger A., and Gruber N.: Ocean Deoxygenation in a Warming World,

Annu. Rev. Mar. Sci., 2, 199-229, 2009.

820 Kennett, J. P., and Huddlestun, P.: Abrupt climatic change at 90,000 yr BP: Faunal

evidence from Gulf of Mexico cores, Quaternary Res., 2, 384-395, 1972.

Kucera, M., Weinelt, M., Kiefer, T., Pflaumann, U., Hayes, A., Weinelt, M., Chen, M.-

T., Mix, A. C., Barrows, T. T., Cortijo, E., Duprat, J., Juggins, S., and

Waelbroech, C.: Reconstruction of sea-surface temperatures from assemblages of

825   planktonic foraminifera: multi-technique approach based on geographically

constrained calibration data sets and its application to glacial Atlantic and Pacific
Oceans, Quaternary Sci. Rev., 24, 951-998, 2005.

Kucera, M.: Chapter six planktonic foraminifera as tracers of past oceanic environments,
Developments in marine geology, **1**: 213-262, 2007.

830   Kuhnt, T., Friedrich, O., Schmiedl, G., Milker, Y., Machensen, A., and Luckge, A.:
Relationship between pore density in benthic foraminifera and bottom-water
oxygen content, Deep-Sea Res. Pt I, 76, 85-96, 2013.

Kuhnt, T., Schiebel, R., Schmiedl, G., Milker, Y., Mackensen, A., and Friedrich, O.:
Automated and manual analyses of the pore density-to-oxygen relationship in

835   *Globobulimina turgida* (Baily), J. Foramin. Res., 44, 1-5, 2014.

Kuroyanagi, A., Kawahata, H., Nishi, H., and Hondo, M.C.: Seasonal changes in
planktonic foraminifera in the northwestern North Pacific Ocean: sediment trap
experiments from subarctis and subtropical gyres, Deep-Sea Res. Pt II, 49, 5627-
5645, 2002.

840   Kuroyanagi A., da Rocha, R. E., Bijma, J., Spero, H. J., Russell, A. D., Eggins, S. M.,
and Kawahata, H.: Effect of dissolved oxygen concentration on planktonic
foraminifera through laboratory culture experiments and implications for oceanic
anoxic events, Mar. Micropaleontol., 101, 28-32, 2013.

Lamb, J. L., and Beard, J. H.: Late Neogene planktonic foraminifers in the

845   Caribbean, Gulf of Mexico, and Italian stratotypes, University of Kansas
Paleontological Institute, 1972.

LeKieffre, C., Spangenberg, J. E., Mabilleau, G., Escrig, S., Meibom, A., and Geslin, E.:
Surviving anoxia in marine sediments: The metabolic response of ubiquitous

benthic foraminifera (Ammonia tepida), PloS One, 12, e0177604, 2017.

850 Levin, L. A.: Oxygen minimum zone benthos: Adaptation and community response to
hypoxia, Oceanogr. Mar. Biol., 41, 41:1-45, 2003.

Levin, L. A.: Manifestation, Drivers, and Emergence of Open Ocean Deoxygenation,
Annu. Rev. Mar. Sci., 10, 229-260, 2017.

Lin, H.: The seasonal succession of modern planktonic foraminfiera: Sediment traps
855 observations from southwest Taiwan waters, Cont. Shelf Res., 84, 13-22, 2010.

Leutenegger, S., and Hansen, H. J.: Ultrastructural and radiotracer studies of pore
function in Foraminifera, Mar. Biol., 54: 11-16, 1979.

Marshall B. J., Thunell R. C., Henehan M. J., Astor Y., and Wejnert, K. E.: Planktonic
foraminiferal area density as a proxy for carbonate ion concentration: A
860 calibration study using the Cariaco Basin ocean time series, Paleoceanography,
28, 363-376, 2013.

Maas, A. E., Frazar, S. L., Outram, D. M., Seibel, B. A., and Wishner, K. F.: Fine-
scale vertical distribution of macroplankton and micronekton in the Eastern
Tropical North Pacific in association with an oxygen minimum zone, J. Plankton
865 Res., 36, 1557-1575, 2014.

Marchant, M., Hebbeln, D., and Wefer, G.: Seasonal flux patterns of planktic
foraminifera in the Peru–Chile Current, Deep-Sea Res. Pt I, 45, 1161-1185, 1998.

Max L., Rippert, N., Lembke-Jene, L., Mackensen, A., Nurnberg, D., and Tiedemann, R.:
Evidence for enhanced convection of North Pacific Intermediate Water to the low-
870 latitude Pacific under glacial conditions, Paleoceanogr. Paleocl. 32, 41-55, 2017.

