Southern California margin benthic foraminiferal assemblages across a modern environmental gradient record recent centennial-scale changes in oxygen minimum zone

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Abstract. Microfossil assemblages provide valuable records to investigate variability in continental margin biogeochemical cycles, including dynamics of the oxygen minimum zone (OMZ). Analyses of modern assemblages across environmental gradients are necessary to understand relationships between assemblage characteristics and environmental factors. Here, we analyzed five cores from the San Diego Margin (32°42'00"N, 117°30'00"W, 300-1175 m water depth) for core top benthic foraminiferal assemblages to understand relationships between community assemblages and spatial hydrographic gradients and down core to identify changes in the oxygen minimum zone through time. Comparisons of benthic foraminiferal assemblages from two size fractions (63-150 and >150 μm) exhibit similar trends across the spatial/environmental gradient, or in some cases exhibit more pronounced spatial trends in the >150 μm fraction. We identify two hypoxic associated species (*B. spissa* and *U. peregrina*), one oxic associated species (*G. subglobosa*) and one OMZ edge-associated species (*B. argentea*). A range of species diversity exists within the modern OMZ (1.5-2.6 H, Shannon Index), suggesting that diversity is not driven by oxygenation alone. Down core analysis of indicator species reveal variability in upper margin of the OMZ (528 m water depth) while the core of the OMZ (800 m) and below the OMZ (1175 m) remained stable in the last 1.5ka. We document expansion of the upper margin of the OMZ beginning 400 ybp on the San Diego Margin that is synchronous with other regional records of oxygenation.

1 Introduction

1.1 Microfossil record of coastal margin biogeochemical change

Ocean oxygen is declining globally; rising ocean temperatures decrease oxygen solubility at the surface and increased stratification inhibits ventilation, leading to decreased oxygen at depth (Breitburg et al., 2018; Levin et al.,
40   2009; Stramma et al., 2010). Expansions of oxygen minimum zones (OMZ) have already been documented and further expansions are predicted (Bograd et al., 2008; Schmidtko et al., 2017; Stramma et al., 2010). Within the California Current system, declines in dissolved oxygen, shoaling of the hypoxic boundary, and decreased pH have been documented (Bakun, 2017; Bograd et al., 2008). Analysis of past expansions and contractions of oxygen minimum zones are critical to developing accurate predictions of future change (Jaccard et al., 2014).

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Continental margin biogeochemical dynamics structure shelf ecosystems across space and time (Levin et al., 2009; Levin and Dayton, 2009). In particular, oxygenation is a key determinant of benthic zonation; seafloor ecosystems are subject to major turnover in response to relatively minor inferred changes in oxygen (Levin, 2003; Levin and Dayton, 2009; Moffitt et al., 2015b). Low-oxygen zones typically contain both low abundance and low diversity of
50   organisms (Levin, 2003; Levin and Dayton, 2009). However, several species of benthic foraminifera are adapted to survive in low-oxygen conditions and are thus present, and often abundant, in such environments (Bernhard and Gupta, 1999; Gooday et al., 2000; Kaiho, 1994, 1999; Keating-Bitonti and Payne, 2016).

Microfossil records from the Southern California Borderlands have been a critical tool for understanding changes in
55   productivity (Cannariato and Kennett, 1999; Emmer and Thunell, 2000; Stott et al., 2000), orbital and millennial scale climate changes (Hendy, 2010; Hendy and Kennett, 2000; Taylor et al., 2015), and climate change through the Holocene (Balmaki et al., 2019; Fisler and Hendy, 2008; Friddell et al., 2003; Roark et al., 2003). Benthic foraminiferal assemblages are also widely used as a proxy for changes in oxygenation through time (Balestra et al., 2018; Bernhard et al., 1997; Bernhard and Gupta, 1999; Cannariato and Kennett, 1999; Gooday, 2003; Moffitt et al.,
60   2014; Ohkushi et al., 2013; Shibahara et al., 2007). Previous studies utilizing benthic foraminiferal assemblages as a proxy for oxygenation demonstrated that the intensity and geographic extent of the CA margin oxygen minimum zone has oscillated in response to changes in climate and ocean temperatures on millennial timescales - weakening during cool periods and strengthening during warm periods (Cannariato and Kennett, 1999; Jaccard et al., 2014; Moffitt et al., 2014, 2015a; Ohkushi et al., 2013). Further work is needed on sub-millennial timescales to quantify
65   recent decadal to centennial changes in oxygen minimum zone dynamics.

Relationships between benthic assemblages and modern environmental conditions were previously developed through analysis of benthic foraminifera along environmental depth gradients and in laboratory culturing studies (Douglas, 1981; Douglas and Heitman, 1979; Loubere, 1991, 1996; Mackensen and Douglas, 1989, 1989). Previous
70   studies of oxygenation change over time from the Southern California margin focus largely on the Santa Barbara and Santa Monica Basins, due to their high sedimentation rates and regular laminations (Balestra et al., 2018; Cannariato and Kennett, 1999; Christensen et al., 1994; Kaiho, 1999; Moffitt et al., 2014; Schimmelmann et al.,

2013), yet significantly fewer studies investigate sediments outside of basin environments. Further analysis is needed to constrain relationships between benthic foraminifera and environmental conditions in the open continental margin where biological and chemical gradients are more extensively distributed.

