

## Response to Reviewer 1

Many thanks for your detailed comments on our manuscript. Each point is addressed individually below.

*“Most importantly, I would strongly suggest to convey analyses of the molecular genetics of the specimens of the two morphotypes (line 394). For unequivocal proof of the species concept, modern papers of the kind presented here may accept the great opportunity of molecular genetics, and not only rely on the morphospecies concept. Also line 404-406: “The shells of *G. hexagonus* in deeper, less oxygenated waters appeared more porous, larger, and less compact than those from shallower, more oxygenated environments.” These specimens may or may not represent two different genotypes”*

We agree that it is possible there are more than one genotype and would love to have genetic data to include. Unfortunately, the preservation of these samples makes them unsuitable for genetic analyses. We also see molecular genetics as an important future step to better understanding these OMZ-affiliated taxa and hope this can be carried out in the coming years.

*“Second most importantly, I would strongly suggest to change the statements in lines 375-379, which are not substantiated by data: “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, low abundance, and the historical dearth of surveys of living planktic foraminifera in low O<sub>2</sub> regions along the western African margin have biased observations of *G. hexagonus* in the modern Atlantic.” – Many studies of sediment trap and net tow samples in the South Atlantic off Namibia (Loncaric and colleagues from Bremen) and the Congo River mouth (Ufkes et al.), as well as surface sediment, would have certainly detected *G. hexagonus* if present. I have myself seen many net tow, sediment trap, and bottom sediment samples from the Atlantic and other ocean basins, including my PhD project on benthic foraminifers from surface sediments in the Gulf of Guinea, and I have never seen a test of *hexagonus* in that region.”*

We have removed reference to the African margin, as we agree that we lack affirmative reporting of *G. hexagonus* in these regions in particular. However, there are reports from Atlantic sediment traps (Smart et al., 2018 as cited) as well as from recent sediments (e.g., the Brown Foraminiferal Database) which demonstrate that *G. hexagonus* is and has been present in the recent past in some regions of the Atlantic.

The following references have all been added as suggested

*“Line 40: please refer to the nice paper of Schmidtko et al. 2017 on modern OMZs”*

*“Line 88: see also: Glock, N., et al. (2018) Nature Communications, 9, 1217, doi:10.1038/s41467-018-03647-5 Glock, N., et al. (2019) PNAS, 116 (8), 2860-2865, doi:10.1073/pnas.1813887116”*

*“Line 327: Please refer to Schiebel et al. (2004) for *T. sacculifer* in another study in a region with a prominent subsurface OMZ, i.e. the Arabian Sea.”*

*“Line 369: refer again to Schiebel et al. (2004)”*

*“Line 75: please add also Warren 1994, see Schiebel and Hemleben 2017”*

The reference from Schiebel and Hemleben (2017) appears to be “Warren, B.A. Context of the suboxic layer in the Arabian Sea. Proc. Indian Acad. Sci. (Earth Planet Sci.) 103, 301–314 (1994). <https://doi.org/10.1007/BF02839540>”. However, this article does not mention

foraminifera or plankton tows as relevant to Line 75. Is it possible that there is another citation that should be added here?

*“Line 125: please give the net strata depths and volume filtered for each net in Wishner et al. 2019, 2020b here as well. This does not consume much space, and saves the reader from consulting for additional literature.”*

These can be found in the supplement, reference to which is included here.

*“Lines 125-126: what was the filtered water volume?”*

This varied between tows and can be found in the supplement, which is now referenced here.

*“Line 227: Foraminifers do not really die in most cases, but reproduce. Therefore, you may change “dead” for “empty” (tests).”*

This is true in most cases and will be altered elsewhere in the manuscript. However, here we specifically reference a few individuals found with cytoplasm (not empty) well below their photic zone habitat. This is suggestive that they may not have successfully reproduced.

*“Lines 299-301: “This species can be considered an indicator of an OMZ habitat and may be useful as an OMZ marker in sedimentary records, as discussed below.” This should possibly be the final statement of the section. BTW: This finding is not new to science; please refer to the respective literature.”*

The sentence has been moved, and while the finding of *G. hexagonus* associated with the OMZ is not new, it has not to the best of our knowledge been used as an indicator of an overlying OMZ in the published literature.

*“Lines 302- 310 present a repetition of the “Results”. Please rewrite.”*

These lines have been rewritten with a greater emphasis on the implications rather than numeric abundances.

*“Line 318: “larger” reads better than “more large” to me.”*

There is a subtle but real distinction here. We don't have data on the distribution of size (“larger”) but are rather arguing that more individual foraminifera in the relatively large size class (> 222 µm) sampled by our nets were present. We have rephrased to clarify.

*“Lines 322-324: “Use of presence/absence of cytoplasm as an indicator for living foraminifera results in an overestimation of live individuals, as dead individuals may retain some cytoplasm while live individuals cannot be devoid of cytoplasm.” This is possibly not entirely true, since decease is most often caused by reproduction, and cytoplasm is consumed and partly converted into offspring (see above).”*

We agree and this has been rephrased as “dead or post-reproductive individuals” as both cases can result in a shell retaining some cytoplasm.

*“Line 427: Buchmann year of publication”*

I'm afraid, I don't understand this comment. Would it be possible for the reviewer to clarify so that we can address this?

*“Lines 431-432: “(e.g., Bijma. . .” Some species increase in weight, others decrease. Please see Beer et al., Geology, 2010, using samples from the Arabian Sea, i.e. another OMZ region.”*

This is an important point, but I would argue not directly relevant to the argument being made in the manuscript. Beer and other authors (for example also Weinkouf et al., 2016) raise the important caveat that carbonate chemistry may not be a primary driver of SNW in all species and regions, pointing to other drivers such as nutrients and temperature. However, it has not been shown, including by Beer et al., 2010, that any planktic foraminifer increases in weight as a response to decreasing carbonate chemistry. Our results are broadly consistent with a widely recognized carbonate ion driver in direction, though we do not explicitly discount other drivers, and given the lack of both in situ carbonate chemistry and other (e.g., nutrient measurements) a further discussion of potential drivers of SNW is really outside of the scope of this manuscript.

*“Line 447: better use outnumber or surpass instead of overwhelm.”*

We have removed this descriptive language so that the phrase reads “However, the increase in size with decreased oxygen availability is such that...”

*“Figure 2: The images may be oriented and organized in a way that makes comparison easier and consumes less space.”*

This figure has been made more compact.

The following changes will be made as suggested:

*“Line 158: you may want to explain the abbreviations F and F-1 at first mention.*

*Lines 212-214, and 220-221: You may skip the sentence on which species were present and absent. Many other species were possibly absent as well, and are not mentioned. The information on the presence and absence of species should also be available from figures and data tables.*

*“Line 108: change reches to reaches”*

*“Line 234: “Empty test assemblages”*

*“Line 453: better “as in some benthic. . .””*

*“Figure 8: upper quartile boxes of F-1 and F-2 are flawed.”*

Many thanks for your thorough review and perspective on our manuscript. Each point is addressed individually below.

*“The morphometric analyses were mainly done, using a normal light microscope. This has the advantage, that the use of the phenotypic plastic traits as paleoproxies can be done without electron-microscopy, which is both cheaper and faster. Unfortunately, this approach has also strong limitations. The pores of foraminifera are typically too small to measure their size correctly under a light microscope. Therefore, the measured total porosity is also likely to be very inaccurate. This might be one reason for the strong scattering in figure 9a and the low R2 of the correlation between porosity and dissolved oxygen.... I would recommend determining the porosity on a few electron microscope pictures and correlating them with the porosity measured on the same individuals using the light microscope method. This would give a coarse estimate about the accuracy of this method. The authors have already done a similar comparison using micro-CT. Nevertheless, micro-CT is also at the limit of resolution, considering the size of pores in foraminiferal tests.”*

We are in full agreement with the reviewer here as to both the limitations and benefits of using light microscopy for measurements of porosity. We have added a line explicitly discussing the trade-offs in using this method in our revised draft. In the case of *G. hexagonus*, the pores are quite large (see images with more to be included), meaning that the greatest limitation in practice has been the curvature of the shells. Images from micro-CT scans were an excellent way to minimize this problem, by generating an essentially unlimited number of angles available from which to measure porosity. We have included additional CT-scan generated images demonstrating both this approach as well as the resolution of the method.