Medina Faull, L., Mara, P., Taylor, G.T., and Edgcomb, V.P.: Imprint of trace dissolved

oxygen on prokaryoplankton community structure in an Oxygen Minimumz Zone, Front. Mar. Sci., 7, 360, 2020, doi:10.3389/fmars.2020.00360.

Meiland, J., Siccha, M., Weinkauf, M. F. G., Jonkers, L., Morard, R., Baranowski, U.,
875   Baumeister, A., Bertlich, J., Brummer, G.-J., Debray, P., Fritz-Endres, T.,
Groeneveld, J., Magerl, L., Munz, P., Rillo, M. C., Schmidt, C., Takagi, H.,
Theara, G. and Kucera, M.: Highly replicated sampling reveals no diurnal vertical
migration but stable species-specific vertical habitats in planktonic foraminifera,
J. Plankton Res., 41, 127-141, 2019.

880   Moffitt S. E., Moffitt, R. A., Sauthoff, W., Davis, C. V., Hewett, K., and Hill, T. M.:
Paleoceanographic insights on recent oxygen minimum zone expansion: Lessons
for modern oceanography, PloS One, 10, e0115246, 2015.

Nomaki, H., Ogawa, N. O, Ohkouchi, N., Suga, H., Toyofuku, T., Shimanaga, M.,
Nakatsuka, T., and Kitazato, H.: (2008) Benthic foraminifera as trophic links
885   between phytodetritus and benthic metazoans: carbon and nitrogen isotopic
evidence, Mar. Ecol. Prog. Ser., 357: 153-164, 2008.

Ohkushi K., Kennett, J. P., Zeleski, C. M., Moffitt, S. E., Hill, T. M., Robert, C.,
Beaufort, L., Behl, R. J.: Quantified intermediate water oxygenation history of the
NE Pacific: A new benthic foraminiferal record from Santa Barbara basin,
890   Paleoceanography, 28, 453-467, 2013.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'hara, R. B.,
Simpson, G. L., Solymos, P., Stevens, M. H. H., and Wagner, H.: Package
'vegan', Community ecology package, 2, 2012.

Orsi, W. D., Morard, R., Vuillemin, A., Eitel, M., Worheide, G., Milucka, J, and Kucera,

895   M.: Anaerobic metabolism of Foraminifera thriving below the seafloor, The
ISME J., 14, 2580-2594.

Ortiz, J. D., Mix, A. C., and Collier, R. W.: Environmental control of living symbiotic
and asymbiotic foraminifera of the California Current, Paleoceanography, 10,
987-1009, 1995.

900   Ortiz, J. D., Mix, A., Rugh, W., Watkins, J., and Collier, R.: Deep-dwelling planktonic
foraminifera of the northeastern Pacific Ocean reveal environmental control of
oxygen and carbon isotopic disequilibria, Geochim. Cosmochim. Acta, 60, 4509-
4523, 1996.

Paulmier, A., Ruiz-Pino, D., and Garçon, V.: The Oxygen Minimum Zone (OMZ) off

905   Chile as intense source of CO_2 and N_2O, Cont. Shelf Res., 28, 2746-2756, 2008.

Paulmier, A. and Ruiz-Pino, D.: Oxygen minimum zones (OMZs) in the modern ocean,
Prog. Oceanogr., 80, 113-128, 2009.

Paulmier, A., Ruiz-Pino, D., and Garçon, V.: CO_2 maximum in the oxygen minimum
zone (OMZ), Biogeosciences, 8, 239-252, 2011.

910   Perez-Cruz, L. L., and Machain-Castillo, M. L.: Benthic foraminifera of the oxygen
minimum zone, continental shelf of the Gulf of Tehuantepec, Mexico, J. Foramin.
Res., 20, 312-325, 1990.

Pflaumann, U., Sarnthein, M., Ficken, K., Grothmann, A., and Winkler, A. (1998).
Variations in eolian and carbonate sedimentation, sea surface temperature, and

915   productivity over the last 3 MY at Site 958 off Northwest Africa. In *Proceedings
of the Ocean Drilling Program, Scientific Results* (Vol. 159, pp. 3-16). Ocean
Drilling Program College Station, TX, 1998.

Pina-Ocoa, E., Hogslund, S., Geslin, E., Cedhagen, T., Revsbech, N. P., Nielse, L. P., Schweizer, M., Jorissen, F., Rysgaard, S., Risgaard-Petersen, N. and Canfield, D.

920   E.: Widespread occurrence of nitrate storage and denitrification among Foraminifera and Gromiida, PNAS, 107, 1148-1153, 2010.