1.2 Regional Setting

The California margin is a well-studied system characterized by southward flow of the California Current, a strong seasonal upwelling regime bringing cold, nutrient rich waters to the surface, high coastal productivity, and a large oxygen minimum zone occurring at intermediate water depths (Checkley and Barth, 2009). The San Diego Margin is dominated by two surface currents: the southward flowing California Current and the seasonal, northward flowing surface counter current, the Davidson Current (Checkley and Barth, 2009).

An important feature of California margin coastal oceanography is the presence of a large, intermediate depth oxygen minimum zone (OMZ) and carbon maximum zone (CMZ), (approx. 500 – 1000 m water depth) (Helly and Levin, 2004; Stramma et al., 2010). Three processes combine to determine the intensity and spatial extent of the modern California margin OMZ: physical mixing of well-oxygenated surface water, biological activity at the surface and at depth, and intrusion of lower oxygen bottom waters (Gilly et al., 2013). Thus, both physical processes (temperature-dependent diffusion from atmosphere, mixing, stratification, deep water circulation) and biological processes (primary productivity at the surface and respiration at depth) control the intensity and extent of OMZs (Gilly et al., 2013; Helly and Levin, 2004).

Here we utilize the spatial variability of the continental margin as a natural laboratory to analyze relationships between core top, modern benthic foraminiferal assemblages and *in situ* measurements of environmental parameters (temperature, oxygenation, carbonate chemistry). We then quantify benthic foraminiferal assemblages downcore to understand past environmental change.

2 Methods

2.1 Study site

The San Diego Margin is located in the Southern California Borderlands (Fig. 1). The margin slopes downward to a depth of approximately 1200 m at a distance of 30 km normal to shore (Fig. 1) and is bounded by a bathymetric rise (600 m water depth) to the west. All hydrographic data and sediment cores used in this study were collected by the San Diego Coastal Expedition aboard the R/V *Melville* in December 2012 by a team from the Scripps Institution of Oceanography.

2.2 Oceanographic data collection

Temperature, salinity, and dissolved oxygen were collected at each core location using a Seabird CTD (SBE9), with a dissolved oxygen probe (Seabird Electronics Sensor SBE43). Carbonate chemistry was completed using *in situ* bottle sampling for pH and total dissolved inorganic carbon (DIC); calculations of carbon dioxide (CO_2) were then

110   completed in CO2SYS and previously published (Nam et al., 2015; Takeshita et al., 2015). Bottom depths were
       measured acoustically at each site.

2.3 Sediment cores

       Five sediment cores collected along a depth transect from 300 to 1175 m depth were selected for use in this study
115   (Figure 1; Table 1). Short (15-31cm) surface sediment cores were collected along the coastal margin using a deep-
       sea multicore with 9 cm diameter cores. Each core was divided into 1 cm intervals aboard the ship and immediately
       frozen. Sediments were not stained upon retrieval; thus, we could not carry out an analysis of live vs. dead or depth
       habitat of these species. Total organic matter of core top sediments was measured as percent ash-free dry weight and
       previously published in Grupe et al. 2015 *(Grupe et al., 2015)*. Subsamples were each disaggregated in deionized
120   water, washed over a 63 μm sieve and oven dried at 50° C.

2.3 Foraminiferal assemblages

       Assemblages were counted from the > 150 μm and 63 - 150 μm fraction for comparison between the size fractions.
       Sediments were split using a sediment splitter; a minimum of 300 foraminifera per sediment sample (in the >150 μm
125   fraction) were counted for all core top samples to provide a representative sample of the whole sediment sample,
       unless fewer than 300 specimens were present in the sample. Assemblages in the 63 – 150 μm fraction were
       quantified from the same fraction as the > 150 μm to allow for comparison of abundance between the two groups.
       Down core assemblages were quantified in the > 150 μm size fraction (see discussion below) and a minimum of 150
       foraminifera per sediment sample were counted in all down core samples unless fewer than 150 specimens were
130   present in the sample.

       Surface sediment (0-1, 1-2 cm) calcareous benthic foraminiferal assemblages were described for all cores. Complete
       down-core records of benthic foraminiferal assemblages were examined at 1 cm intervals for cores MV1217-2-3
       (528 m), MV1217-1-3 (800 m) and MV1217-4-3 (1175 m).

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       Shannon Index of diversity was used to describe foraminifera diversity (Peet, 1974). Distance-based redundancy
       analysis (dbRDA) with Bray–Curtis distances was used to ordinate core top assemblages and examine relationship
       to environmental variables. Non-metric multidimensional scaling ordination, using square root transformation of
       assemblage species counts and Bray-Curtis similarities, were completed to identify relatedness between assemblages
140   through time. All multivariate analyses were completed using the Vegan R package (Myhre et al., 2017; Oksanen et
       al., 2013).