In this particular case, SEM has the disadvantage of being a functionally destructive analysis. This is due to the need to mount quite fragile shells on carbon tape, coat them, and in some cases amputate chambers (to look at internal porosity). Given the limited number of shells available, and the limited benefits of SEM in addition to CT analyses, we have opted not to image our shells in that way. We leave open the possibility that this may be a preferable method for the development of a quantitative porosity-based proxy for oxygenation in *G. hexagonus*, but such a quantitative assessment is beyond the scope of the current paper, and likely this sample set. At this point, we are only able to demonstrate an empirical trend, captured by two very different approaches. We have tried to be explicit about these caveats, stating “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 would 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.”

*“Regarding this correlation: What kind of fit has been used to determine R2 and P. Was it a linear fit? Is it possible to give the equation of the fit in the paper?”*

*“In this context the authors state: “A comparison of the two methods carried out on a subset of shells (n = 31) showed that the results from the two approaches are correlated (R2 = 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 CTbased approach.” In my opinion a correlation coefficient of 0.37 is too low, to make such a statement, when comparing the two methods”.*

This is a linear fit and the equation has been included in the results ( $y = x \cdot 0.23 + 2.64$ ). The comparison is simply meant to demonstrate that multiple methods result in the same trend, but we would caution that due to the low predictive power of this relationship, light microscopy should not be used to estimate CT-based porosity. The two methods are not interchangeable, though both capture the same trend. We have tried to clarify this in our added discussion.

*“G. hexagonus and H. parapelagica seem to be well adapted to oxygen depleted environments. This is a very interesting finding for planktic foraminifers. What I miss in this paper is a small discussion about different survival strategies of (benthic) foraminifera to oxygen depletion. They might apply to planktic foraminifera, too.”*

We have added an additional short discussion of denitrification, dormancy, and specialized morphology in benthic foraminifera.

*“The finding that the size G. hexagonus specimens increases with decreasing oxygen is counterintuitive but very intriguing. A similar observation has been done on benthic foraminifera from the same region (Keating-Bitonti and Payne, 2017). The paper is already cited but it might be worth to mention the finding from above in the discussion.”*

We have included a clause on their results as to size, in particular that only two of four species analyzed demonstrate the expected decrease in size with decreasing oxygen concentrations.

*“The porosity of G. hexagonus seems to decrease with ontogeny. This seems to be the opposite trend than in benthic foraminifera. As far as I know, usually the last chamber is the most porous. The ontogenetic trend might be a problem for the application as a paleoproxy. Could the authors think about a method, that minimizes the influence of this ontogenetic trend?”*

The reviewer raises a very good point. Unfortunately, all of these analyses were carried out on plankton tow specimens which may have been at different stages of (late) ontogeny, which complicates the meaning of a “last” chamber. It will probably be necessary for more work to be done, in particular on shells at their terminal stage, before the findings presented here could be presented as a quantitative paleoproxy. We have tried to be more explicit about this limitation in our statement “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 would 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.”

*“Line 439: “is consistent with a reduction of overall calcification in low oxygen, DIC rich environments, where precipitation and maintenance of a shell may be more metabolically expensive.” Is there a reference that calcite precipitation is metabolically more expensive under oxygen depletion? Otherwise, this is very speculative. The formation of biomass, for example, is energetically favorable under oxygen depletion.”*

The implication is not meant to be that calcite precipitation is metabolically more expensive under oxygen depletion (this may or may not be the case, but we whole-heartedly agree that there is currently no evidence), but under a DIC-rich environment coincident with the OMZ. This has been rephrased as “...reduction of overall calcification in low calcite saturation states associated with the OMZ...”

*“Line 426: The authors write that nitrate increased with depth. Is there a correlation between shell size and nitrate availability? In this case, the increased porosity might be just a secondary feature, due to the lower surface to volume ratio in larger individuals.”*

Nitrate availability increases in the region with depth as does size, however as we do not have data from the same tows, attempting to correlate these two parameters directly would probably be overreach. That increased porosity could in a sense be compensating for lower surface/volume ratio is an interesting possibility and will be added to the discussion.

*“The following paper might be worth to be considered in the discussion: “Richirt, J., Champmartin, S., Schweizer, M. et al. Scaling laws explain foraminiferal pore patterns. Sci Rep 9, 9149 (2019). <https://doi.org/10.1038/s41598-019-45617-x>””*

The findings of this paper are now referenced.

*“I think the pictures of *G. hexagonus* in figure 2 are not very representative of this species. Is it possible to add electron-micrographs of the two species from this figure, focusing on the morphological traits that characterize these species?”*

We stated in our initial response that “We will add additional CT-scan images of *G. hexagonus* to a new panel in Figure 9, to demonstrate a greater range of the morphologies observed.”

However, we ultimately chose to add these scans to a new Figure (10) as a better way to address the reviewer’s suggestion.

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

Deleted: shell

Catherine V. Davis<sup>1</sup>, Karen Wishner<sup>2</sup>, Willem Renema<sup>3,4</sup> & Pincelli M. Hull<sup>1,5</sup>

Deleted: <sup>4</sup>

5 <sup>1</sup>Department of Earth and Planetary Sciences, Yale University, New Haven CT 06511,  
USA

<sup>2</sup>Graduate School of Oceanography, University of Rhode Island, Narragansett, RI 02882,  
USA

<sup>3</sup>[Department of Ecosystem & Landscape Dynamics, Institute for Biodiversity &  
Ecosystem Dynamics \(IBED\), University of Amsterdam, Amsterdam, the Netherlands](#)

Deleted: <sup>3</sup>Naturalis

<sup>4</sup>[Naturalis](#) Biodiversity Center, Leiden, the Netherlands

<sup>5</sup>[Peabody](#) Museum of Natural History, Yale University, New Haven 06511, USA

Deleted: <sup>4</sup>Peabody

15 **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

Deleted: of a

Deleted: deoxygenated

20 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

Deleted: shells

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.

Deleted: shells

Deleted: shell

Deleted: shells

## 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

Deleted: and



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  
60 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  
65 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  
70 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.

75 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

Deleted: shells

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., 85 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 90 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 95 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 100 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

**Deleted:** ; LeKieffre et al., 2017; Gooday, et al. 2020).

105 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  
110 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  
115 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

120

#### 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  
125 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).

Deleted: reches

## 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<sup>2</sup> 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 26<sup>th</sup> and February 7<sup>th</sup> 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

Deleted: A 1 m<sup>2</sup>

Deleted: eight or nine

Deleted: 8

Deleted: 9

Deleted: Wishner et al. 2019, 2020b

formalin at sea. Isolation of foraminifera from samples occurred in 2017-2019 at the University of Rhode Island. Between 3/10<sup>ths</sup> and 1/125<sup>ths</sup> of material in a net was examined, depending upon abundance of foraminifera, and all intact tests were isolated from the split.

Deleted: sample

Deleted: shells

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.

Deleted: shells

## 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<sup>-3</sup> 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).