Podlaska, A., Wakeham, S. G., Fanning, K. A., and Taylor, G. T.: Microbial community structure and productivity in the oxygen minimum zone of the eastern tropical North Pacific, Deep-Sea Res. Pt 1, 66, 77-89, 2012.

925   R Core Team: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, 2017

Rao, K. K., Jayalakshmy, K. V., Kumaran, S., Balasubramanian, T., and Kutty, M. K.: Planktonic foraminifera in waters off the Coromandel coast, Bay of Bengal, Indian J. Mar. Sci., 18, 1-7, 1989.

930   Rathburn, A. E., Willingham, J., Ziebis, W., Burkett, A.M., and Corliss, B. H.: A new biological proxy for deep-sea paleo-oxygen: Pores of epifaunal benthic foraminifera, Sci. Rep., 8, 9456, doi:10.1038/s41598-018-27793-4, 2018.

Ravelo, A. C., and Fairbanks, R. G.: Oxygen isotopic composition of multiple species of planktonic foraminfera: Recorders of the modern photic zone temperature,

935   Paleoceanography, 7, 815-831, 1992.

Rebotim, A., Voelker, A. H. L., Jonker, L., Waniek, J. J., Meggers, H., Schiebel, R., Fraile, I., Schulz, M., and Kucera, M.: Factors controlling the depth habitat of planktonic foraminifera in the subtropical eastern North Atlantic, Biogeosciences, 14, 827-859, doi:10.5194/bg-14-827-2017, 2017.

940   Regenberg, M., Steph, S., Nurnberg, D., Tiedemann, R., and Garbe-Schonberg, D.: Calibrating Mg/Ca ratios of multiple planktonic foraminiferal species with d18O-calcification temperatures: Paleothermometry for the upper water column, Earth Planet. Sci. Lett., 278, 324-336, 2009.

Richirt, J., Champmartin, S., Schweizer, M., Mouret, A., Petersen, J., Ambari, A., and

945   Jorissen, F. J.: Scaling laws explain foraminiferal pore patterns, Scientific Reports, 9, 9149, 2019.

Rippert, N., Nurnberg, D., Raddatz, J., Maier, E., Hathorne, E. C., Bijma, J., and Tiedemann, R.: Constraining foraminiferal calcification depths in the western Pacific warm pool, Mar. Micropaleontol., 128, 14-27, 2016.

950   Rippert, N., Max, L., Mackensen, A., Cacho, I., Povea, P., and Tiedemann, R.: Alternating influence of northern versus southern-sourced water masses on the equatorial Pacific subthermocline during the past 240 ka, Paleoceanogr. Paleocl., 32, 1256-1274, 2017.

Risgaard-Petersen, N., Langezaal, A. M., Ingvardsen, S., Schmid, M. C., Jetten, M. S. M.,

955   Op den Camp, H. J. M., Derksen, J. W. M., Pina-Ochoa, E., Eriksson, S. P., Nielsen, L. P., Revsbech, N. P., Cedhagen, T. and van der Zwaan, G. J.: Evidence for complete denitrification in a benthic foraminifer, Nature, 443, 93-97, 2006.

Ross, B. J. & Hallock, P.: Dormancy in the Foraminfiera: A review, J. Foramin. Res., 46(4), 358-368.

960   Russell, A. D., Honisch, B., Spero, H. J., and Lea, D. W.: Effects of seawater carbonate ion concentration and temperature on shell U, Mg, and Sr in cultured planktonic foraminifera, Geochim Cosmochim Acta, 68, 4347-4361, 2004.

Saito, T., P. R. Thompson, and D. Breger, 1976, Skeletal ultramicrostructure of some

elongate chambered planktonic foraminifera and related species, in Y.

965   Takayanagi, and T. Saito, eds., Progress in Micropaleontology. New York: The

American Museum of Natural History, pp. 278-304.

Sautter, L. R. and Thunell, R. C.: Seasonal variability in the d18O and d13C of planktic

foraminifera from an upwelling environments: sediment trap results from the San

Pedro Basin, Southern California Bight, Paleoceanography, 6, 307-334, 1991.

970   Schiebel, R., Zeltner, A., Treppke, U.F., Waniek, J.J., Bollmann, J. Rixen, T., &

Hemleben, C.: Distribution of diatoms, coccolithophores and planktic

foraminifers along a trophic gradient during SW monsoon in the Arabian Sea,

Marine Micropaleontology, 3-4, 345-371, 2004.

Schiebel, R., & Hemleben, C.: *Planktic foraminifers in the modern ocean* (pp. 1-

975   358). Berlin: Springer, 2017.

Schmidtko, S., Stramma, L., & Visbeck, M.: Decline in global oceanic oxygen content

during the past five decades, Nature, 542, 335-339, 2017.