2.4 Radiocarbon based chronology

       Cores from two sites (528 m water depth, MV1217-2-3, 1175 m water depth MV1217-4-1 and MV1217-4-3) were
145   selected for radiocarbon (^{14}C) dating using mixed bulk planktonic foraminifera. Core MV1217-2-3 (528 m) was
       sampled at three 1-cm intervals (11-12 cm, 16-17 cm, 25-26 cm). Core MV1217-4-3 (1175 m) was sampled at one

1-cm intervals (5-6 cm) and core MV1217-4-1 (1175 m) was sampled at two 1-cm intervals (10-11 cm, 20-21 cm) (Table 2). Radiocarbon analysis was completed at the Lawrence Livermore National Laboratory using $\delta^{13}C$ assumed values following the convention of Stuiver and Polach 1977 (Stuiver and Polach, 1977). The quoted age was given

150 in radiocarbon years using the Libby half-life of 5568 years. The Calib7.1 calibration program was used to calibrate ages using a reservoir age of 220.0 +/- 40.0 (Ingram and Southon, 1996; Stuiver and Polach, 1977).

3.0 Results

3.1 Vertical profiles, sediment characterization of San Diego Margin

155 Across the depth profile, temperature decreased steadily with depth (300 m to 1175 m) ranging from 8.6°C (300 m) to 3.8°C (1175 m) (Figure 2, Table 1). Salinity (not plotted here) had a mean of 34.4 psu with a total range of 34.1 to 34.5 psu. Water column dissolved oxygen (DO) concentration documents a low oxygen zone, with a minimum occurring at 700 m water depth (0.26 ml/L; Figure 2, Table 1), compared to 1.54 ml/L at 300 m and 0.58 ml/L at 1175 m. Minimum pH is documented at 700 m (7.55) and is higher above (300 m, 7.65) and below (1175 m, 7.59)

160 the intermediate depth low pH zone (Figure 2, Table 1). Total organic matter increased with depth (6.8-14.7% AFDW). These results are consistent with previous analyses of the California margin OMZ/CMZ (Helly and Levin, 2004).

3.2 Benthic foraminiferal assemblage across modern environmental gradient

165 Relative abundance of benthic foraminifera was quantified for all sites in the 0-1 and 1-2 cm intervals. We compared the 0-1 cm interval to the 1-2 cm interval to assess if depth habitat of any species was determining their relative abundance in the core top assemblage. Specimens were not Rose Bengal stained, thus their presence in any interval does not indicate that they were living at the time of collection. We do not identify any significant relationship between relative abundance of a species and depth interval (in all cases $p>0.05$ or r^2 is <0.001). Foraminiferal

170 abundance is low (<100 individuals) in some of the samples from 0-1 cm. Thus, in order to utilize sufficient numbers of individuals and because there were no significant differences in abundance of species between 0-1 cm and 1-2 cm, for the rest of the discussion we refer to the 0-2 cm fraction as the core top material. Calcareous taxa dominated the assemblage at every site; agglutinated foraminifera made up 0-17.7% of the assemblage. The site at 700 m, at the core of the OMZ, had the largest relative abundance of agglutinated foraminifera comprising 17.7% of

175 the assemblage. Due to their propensity for degradation and to remain consistent with other regional studies, we exclude agglutinated taxa and all values are reported as percent of total calcareous taxa for the remainder of the text.

Total abundance of foraminifera decreases with depth (Figure 2). Core top assemblages were dominated by *Bolivina argentea, Uvigerina peregrina, Globocassidulina subglobosa, Epistominella* sp1*, Cassidulina carinata,* and

180 *Bolivina spissa,* in order of decreasing abundance. These dominant taxa make up more than 84% of all foraminifera counted across all core top samples. All other species each account for <4% of total assemblage across all core tops. The following taxa are found at all five water depths: *Bolivina argentea, Bolivina spissa, Bulimina* sp., *Cibicidoides*

sp*., Epistominella* sp*., Globobulimina pacifica, Globocassidulina subglobosa, Globobulimina ovata, Nonionella stella, Quinqueloculina* sp*.* and *Uvigerina peregrina.*

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First, we report the benthic foraminiferal assemblage from the >63 μm size fraction; we then report on a comparison between the 63 - 150 μm and >150 μm size fractions. The assemblage at 300 m is dominated by *G. subglobosa* (28%), *B. argentea* (25%), *U. peregrina* (10%), *E. pacifica* (8%), *Bolivina spissa* (6%); the species richness is 25 and diversity (Shannon Index, H) is 2.167. The assemblage at 528 m is dominated by *B. argentea* (34%), *U.*

190 *peregrina* (21%), *Epistominella* sp1. (17%), *C. carinata* (8%) and *G. subglobosa* (5%); the species richness is 26 and diversity (Shannon Index, H) is 1.945. The assemblage at 700 m is dominated by *Epistominella* sp1. (28%), *C. carinata* (15%), *U. peregrina* (13%), %), *G. subglobosa* (11%), and *B. spissa* (15%); the species richness is 24 and diversity (H) is 2.297. The assemblage at 800 m is dominated by *B. spissa* (16%), *U. peregrina* (16%), *Epistominella* sp1. (13%), *C. carinata* (10%), *Cibicidoides* sp. (10%), and *Globobulimina ovata* (13%); the species

195 richness is 26 and diversity (H) is 2.613. The assemblage at 1175 m is dominated by *C. carinata* (25%), *Epistominella* sp1. (20%), *G. subglobosa* (8%), *B. spissa* (6%), *Epistominella smithi* (6%); the species richness is 26 and diversity (Shannon Index) is 2.529 (Figure 3).