### 185 2.3 Morphological Analyses

All individuals of the species *G. hexagonus* were weighed on a Mettler Toledo ultramicrobalance ( $\pm 1 \mu\text{g}$ ) 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  
190 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  
195 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  
200 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.

Deleted: shell

Deleted: by

Deleted: shell

Deleted: shells

Deleted: Shell

Deleted: shell

Deleted: shell

Deleted: shell

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  $\mu\text{m}$ ; realized resolution varied from 0.4-0.7  $\mu\text{m}$ . 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).

Deleted: analysed

### 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  $\text{ml L}^{-1}$  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  $[\text{O}_2] > 2.45 \text{ ml L}^{-1}$  (109  $\mu\text{M}$ ) as oxic, between 2.45  $\text{ml L}^{-1}$  and 1.4  $\text{ml L}^{-1}$  (63  $\mu\text{M}$ ) as transitional (“mild hypoxia” in previous literature), and  $< 1.4 \text{ ml L}^{-1}$  as OMZ conditions (“hypoxia” and below). Previous authors have distinguished between intermediate (0.5-1.4  $\text{ml L}^{-1}$ ) and severe hypoxia ( $< 0.5 \text{ ml L}^{-1}$ ).

235  $l^{-1}$ ; 22  $\mu M$ ), 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  
240 above, can be divided into three categories: those living in oxic conditions (minimum  
[O<sub>2</sub>] within a net > 2.45 ml L<sup>-1</sup>), OMZ conditions (maximum [O<sub>2</sub>] within a net < 1.4 ml L<sup>-1</sup>), 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<sup>-3</sup> and  
245 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  
250 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<sup>-3</sup>. This  
255 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.*

**Deleted:** (%). *Globigerinita glutinata*, *Hastigerina digitata*, *Globigerinoides conglobatus*, *Sphaeroidinella dehiscens*, *Candeina nitida*, *Globigerinella calida*, *Globigerina falconensis*, and *Neogloboquadrina dutertrei* were absent (Table 1; Fig....



*obliquiloculata*, and *G. bulloides* were found in low abundance (<1%) (Table 1; Fig. 6).

Deleted: %, and all other species were absent

265 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<sup>-3</sup>. 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<sup>-3</sup>)

270 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).

Deleted: is not

Deleted: comparable

### 3.3 ~~Empty Test~~ Foraminiferal Assemblages

Deleted: Dead

280 ~~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<sup>-3</sup> 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

Deleted: Dead

Deleted: in

Deleted: shells

Deleted: dead

295 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

300 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  
305 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  
310 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  
315 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),

Deleted: shell

Deleted: shell

Deleted: shells

Deleted: .

and with ontogeny within individuals (Fig. 8), demonstrating an interaction between size, ontogeny, and porosity.

#### 3.4.2 Size and Chamber Number

325 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<sup>-1</sup> (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  
330 occurred between 0.1 and 0.2 ml L<sup>-1</sup> O<sub>2</sub>, 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).

Deleted: shells

#### 3.4.3 Size-normalized Weight

335 *Globorotaloides hexagonus* ~~tests~~ were light for their size, with individual ~~test~~ weights averaging just 7.7  $\mu\text{g}$ , and ranging from 1 to 22  $\mu\text{g}$  for ~~tests~~ sized between 297 and 631  $\mu\text{m}$  in length. Size-normalized weight increased with oxygenation, especially below 0.2 ml L<sup>-1</sup> O<sub>2</sub> (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  
340 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),

Deleted: shells

Deleted: shell

Deleted: shells

although in our study the variance in size-normalized weight explained by size was low ( $R^2 = 0.10$  p-value  $< 0.001$ ).

#### 350 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.

Deleted: shell

Deleted: shell

### 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*.

Deleted: This species can be considered an indicator of an OMZ habitat and may be useful as an OMZ marker in sedimentary records, as discussed below.

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

365

375 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  
380 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  $\mu\text{m}$ ) of this species were likely to be present in our nets just prior  
385 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-  
390 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  
395 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-

Deleted: comprising 33% of the total assemblage

Deleted: and thus sampled

Deleted: 222  $\mu\text{m}$  mesh

Deleted: dead

Deleted: shells

bearing ~~tests~~ in OMZ nets, while only found in low abundances in surface assemblages.

**Deleted:** shells

This suggests that these two species are truly endemic to deeper hypoxic waters.

405 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  
410 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<sup>-3</sup> 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  
415 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,~~  
420 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.

**Deleted:** was

**Deleted:** Future sampling at higher vertical resolution through the oxycline is required to test this hypothesis.

#### 4.2 *Globorotaloides hexagonus* as an OMZ Indicator Species

*Globorotaloides hexagonus* was consistently found within our low oxygen nets,  
430 though individuals were sparsely distributed (mean density of 0.2 individual m<sup>-3</sup>), 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  
435 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  
440 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  
445 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  
450 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

**Deleted:** However, the

**Deleted:** frequently

**Deleted:** The

**Deleted:** shells

**Deleted:** ,

**Deleted:** , and the historical dearth of surveys of living planktic foraminifera in low O<sub>2</sub> regions along the western African margin

460 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  
465 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  
470 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).

475

#### 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  
480 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-  
485 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  
490 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  
495 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:

500 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

505 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

Deleted: shells

Deleted: shell

Deleted: .)

Deleted: shell

Deleted: shell

Deleted: shells

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 would 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).

Deleted: increased

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

Deleted: Shells

Deleted: shell

540 calcite saturation states associated with the OMZ, where precipitation and maintenance of a test may be more metabolically expensive.

Deleted: oxygen, DIC rich environments

Deleted: shell

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

Deleted: Shells

Deleted: .

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

Deleted: overwhelmed these other morphological features,

Deleted: had

545 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.

550 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.*

555 *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.

Deleted: shell

570

## 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.*

575 *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

Deleted: shell

(size-normalized weight, porosity) under the low oxygen and/or carbonate saturation state

Deleted: states

580 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

Deleted: shells

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

585 exclusively in the OMZ, recovery of *G. hexagonus* tests from sediments would be a

Deleted: shells

strong indication of low-oxygen mid-waters. Moreover, large tests with high porosity,

Deleted: shells

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  
595 conspecifics.

#### **Data Availability**

All data associated with this article is available in the supplement or has been previously  
600 published and archived on the BCO-DMO database found at [http://lod.bco505  
dmo.org/id/dataset/755088](http://lod.bco505<br/>dmo.org/id/dataset/755088).

#### **Competing Interests**

The authors declare that they have no conflict of interest.

Deleted: ¶

Formatted: Font: Bold

Formatted: Line spacing: Double

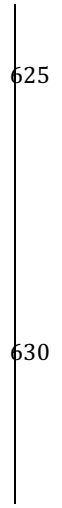
Formatted: Font: Bold

#### 605 **Acknowledgements**

Many thanks to D. Outram for laboratory assistance and 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  
610 Research Fellowship to P.M.H.