Siccha, M., & Kucera, M.: ForCenS, a curated database of planktonic foraminifera

census counts in marine surface sediment samples. Scientific data, 4, 170109,

980   2017.

Smart, S. M., Ren, H., Fawcett, S. E., Schiebel, R., Conte, M., Rafter, P. A., Ellis, K. K.,

Weigand, M. A., Oleynik, S., Haug, G. H., and Sigman, D. M.: Ground-truthing

the planktic foraminifer-bound nitrogen isotope paleo-proxy in the Sargasso

Sea. Geochim. Cosmochim. Acta, 235, 463-482 2018.

985   Stramma, L., Johnson, G. C., Sprintall, J., and Mohrholz, V.: Expanding Oxygen-

Minimum Zones in the Tropical Oceans, Science, 320, 655-658, 2008.

Stramma, L., Johnson, G. C., Firing, E., and Schmidtko, S.: Eastern Pacific oxygen minimum zones: Supply paths and multidecadal changes, J. Geophys. Res. Oceans, 115, C9, 2010.

990   Stramma, L., Prince, E. D., Schmidtko, S., Luo, J., Hoolihan, J. P., Visbeck, M., Wallace, D. W. R., Brandt, R., and Kortzinger, A.: Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes, Nat. Clim. Change, 2, 33-37, 2012.

USNO Astronomical Applications Department,

995   http://aa.usno.navy.mil/data/docs/MoonPhase.php, accessed: 10/10/2019.

Venancio, I. M., Franco, D., Belem, A. L., Mulitza, S., Siccha, M., Albuquerue, A. L. S., Schulz, M., and Kucera, M.: Planktonic foraminifera shell fluxes from a `weekly resolved sediment trap record in the southwestern Atlantic: Evidence for synchronized reproduction, Mar. Micropaleontol., 125, 25-35, 2016.

1000   Wejnert, K. E., Thunell, R. C., and Astor, Y.: Comparison of species-specific oxygen isotope paleotemperature equations: Sensitivity analysis using planktonic foraminifera from the Cariaco Basin, Venezuela, Mar. Micropaleontol., 101, 76-88, 2013.

Weiner, A., Aurahs, R., Kurasawa, A., Kitazato, H., and Kucera, M.:Vertical niche

1005   partitioning between cryptic sibling species of a cosmopolitan marine planktonic protist, Mol. Ecol., 21, 4063-4073, 2012.

Wishner, K. F., Ashjian, C. J., Gelfmann, C., Gowing, M. M., Kann, L., Levin, L. A., Mullineaux, L. S. and Saltzman, J.: Pelagic and benthic ecology of the lower

interface of the Eastern Tropical Pacific oxygen minimum zone, Deep-Sea Res. Pt
1010   1, 42, 93-115, 1995.

Wishner, K. F., Gowing, M. M., and Gelfman, C.: Mesozooplankton biomass in the
upper 1000 m in the Arabian Sea: overall seasonal and geographic patterns, and
relationship to oxygen gradients, Deep-Sea Res. Pt II, 45, 2405-2432, 1998.

Wishner, K. F., Outram, D. M., Seibel, B. A., Daly, K. L., and Williams, R. L.:
1015   Zooplankton in the eastern tropical north Pacific: Boundary effects of oxygen
minimum zone expansion, Deep-Sea Res. Pt I, 79, 122-140, 2013.

Wishner, K. F., Seibel, B. A., Roman, C., Deutsch, C., Outram, D., Shaw, C. T., Birk, M
A., Mislan, K. A. S., Adams, T. J., Moore, D., and Riley, S.: Ocean
deoxygenation and zooplankton: Very small oxygen differences matter, Sci. Adv.
1020   4, eaau5180, 2018.

Wishner, K., Seibel, B., and Roman, C.: Event log from R/V Sikuliaq SKQ201701S
from January to February 2017. Biological and Chemical Oceanography Data
Management Office (BCO-DMO). http://lod.bco-dmo.org/id/dataset/755088,
access date: May 27, 2020, 2020.

1025 Wishner, K. F., Seibel, B., and Outram, D.: Ocean deoxygenation and copepods:
coping with oxygen minimum zone variability, Biogeosciences, 17, 2315-2339,
doi:10.5194/bg-17-2315-2020, 2020.

Woehle, C., Roy, A.-S., Glock, N., Wein, T., Weissenbach, J., Rosenstiel, P., Hiebenthal,
C., Michels, J., Schonfeld, J., and Dagan, T.: A novel eukaryotic denitrification
1030   pathway in foraminifera, Curr. Biol., 28, 2536-2543, 2018.