3.3 Comparison of benthic foraminifera in two size fractions

200 Comparison of abundance of foraminifera between the 63-150 μm and 150 μm shows higher abundance in the small fraction at 300 m, 700 m and 1175 m, and higher abundance in the large size fraction at 528 m and 800 m. Several taxa are found in both size fractions at all five water depths: *Globocassidulina subglobosa, Epistominella* sp1. Three species have significantly different relative abundances between size classes; three are more likely to be found in the 63-150 μm (*Cassidulina carinata, Epistominella* sp1 and *G. subglobosa*) and one species (*U. peregrina*) is

205 significantly more likely to be found in the 150 μm size fraction (ANOVA, $p < 0.05$ for all).

In the >150 μm size fraction, species diversity ranges from 1.31 – 2.80 (Shannon Index, H); minimum diversity is found at 528 m (1.31) and maximum diversity is found at 1175 m (2.80). Species richness ranges from 21-25, with the highest and lowest values at 1175 m and 700 m respectively. In comparison, in the 63-150 μm size fraction,

210 species diversity ranges from 1.97 – 2.69 (Shannon Index, H); minimum diversity is found at 300 m (1.97) and maximum diversity is found at 700 m (2.69). Species richness is lower in the 63-150 μm fraction relative to >150 μm fraction at all sites; richness ranges from 16 (at 700 m) to 21 (at 300 m).

When we consider the complete assemblage (>63μm) we can classify the most abundant species into four groups

215 based on their trends relative to the oxygen minimum zone. Two species are more abundant within the OMZ: *B. spissa,* and *U. peregrina*; we identify these species as dysoxic indicator species. One species is less abundant within the OMZ relative to above and below the OMZ: *G. subglobosa*; we identify this species as an oxic indicator species. Two species increase in abundance with water depth: *C. carinata* and *Epistominella* sp. One species is most abundant near the uppermost edge of the OMZ: *B. argentea*; this species may be edge-associated. Importantly, when

220   we consider only the >150 µm size fraction, we observe the same trends: high abundance in OMZ (*B. spissa, U. peregrina*), low abundance in OMZ (*G. subglobosa*), increased abundance with depth (*C. carinata* and *Epistominella* sp.), and edge-dominant (*B. argentea*). Generally, we find that trends across depth are similar between the complete (>63 µm) and large size fraction (>150 µm) or are more pronounced in the >150 µm size fraction compared to the 63-150 µm size fraction (Figure 3). In some taxa, trends in both size fractions have similar trends

225   across depth (*B. spissa, Epistominella* sp1., *G. subglobosa, C. carinata).* For other taxa, we observe a low relative abundance of a species in the (63-150 µm) fraction throughout all water depths, while for the same species in the 150 µm size fraction, we observe a pronounced trend through depth (*U. peregrina*, *B. argentea*).

         To further analyze these trends, we completed pairwise analysis of relative abundances of benthic foraminifera and

230   environmental parameters. DO concentrations and pH are correlated at all water depths; here we chose to compare foraminiferal abundances to dissolved oxygen, yet we acknowledge that these affiliations may be driven by the combined effect of the oxygen minimum/carbon maximum zone. When we analyze the complete assemblage (>63 µm) we identify a significant positive correlation between *G. subglobosa* and dissolved oxygen (r^2=0.76, p<0.05) and temperature (r^2=0.64, p<0.05) and a significant negative correlation between *G. subglobosa* and total organic

235   matter (r^2=-0.72, p<0.05). If we analyze the >150 µm size fraction only, we identify the same significant positive correlation between DO and *G. subglobosa* (r^2=0.96, p<0.05) and also identify a positive correlation between *C. carinata* and water depth; abundance of this species increases with depth (r^2=0.93, p<0.05). When we analyze the 63-150 µm size fraction alone, we identify the same trends as observed in the >150 µm fraction: a significant positive correlation between *G. subglobosa* and dissolved oxygen (r^2=0.90, p<0.05). and a significant positive

240   correlation between *C. carinata* and water depth (r^2=0.88, p<0.05). In the 63-150 µm fraction we also identify a significant negative correlation between *U. peregrina* and water depth (r^2=-0.95, p<0.05). We do not identify significant correlations between any other taxa and environmental parameter.

3.4 Multivariate analyses of benthic foraminiferal assemblage

245   Multivariate statistical analysis (using distance-based redundancy analysis) of core top assemblages identifies several taxa that contribute most strongly to the ordination of the assemblages (*G. subglobosa, Epistominella* sp1., *U. peregrina, B. argentea*) (Figure S1). Oxygenation operates on an axis - separating sites at 300 m and 1175 m from the three OMZ sites 528 m, 700 m, and 800 m. Temperature operates on a second axis (Figure S1). Our findings support previous work that identify *Globocassidulina subglobosa* with higher oxygen environments and

250   *Bolivina argentea* and *Uvigerina peregrina* with lower oxygen environments (Bernhard et al., 1997; Kaiho, 1994, 1999; Moffitt et al., 2014).

3.5 Age model development

         Radiocarbon dating of two cores yielded variable sedimentation rates, from 6.1 to 42.2 cm/ka (error of +/- 11.3, see

255   Table 2). An age model was developed for each core based on linear interpolation between radiocarbon dates (Figure S2). Core MV1217-3-3 (800 m water depth) was not radiocarbon dated; for this core we apply an average

sedimentation rate (19.6 cm/ka) generated from the core above (528 m) and below (1175 m) this core. All following results will be discussed in age (years before present).