615

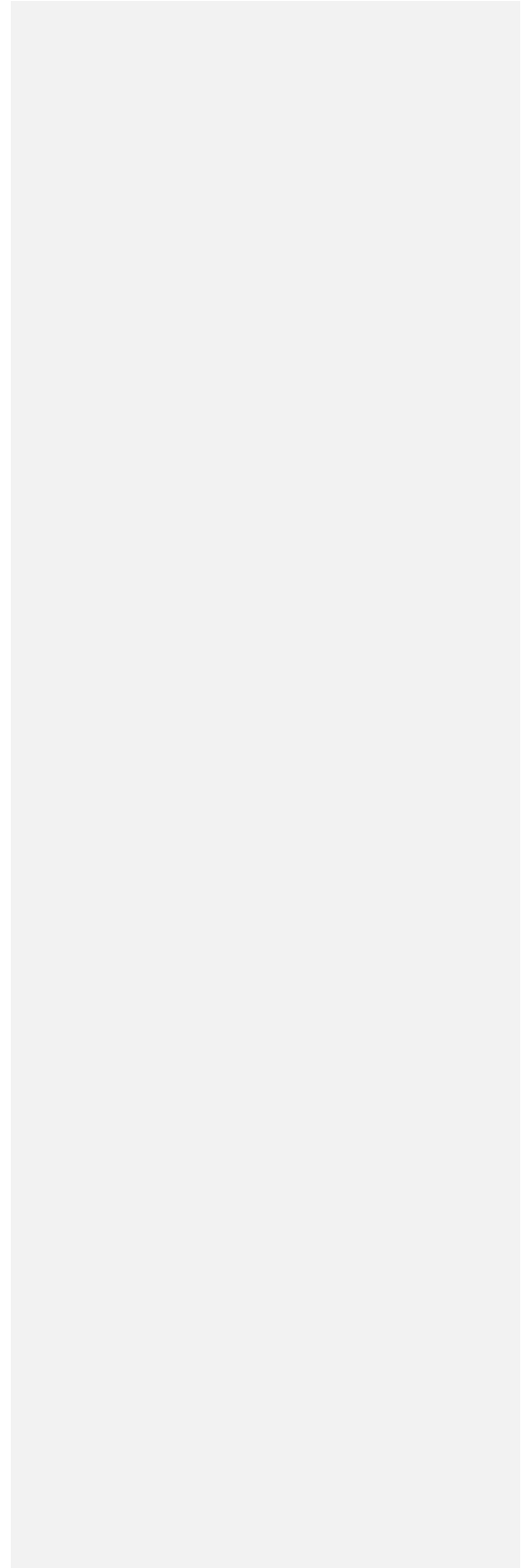
620



625

630

**Figures**

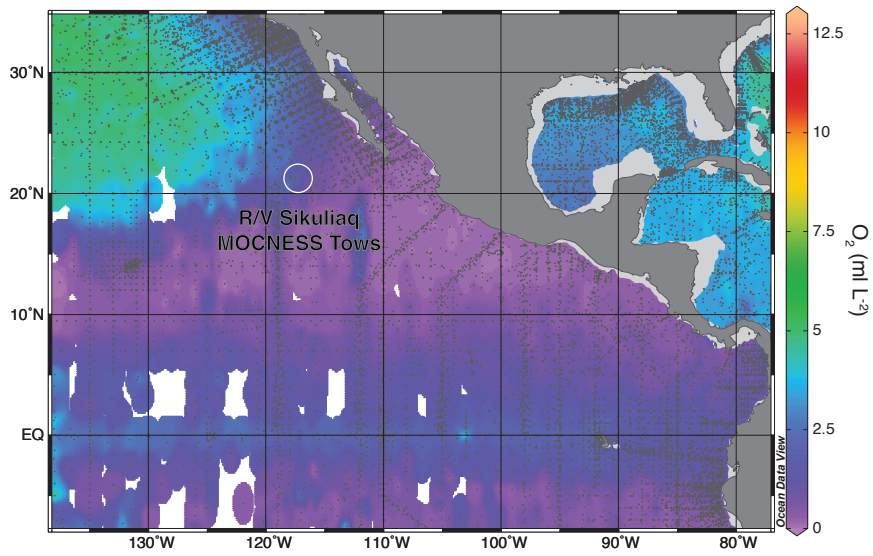


Species	% of Oxic Assemblage	% of Transitional Assemblage	% of OMZ Assemblage
<i>T. sacculifer</i>	74.6	22.1	3.6
<i>G. ruber</i>	5.4	0.6	0.3
<i>H. pelagica</i>	5.0	3.9	1.4
<i>G. siphonifera</i>	4.0	9.6	1.0
<i>O. universa</i>	3.5	5.5	0.1
<i>G. hexagonus</i>	3.1	40.7	86.1
<i>G. bulloides</i>	1.9	0.0	0.1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

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

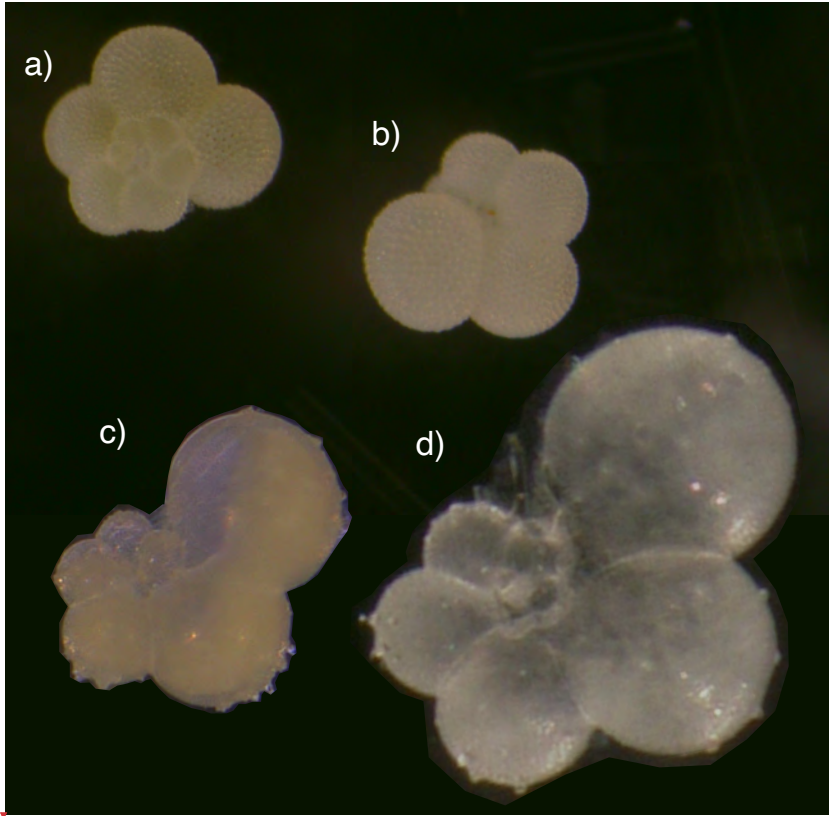
Deleted:

635 **Table 1.** The relative abundance of planktic foraminifera within oxygen defined assemblages: an oxic assemblage (minimum O<sub>2</sub> within a net O<sub>2</sub> > 2.45 ml L<sup>-1</sup>), transitional assemblage, and OMZ assemblage (maximum O<sub>2</sub> within a net < 1.4 ml L<sup>-1</sup>).

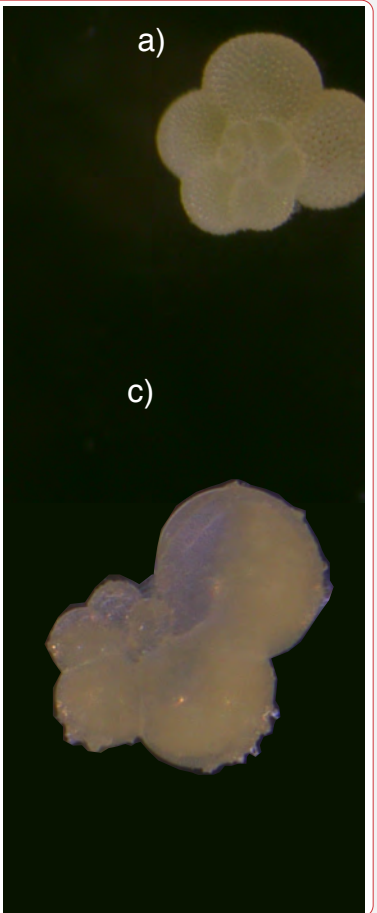


**Fig. 1.** Location of MOCNESS tows (white circle) taken onboard the *R/V Sikuliaq* shown on a map of dissolved oxygen measured at 200 m below the sea surface. Oxygen data are aggregated from the World Ocean Atlas (Garcia et al., 2018) and plotted using Ocean

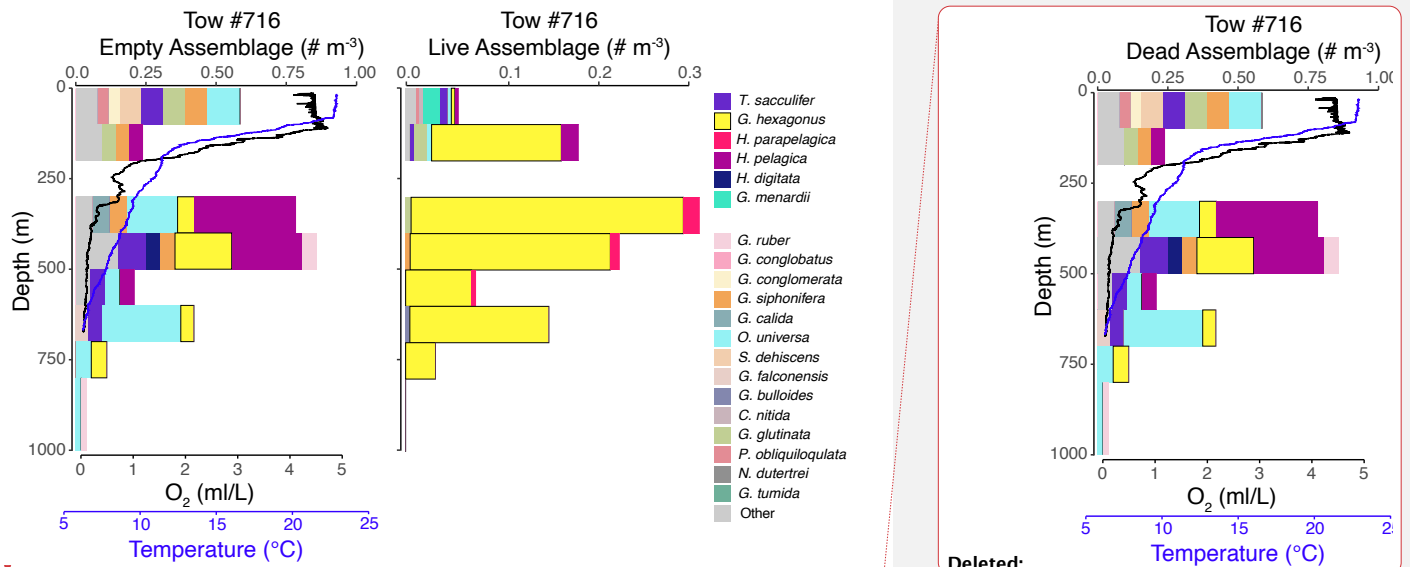




**Fig. 2.** A side-by-side comparison from the same tow of (a) a dorsal view of a live (cytoplasm containing) *G. hexagonus* and (b) a ventral view of ~~the empty test of~~ *G. hexagonus*, as well as (c) a live and (d) ~~empty~~ *H. parapelagica*