3.6 Temporal change in benthic foraminiferal assemblages

Downcore assemblages were quantified in three cores (from 528, 800, and 1175 m water depth) in the >150 μm size fraction only, following results from core top analysis (see Discussion section). Downcore assemblages contained similar species to core top. Downcore assemblages were dominated by *Uvigerina peregrina, Bolivina spissa, Bolivina argentea, Globobulimina sp, Cibicidoides sp,* and *Epistominella* sp1, in that order. These dominant taxa make up more than 75% of all foraminifera counted across all cores and subsamples. All other species each account for less than 5% of total assemblage across all cores and depths. The total number of species in each sample ranged from 11 to 26, comparable to the number of species found in the core tops.

Multivariate statistical analysis of down core assemblages and core top assemblages shows that, through time, assemblage similarity within sites exceeds similarity to assemblages at any other site (Figure S3). We do not document any trended change in assemblages over time at any one site that is equal in magnitude to the spatial difference between modern sites. For this reason, we subsequently discuss change in assemblage through time at each site independently.

At 528 m water depth, we document variability in foraminiferal assemblages through time, with a notable shift occurring at 400 ybp. Diversity decreases from 400 ybp to present; oxic indicator taxa (*G. subglobosa*) decrease from 10% of the assemblage at 400 ybp to nearly absent from the assemblage in more recent sediments (Figure 4). Dysoxic indicator taxa exhibit complex trends: *B. spissa* stays at a very low relative abundance (<6% of assemblage) while *U. peregrina* increases to over 30% of the assemblage (Figure 4). We also document a major increase in the proportion of *B. argentea*; as discussed above, this is a species that we document occurring at the upper margin of the OMZ in the modern environment.

At 800 m water depth, we do not document a significant shift in relative abundance of oxic indicators or dysoxic indicators over time, or a significant change in diversity over the interval examined (Figure 4). We interpret these assemblages to reflect environmental stability over the past 1.5ka (Figure 4). At 1175 m water depth, we document little change in relative abundance of oxic and dysoxic indicator species from 200-800 ybp. Beginning at 200 ybp, we document an increase in *B. spissa*, but no change in *U. peregrina* (Figure 4)*.

4 Discussion

4.1 Benthic foraminiferal assemblages across modern environmental gradient

Analysis of benthic foraminifera from two size fractions (63-150 μm and >150 μm) across a modern environmental gradient improves our understanding of benthic foraminifera as a proxy for past change. At all sites measured here, species richness is greater in the >150 μm relative to the 63-150 μm fraction, yet there is no consistent relationship between diversity and size fraction. This may be due to the fact that in some species, we observe significant

variability in relative abundance across space in the >150 µm fraction, while in the 63-150 µm fraction there is little
change in relative abundance across sites. Total number of foraminifera in each size class varies with depth and we
295   do not see a trend of higher proportions of small foraminifera within the OMZ as shown in previous studies
(Venturelli et al., 2018). A full range of species diversity exists within the modern OMZ (1.3-2.6 H, Shannon Index),
suggesting that diversity is not driven by oxygenation alone. Importantly, the range in diversity across the gradient is
reduced when the complete assemblage is included, due to low diversity in the >150 µm fraction at 528 m.

300   In most cases, trends of relative abundance of benthic foraminifera across space are either 1) similar between the
complete assemblage (>63µm) and the >150 µm size fraction or 2) trends in the >150 µm size fraction are more
pronounced than in the complete assemblage. Trends across the OMZ gradient are similar in both size fractions in
G. subglobosa, Epistominella sp1, and *C. carinata.* If one were to interpret the combined assemblage or the >150
µm assemblage in these species, the results would be similar, despite the fact that these species are in higher
305   abundances in the small size fraction. Two species are present in the small size fraction in all sites in similar (low)
relative abundance, while in the >150 µm fraction, we document distinct trends in relative abundance across space
(*B. argentea* and *U. peregrina*). This is noteworthy as it may indicate that these species are able to tolerate a range
of environmental conditions, and thus are present in small numbers and small shell sizes at all sites, but that in
certain environments, these species are able to thrive and out-compete other species, thus allowing them to grow to
310   larger sizes (De Villiers, 2004; Gooday, 2003; Levin et al., 2010).

In the Southern California Borderlands, the disciplinary convention has largely been to focus on the >150 µm size
fraction and thus, quantifying this fraction is necessary for comparison to previously published studies (Balestra et
al., 2018; Cannariato and Kennett, 1999; Moffitt et al., 2014). Our findings show that spatial trends in the >150 µm
315   size fraction generally reflect those found in the >63 µm size fraction or are muted by the inclusion of the 63-150
µm. Thus, we recommend that workers utilize the >150 µm size fraction for analysis when targeting indicator taxa
such as *B. argentea, B. spissa, U. peregrina, G. subglobosa* or when assessing trends across the OMZ gradient.
However, it is useful to quantify the complete >63µm assemblage in a subset of samples to ascertain whether there
are important species or trends being missed. If the target of a project is to quantify changes in the ecology of a site
320   or in specific metrics such as diversity, shell size, or shell weight, we recommend the inclusion of the complete
assemblage (>63 µm). We acknowledge that the identification of microfossils as a tool for paleoceanographic
interpretation contains inherent uncertainty due to variability in identification of species between observers and
within single observers (Al-Sabouni et al., 2018; Fox et al., 2018; Hsiang et al., 2019). Further, it has been shown
that there is a correlation between size of specimen and accuracy of identification, meaning that the inclusion of the
325   smaller specimens in the >63 µm fraction may reduce the accuracy of identification (Fox et al., 2018). Given this
uncertainty, in subsequent text we focus only on spatial/environmental trends that change by a minimum of 10%
relative abundance across the depth transect or through time.