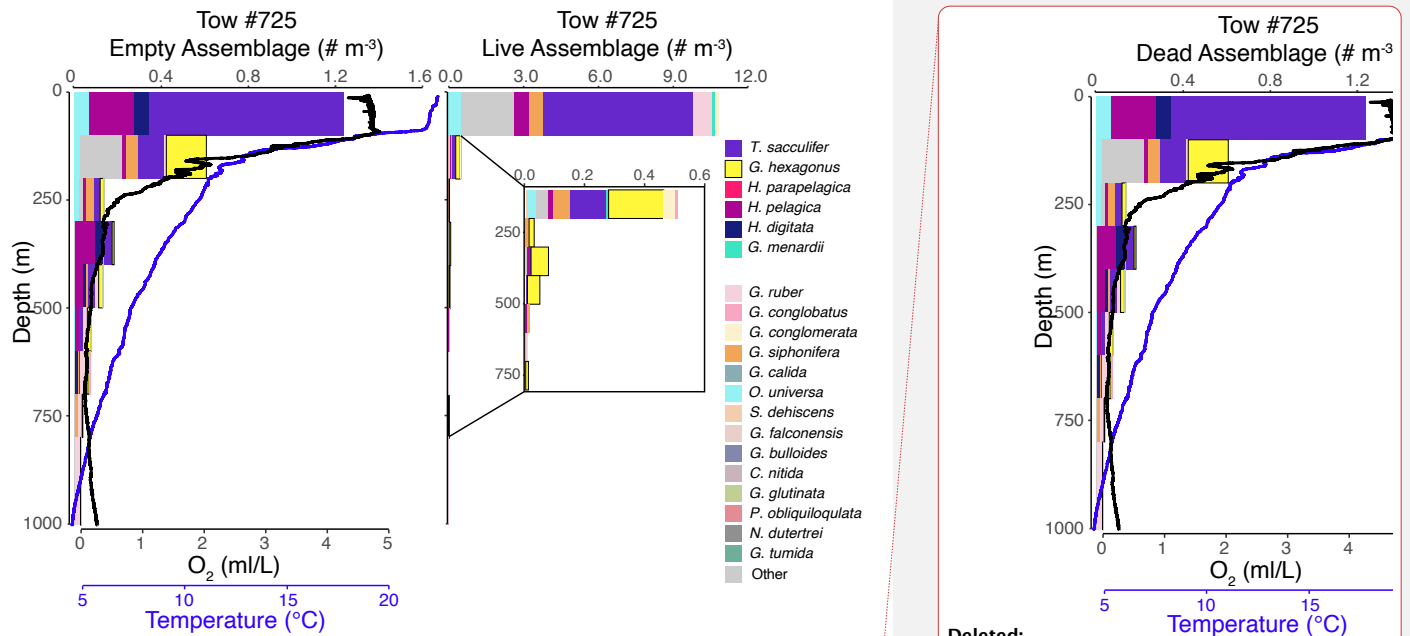


**Deleted:**  
**Deleted:** a dead (  
**Deleted:** )  
**Deleted:** dead



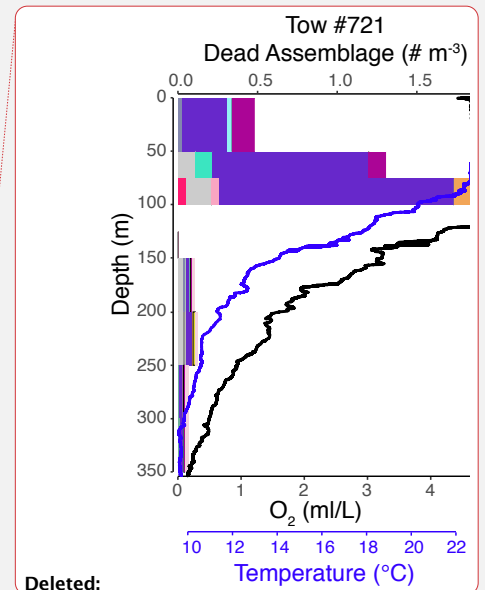
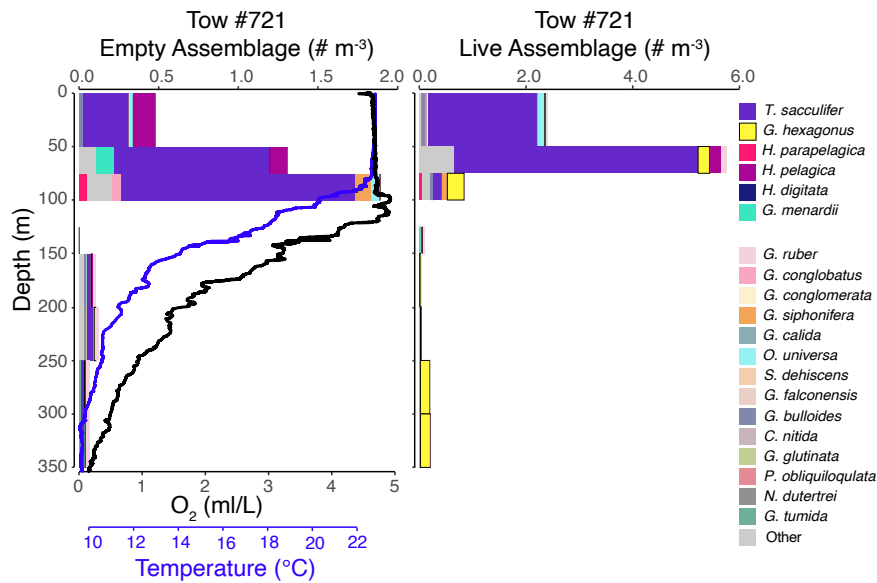
655 **Fig. 3.** Vertical profiles of the empty test assemblage, dissolved oxygen and temperature (left) and live foraminiferal assemblage (right) from tow #716 (0-1000 m). Each color represents a different species (see legend), with brighter colors for the six most salient species across nets and depths.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

Deleted: dead foraminiferal



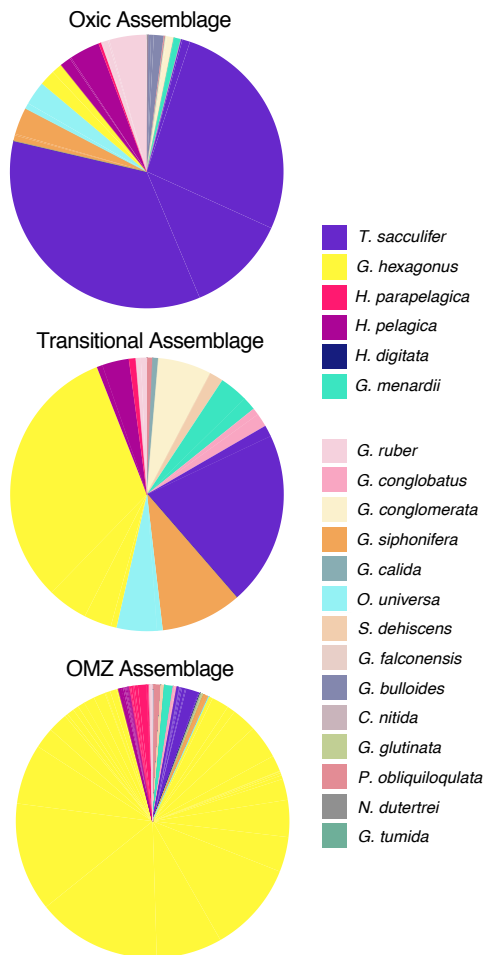
**Fig. 4.** Vertical profiles of the empty test assemblage, dissolved oxygen and temperature (left) and live foraminiferal assemblage (right) from tow #725 (0-1000 m). Each color represents a different species (see legend). Abundance axes vary, with the inset showing

665 an enlargement of abundance data in that part of the water column.

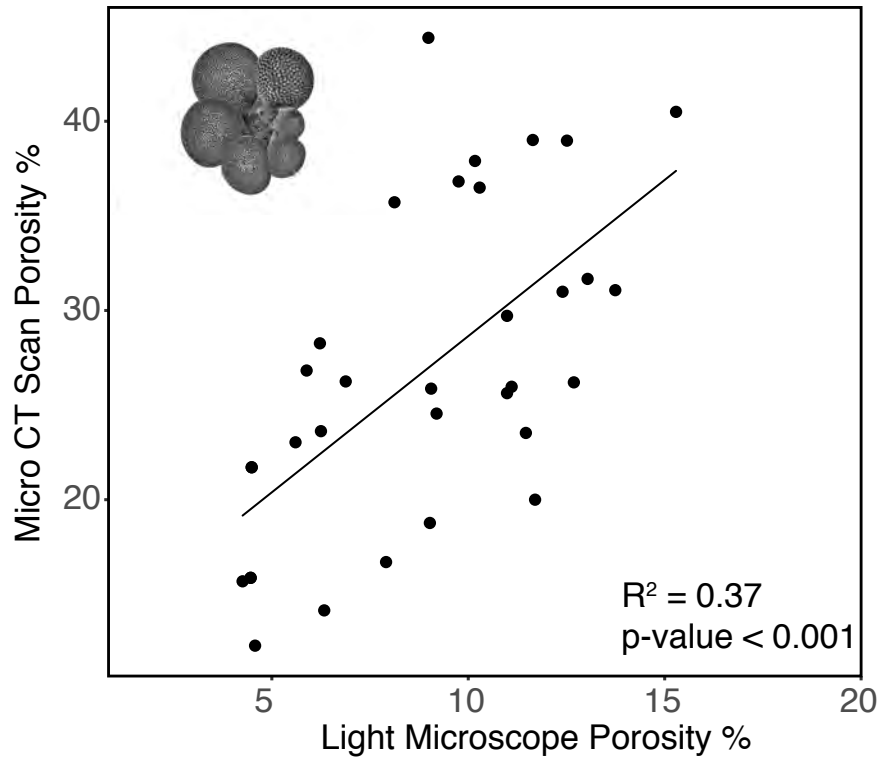


Deleted: dead foraminiferal

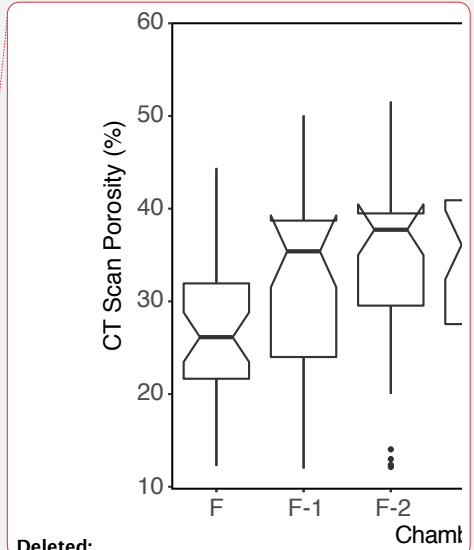
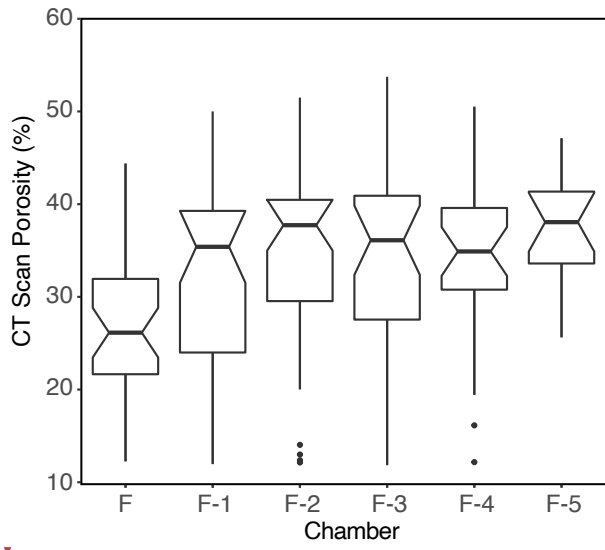
670 **Fig. 5.** Vertical profiles of the empty test assemblage, dissolved oxygen and temperature (left) and live foraminiferal assemblage (right) from tow #721 (0-350 m). Each color represents a different species (see legend). Abundance axes vary between panels.