In order to better compare to other similar studies from the Southern California Borderlands, for the remainder of the discussion we analyze the >150 μm fraction only. We identify two hypoxic associated species (*B. spissa* and *U. peregrina*), one oxic associated species (*G. subglobosa*) and one OMZ edge-associated species (*B. argentea*). These trends are shown in both the >150 μm assemblage and in the complete assemblage (>63 μm). Not surprisingly, these taxa are commonly used as indicator species in previous studies (Balestra et al., 2018; Cannariato and Kennett, 1999; Moffitt et al., 2014). The species we identify as dysoxic and edge associated (*B. spissa, U. peregrina*, and *B. argentea*) are elongated in shape and are infaunal species. In comparison, *G. subglobosa* is more abundant in higher oxygen environments and is a spherical, epifaunal species. This supports previous findings that infaunal vs. epifaunal habitat preference impacts the species distribution across the oxygenation gradient (Kaiho, 1999; Venturelli et al., 2018). Infaunal species are more common within the OMZ, while epifaunal are more common in well-oxygenated areas.

Previous studies have categorized benthic foraminifera into three categories of oxygenation: oxic (>1.5 ml/L DO), suboxic (0.3-1.5 ml/L) and dysoxic (0.3ml/L) based upon similar studies combining *in situ* environmental conditions and assemblage data (Cannariato and Kennett, 1999; Douglas and Heitman, 1979; Kaiho, 1994; Moffitt et al., 2014). Our findings indicate that region (or environment) specific oxygen species associations may be necessary, as our findings do not align directly with previous categorization of species. Several species that are well recognized as low-oxygen indicators (*B. argentea, B. spissa,* and *U. peregrina*) were found at all water depths in this study, but we find only very low abundances of two well-documented low-oxygen indicator species, *Nonionella stella* and *Bolivina tumida* (Bernhard et al., 1997; Bernhard and Gupta, 1999; Cannariato and Kennett, 1999; Moffitt et al., 2014). These taxa have documented adaptations to extreme environments; *B. tumida* is associated with methane seep environments (Hill et al., 2003) and *N. stella* is known to sequester symbionts or plastids in extreme conditions (Bernhard and Bowser, 1999). We hypothesize that the marginal environment studied here does not reach the extreme hypoxic to anoxic conditions that are suitable for *B. tumida* or *N. stella.* Several species of documented oxic indicators (*Cibicidoides* sp. and *Quinqueloculina* sp.) are found across all depths (300 – 1175 m) and oxygenation environments (0.26-1.54 ml/L) in the San Diego Margin. Many past categorizations of these species were generated using species from very low oxygen basins (e.g., Santa Barbara Basin) where seasonal anoxia is present. The presence of oxic indicator species across all water depths may provide evidence for periodic flushing of high oxygen water or a selection for species that can tolerate a range of environmental conditions rather than a specific threshold of oxygenation. Oxygen concentrations may simply be within a range in which previously categorized 'suboxic' taxa thrive and that is not as extreme as environments in which previous studies were completed, Alternatively, the environment along the San Diego Margin may be more variable (has a wider range of oxygenation) than these extreme taxa can tolerate. Further, habitat heterogeneity, including grain size (not measured here), has been shown to play a role in the determination of species assemblages, particularly in low-oxygen environments in which the nature of the sediment matrix determines within sediment oxygenation (Levin et al., 2010; Venturelli et al., 2018).

365   We identify an anomalous assemblage at 528 m water depth; this assemblage is the least diverse (H=1.32).
      Importantly, the low diversity at this site is driven by the dominance of a single species, *B. argentea*. We observe the
      dominance of *B. argentea* at 528 m water depth, near the modern upper margin of the oxygen minimum zone and a
      lower relative abundance of this species at 700 and 800 m water depth, in the heart of the OMZ (Figure 3). This
      pattern of *B. argentea* at high abundances near the upper margin of the OMZ has been previously observed

370   (Douglas, 1981) and these species are often used as indicators of dysoxic environments (Bernhard et al., 1997;
      Kaiho, 1999). We document the presence of members of the *Bolivina* genera at all water depths. In some intervals
      described here, bolivinids make up more than fifty percent of the total assemblage, therefore, any changes in
      abundance of this genera alone can drive changes in the assemblages as a whole. While bolivinids are widely
      accepted as low-oxygen dwelling species, specifically, *Bolivina argentea* has been utilized as a low-oxygen

375   indicator taxon, analysis of their abundance and distribution requires careful scrutiny. Within-species variation of
      morphologic traits have been correlated with affinities for certain environmental conditions (Lutze, 1964), yet
      congeneric gradations such as those observed here in the bolivinid genera merit further investigation.

      We attribute some of the unexpected variability in benthic communities that does not correlate with bottom water

380   oxygenation to "edge effects" of the OMZ. Specifically, there is more biologically available nitrate and nitrifying
      bacteria at the edges of the OMZ as compared to the center, thus we expect greater nutrient concentrations and
      larger food availability due to the presence of these bacteria (Mullins et al., 1985). Seasonal or annual variability in
      oxygenation of the upper margin of the oxygen minimum zone causing a variable oxygenation regime at 528 m may
      drive selection for species that can tolerate a range of environmental conditions rather than a specific threshold of

385   oxygenation. Further, environmental and ecological factors may combine to drive assemblage diversity; the
      interactive effects of competition and environmental adaptation may promote habitat specialization at this water
      depth (Fine et al., 2004). While the sites measured here document effects of the upper margin of the OMZ (528 m
      site), they may exclude the lower margin of the OMZ due to sampling depths.

390   **4.2 Temporal change in benthic foraminiferal assemblages record environmental change through time**
      Following results of analysis across modern core tops, all down core benthic foraminiferal assemblages were
      collected from the >150 μm size fraction. The combination of analysis from three distinct modern environments
      (upper margin of the OMZ (528 m), the core of the OMZ (800 m) and below the OMZ (1175 m)) allows for
      reconstruction of oceanographic change through the water column. We acknowledge that the environment is more

395   variable than we can describe given the record available. Oxygenation varies on seasonal, annual, and decadal
      timescales - yet each interval of sediment analyzed represents >35 years, thus we are capturing a time-averaged
      signal. Further, several factors complicate our ability to interpret benthic assemblage records: relative preservation
      of various shell types, post-depositional changes in sediment, dominant fauna within some assemblages that
      dominate responses, and high frequency variability not captured in the record. Yet, we are still able to analyze

400   benthic foraminiferal assemblages to identify environmental changes through the time interval described here.

Integrating analysis of cores from multiple depths reveals decadal to centennial variability in oxygenation at the upper margin of the OMZ (528 m) during the last 1.5 ka, but little to no change in the oxygenation at the core of the OMZ (800 m) or below the OMZ (1175 m) (Figure 4). The change in assemblage at 528 m beginning at 400 ybp

405 indicates a transition to the OMZ 'edge' environment in which *B. argentea* and *U. peregrina* species dominate in the modern. The formation of an assemblage that is similar to modern at 400 ybp implies the onset of modern conditions at this site which would include relatively low oxygen with variable oxygenation on seasonal to yearly timescales. We interpret the transition in assemblage as a decrease in oxygenation at this depth and a shoaling of the upper margin of the OMZ beginning at 400 ybp and continuing to present. The combined suite of foraminiferal

410 assemblages reveals shoaling of the upper margin of the OMZ in the last 400 years, while the core of the OMZ and below the OMZ remained stable (Figure 4). As such, we document an expansion of the upper margin of the oxygen minimum zone beginning ∼ 1600 CE and continuing to the present.

Our findings are consistent with observations from other regional records of oxygenation, including those from well-

415 resolved records in nearby basins. Santa Monica Basin (SMB) and Santa Barbara Basin (SBB) are silled basins that experience periodic flushing; changes in the strength or oxygen content of North Pacific Intermediate Water, stratification or surface productivity can lead to changes in oxygenation within each basin (Balestra et al., 2018; Cannariato and Kennett, 1999; Schimmelmann et al., 2013). Marine sediment records from Santa Monica Basin show non-annual laminations (indicating a low-oxygen to anoxic environment) beginning 1600 CE and document

420 shoaling of the low-oxygen zone within the basin from 1600 CE to present (Christensen et al., 1994). Santa Barbara Basin has well-documented sediment laminations through most of the Holocene indicating persistent low oxygen, but also shows gradual intensification of the oxygen minimum zone within SBB since 1850 (Wang et al., 2017).

The synchronous decrease in oxygenation in Santa Monica Basin (Christensen et al., 1994) and San Diego Margin

425 (this study) from ∼1600 CE to present indicates that this deoxygenation is not driven by basinal changes alone; rather it is likely driven by regional scale phenomena. The decrease in oxygenation across the Southern California margin since 1600 CE could be attributed to 1) a change in oxygenation or strength of North Pacific Intermediate Water, 2) an increase in organic carbon flux from sea surface to depth driven by changes in surface productivity, or 3) decrease in bottom water mixing or ventilation as a result of changes in surface water temperatures. We note that

430 within the San Diego Margin and Santa Monica Basin records, deoxygenation trends begin ∼400 ybp but continue or intensify in the last 200 years. In the last 150 years, deoxygenation is synchronous across SBB, SMB and SDM. In this interval, decreases in oxygenation are potentially due to an increase in organic carbon supply from terrestrial sources due to human land use change in the Southern CA region (Tomasovych and Kidwell, 2017; Wang et al., 2017). Investigation of oxygenation change over time requires further research to identify forcing mechanisms for

435 changes in the upper margin of the OMZ and to discern the relative impact of human and natural forcing in changing oxygenation across the last century.