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



**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.

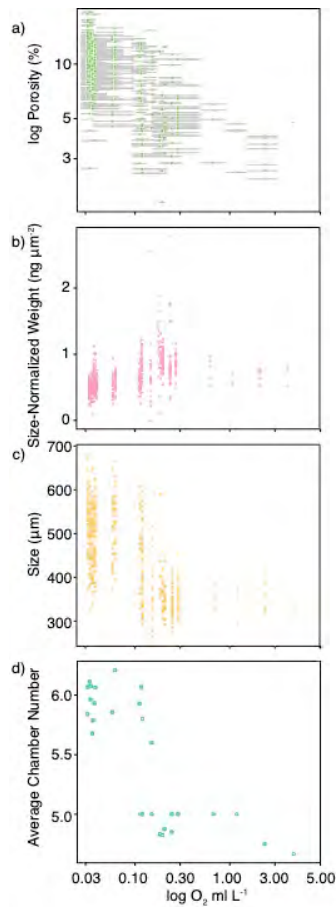


Deleted:

Deleted: shell

685

**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.



690

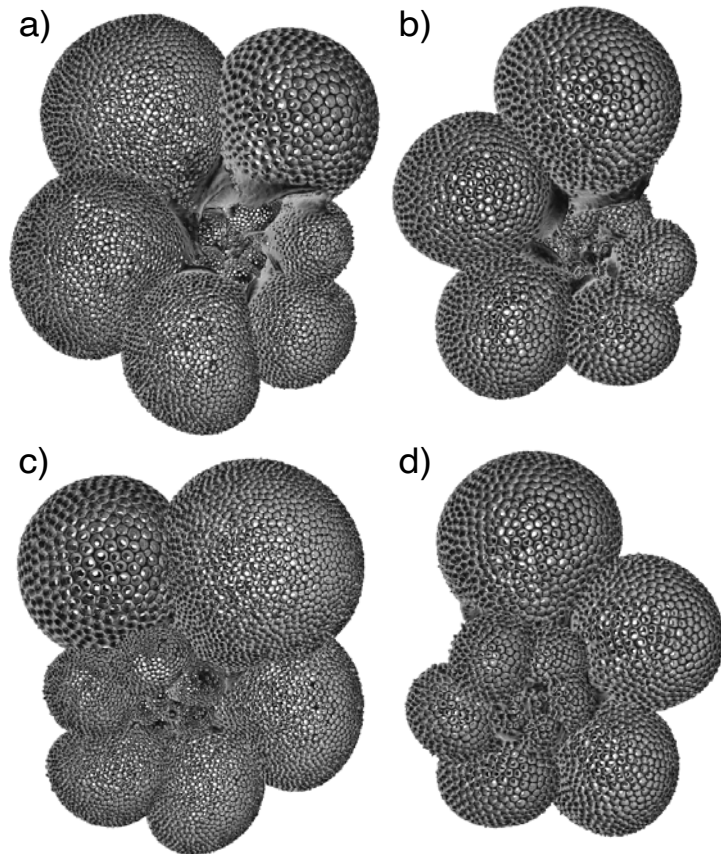
**Fig. 9.** Morphological traits of *G. hexagonus* tests plotted against the average dissolved oxygen (log scale) measured in the nets in which they were collected. The depicted characteristics are a) log of porosity, b) size-normalized weight (using the area-density method), c) size as measured by the 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.

695

Deleted: shells

Formatted: Font: Not Bold





700 **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.

705

## References

710 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. Foramin. Res.*, 16, 207-215, 1986.

715 [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 estimate dysoxic bottom-water oxygen concentrations; Santa Barbara Basin, US Pacific continental margin, *J. Foramin. Res.*, 27, 301-310, 1997.

720 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.

725 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, *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. *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

Formatted: Pattern: Clear (White)

- 730 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.
- 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,  
735 1990.
- Bijma, J., Faber, W. W., and Hemleben, C.: Temperature and salinity limits for  
growth and survival of some planktonic foraminifers in laboratory cultures, *J.*  
*Foramin. Res.*, 20, 95-116, 1990.
- Bijma, J., Honisch, B., and Zeebe, R. E.: Impact of the ocean carbonate chemistry on  
740 living foraminiferal shell weight: 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.
- Birch H., Coxall H. K., Pearson P. N., Kroon D., and O'Regan M.: Planktonic  
foraminifera stable isotopes and water column structure: Disentangling ecological  
745 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  
different ecological strategies within the genus *Neogloboquadrina* (planktonic  
foraminifer). *PloS one*, 13(1), e0191653.
- 750 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,

- K. A., Seibel, B. A., Telszewski, M., Yasuhara, M., and Zhang, J.: Declining oxygen in the global ocean and coastal waters, *Science*, 359, 2018.
- 755 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.
- 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.
- 760 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 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.
- 765 Cassman, N., Prieto-Davo, A., Walsh, K., Silva, G. G. Z., Angly, F., Akhter, S., Barott, 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.
- 770 Cignoni, P., Callieri, M., Corsini, M., Dellepiane, M., Ganovelli, F., and Ranzuglia, G.: MeshLab: an open-source mesh processing tool, Sixth Eurographics Italian Chapter Conference, 129-136, 2008.
- 775 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 digitate planktonic foraminifera, *Paleobiology*, 33, 495-516, 2007.

780 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 water-column denitrification derived from nitrogen gas measurements, *Nature Geosci.*, 5, 547, 2012.

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

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

795 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

foraminifera: Lunar reproduction cycle in *Globigerinoides sacculifer* (Brady),  
*Paleoceanography*, 6, 295-306, 1991.

800 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.

Fairbanks, R. G., Sverdrlove, M., Free, R., Wiebe, P. H., and Be, A. W. H.: Vertical  
distribution and isotopic fractionation of living planktonic foraminifera from the  
805 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*,  
19, PA2014, doi:10/1029/2003PA000970, 2004.

Fiedler P. C. and Talley L. D.: Hydrography of the eastern tropical Pacific: A  
810 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  
Ocean Atlas 2018, Volume 3: Dissolved Oxygen, Apparent Oxygen Utilization,  
and Oxygen Saturation. A. Mishonov Technical Ed.; NOAA Atlas NESDIS 83,  
815 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  
maximum of the northeastern tropical Pacific Ocean, *J. Mar. Res.*, 41, 747-768,  
1983.

820 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
- 825 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 Origin, Life in Extreme Habitats and Astrobiology*, eds Altenbach A. V., Bernhard J. M., and Seckbach J. (Springer Netherlands), Vol 21, 537-552, 2012.
- 830 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, 1217, 2018.
- 835 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.
- 840 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 the dark ocean – Challenging the paradigms of deep-sea ecology with special

- emphasis on foraminiferans and naked protists. *Eur. J. Protistol.*, 75: 125721.
- 845 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., Chalk, T. B., Stewart, J. A., Alt, C. H. S., Durrant, J. and Hull, P. M.: Size-dependent response of foraminiferal calcification to seawater carbonate
- 850 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, 2011.
- Hogslund, S., Revsbech, N. P., Cedhagen, T., Nielsen, L. P., and Gallardo, V. A.:
- 855 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., Kelly, A., Liu, Y., and Hull, P. M.: *Automorph*: Accelerating morphometrics with automated 2D and 3D image processing and shape extraction, *Methods Ecol.*
- 860 *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 Bay, California, *Limnol. Oceanogr.* 56, 562-576, 2011.
- Jorissen F. J., Fontanier C., and Thomas, E.: Chapter seven paleoceanographical proxies
- 865 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 shell flux of planktonic foraminifera in the Gulf of Mexico, *Biogeosciences*, 12, 30161-3070, 2015.
- 870 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 Wright, J. D.: Traditional and emerging geochemical proxies in foraminifera, *J. Foramin. Res.*, 40, 165-192, 2010.
- 875 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.
- Keating-Bitonti, C. R., and Payne, J. L.: Ecophenotypic responses of benthic foraminifera to oxygen availability along an oxygen gradient in the California Borderland, *Mar. Ecol.*, 38, e12430, 2017.
- 880 Keeling R. F., Körtzinger A., and Gruber N.: Ocean Deoxygenation in a Warming World, *Annu. Rev. Mar. Sci.*, 2, 199-229, 2009.
- Kennett, J. P., and Huddleston, P.: Abrupt climatic change at 90,000 yr BP: Faunal evidence from Gulf of Mexico cores, *Quaternary Res.*, 2, 384-395, 1972.
- 885 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 Waelbroeck, C.: Reconstruction of sea-surface temperatures from assemblages of planktonic foraminifera: multi-technique approach based on geographically

- constrained calibration data sets and its application to glacial Atlantic and Pacific  
890 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.
- Kuhnt, T., Friedrich, O., Schmiedl, G., Milker, Y., Machensen, A., and Luckge, A.:  
Relationship between pore density in benthic foraminifera and bottom-water  
895 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  
*Globobulimina turgida* (Baily), *J. Foramin. Res.*, 44, 1-5, 2014.
- Kuroyanagi, A., Kawahata, H., Nishi, H., and Hondo, M.C.: Seasonal changes in  
900 planktonic foraminifera in the northwestern North Pacific Ocean: sediment trap  
experiments from subarctic and subtropical gyres, *Deep-Sea Res. Pt II*, 49, 5627-  
5645, 2002.
- 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  
905 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  
Caribbean, Gulf of Mexico, and Italian stratotypes, University of Kansas  
Paleontological Institute, 1972.
- 910 LeKieffre, C., Spangenberg, J. E., Mabilieu, 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.
- Levin, L. A.: Oxygen minimum zone benthos: Adaptation and community response to hypoxia, *Oceanogr. Mar. Biol.*, 41, 41:1-45, 2003.
- 915 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 foraminifera: Sediment traps observations from southwest Taiwan waters, *Cont. Shelf Res.*, 84, 13-22, 2010.
- Leutenegger, S., and Hansen, H. J.: Ultrastructural and radiotracer studies of pore  
920 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 calibration study using the Cariaco Basin ocean time series, *Paleoceanography*, 28, 363-376, 2013.
- 925 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 Res.*, 36, 1557-1575, 2014.
- Marchant, M., Hebbeln, D., and Wefer, G.: Seasonal flux patterns of planktic  
930 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-latitude Pacific under glacial conditions, *Paleoceanogr. Paleocl.* 32, 41-55, 2017.

- 935 Medina Faull, L., Mara, P., Taylor, G.T., and Edgcomb, V.P.: Imprint of trace dissolved oxygen on prokaryoplankton community structure in an Oxygen Minimum Zone, *Front. Mar. Sci.*, 7, 360, 2020, doi:10.3389/fmars.2020.00360.
- Meiland, J., Siccha, M., Weinkauff, M. F. G., Jonkers, L., Morard, R., Baranowski, U., Baumeister, A., Bertlich, J., Brummer, G.-J., Debray, P., Fritz-Endres, T., 940 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.
- Moffitt S. E., Moffitt, R. A., Sauthoff, W., Davis, C. V., Hewett, K., and Hill, T. M.: 945 Paleooceanographic 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 between phytodetritus and benthic metazoans: carbon and nitrogen isotopic 950 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, *Paleoceanography*, 28, 453-467, 2013.
- 955 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,  
M.: Anaerobic metabolism of Foraminifera thriving below the seafloor, The  
960 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.

Ortiz, J. D., Mix, A., Rugh, W., Watkins, J., and Collier, R.: Deep-dwelling planktonic  
965 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  
Chile as intense source of CO<sub>2</sub> and N<sub>2</sub>O, *Cont. Shelf Res.*, 28, 2746-2756, 2008.

970 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<sub>2</sub> maximum in the oxygen minimum  
zone (OMZ), *Biogeosciences*, 8, 239-252, 2011.

Perez-Cruz, L. L., and Machain-Castillo, M. L.: Benthic foraminifera of the oxygen  
975 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  
productivity over the last 3 MY at Site 958 off Northwest Africa. In *Proceedings*

- 980 *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.  
E.: Widespread occurrence of nitrate storage and denitrification among  
985 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.
- R Core Team: A language and environment for statistical computing. R Foundation for  
990 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.
- Rathburn, A. E., Willingham, J., Ziebis, W., Burkett, A.M., and Corliss, B. H.: A new  
995 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 foraminifera: Recorders of the modern photic zone temperature,  
Paleoceanography, 7, 815-831, 1992.
- 1000 Rebotim, A., Voelker, A. H. L., Jonker, L., Waniek, J. J., Meggers, H., Schiebel, R.,  
Fraille, 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.

Regenberg, M., Steph, S., Nurnberg, D., Tiedemann, R., and Garbe-Schonberg, D.:

1005 Calibrating Mg/Ca ratios of multiple planktonic foraminiferal species with  $\delta^{18}\text{O}$ -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](#)

1010 [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.

Rippert, N., Max, L., Mackensen, A., Cacho, I., Povea, P., and Tiedemann, R.:

1015 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., Ingvarnsen, S., Schmid, M. C., Jetten, M. S. M.,

1020 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 Foraminifera: A review, \*J. Foramin. Res.\*,](#)

[46\(4\), 358-368.](#)

1025 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 ultrastructure of some elongate chambered planktonic foraminifera and related species, in Y. Takayanagi, and T. Saito, eds., *Progress in Micropaleontology*. New York: The American Museum of Natural History, pp. 278-304.

1030 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.

1035 ~~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. 1-358). Berlin: Springer, 2017.~~

1040 ~~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, 2017.

1045 Smart, S. M., Ren, H., Fawcett, S. E., Schiebel, R., Conte, M., Rafter, P. A., Ellis, K. K.,

Formatted: Font color: Auto, Pattern: Clear

Formatted: EndNote Bibliography, Indent: Left: 0", Hanging: 0.5"

Deleted: & Hemleben, C. (2017). *Planktic foraminifers in the modern ocean* (pp. 1-

Formatted: Font color: Auto, Pattern: Clear



- 1050 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.
- Stramma, L., Johnson, G. C., Sprintall, J., and Mohrholz, V.: Expanding Oxygen-  
Minimum Zones in the Tropical Oceans, *Science*, 320, 655-658, 2008.
- 1055 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.
- 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.
- 1060 USNO Astronomical Applications Department,  
<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., Albuquerque, 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  
1065 synchronized reproduction, *Mar. Micropaleontol.*, 125, 25-35, 2016.
- 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.
- 1070 Weiner, A., Aurahs, R., Kurasawa, A., Kitazato, H., and Kucera, M.: Vertical niche

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

1075 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 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.

1080 Wishner, K. F., Outram, D. M., Seibel, B. A., Daly, K. L., and Williams, R. L.: Zooplankton in the eastern tropical north Pacific: Boundary effects of oxygen minimum zone expansion, *Deep-Sea Res. Pt I*, 79, 122-140, 2013.

1085 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.* 4, eaau5180, 2018.

1090 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.

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.

1095 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  
pathway in foraminifera, *Curr. Biol.*, 28, 2536-2543, 2018.