5 Conclusion

440 This spatial analysis of benthic foraminifera assemblages across a modern oxygenation gradient on the San Diego
Margin improves our understanding of the relationship between assemblages and their environment. Comparison of
the relative abundance of benthic foraminifera in two size classes (63-150 and >150 μm) across the modern OMZ
shows that trends are either similar in both size classes or are more pronounced in the larger size fraction. As a
result, we conclude that analysis of the >150 μm assemblage for this site provides the most useful record for

445 interpreting benthic foraminifera as a proxy for past change. We identify two hypoxic associated species (*B. spissa,*
and *U. peregrina*), one oxic associated species (*G. subglobosa*) and one OMZ edge-associated species (*B. argentea*).
Down core analysis of indicator species reveals variability in upper margin of the OMZ while the core of the OMZ
remained stable in the last 1.5ka. We document expansion of upper margin of OMZ beginning 400 ybp on San
Diego Margin that is synchronous with regional records of oxygenation.

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Data Availability

All data collected for this paper is electronically archived by the NOAA Paleoclimatology Database as "San Diego Margin Benthic Foraminiferal Assemblages from Late Holocene."

455 **Author Contributions**

HMP, SEM, and TMH conceptualized and designed the project. HMP, SEM, JTD, and KRR completed data collection. HMP, TMH, and PDR completed data analysis. HMP wrote the manuscript. All authors contributed to editing of the manuscript.

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Figures
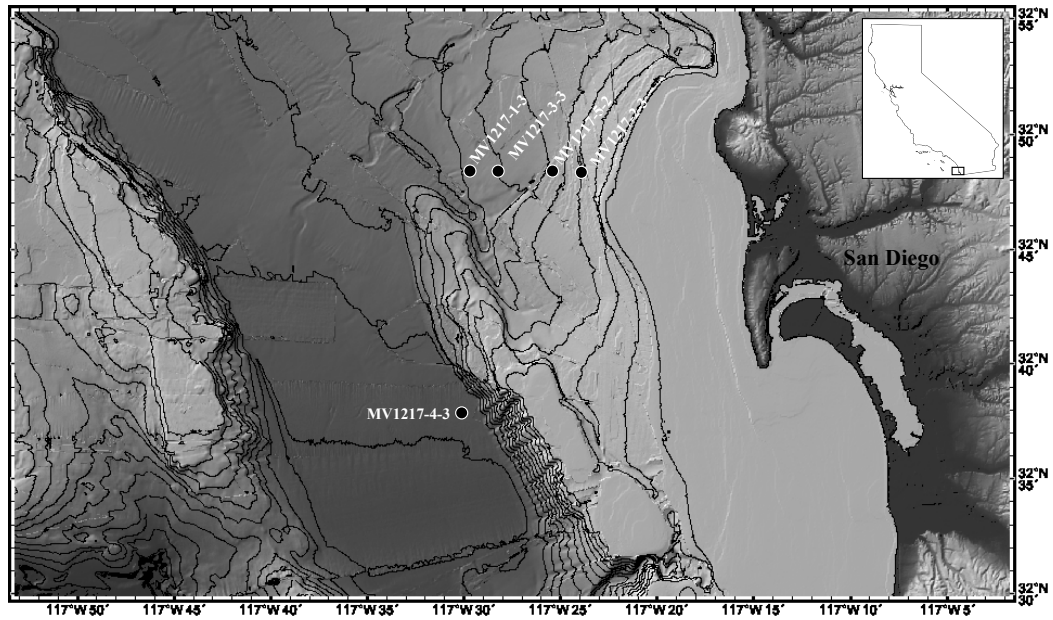
Figure 1. Map of cores used in this study

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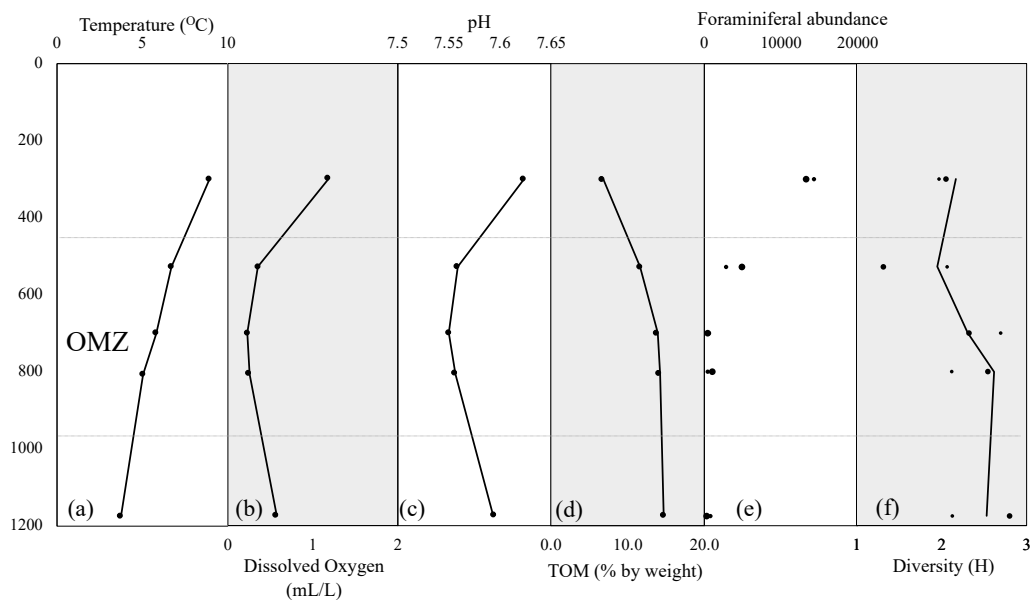


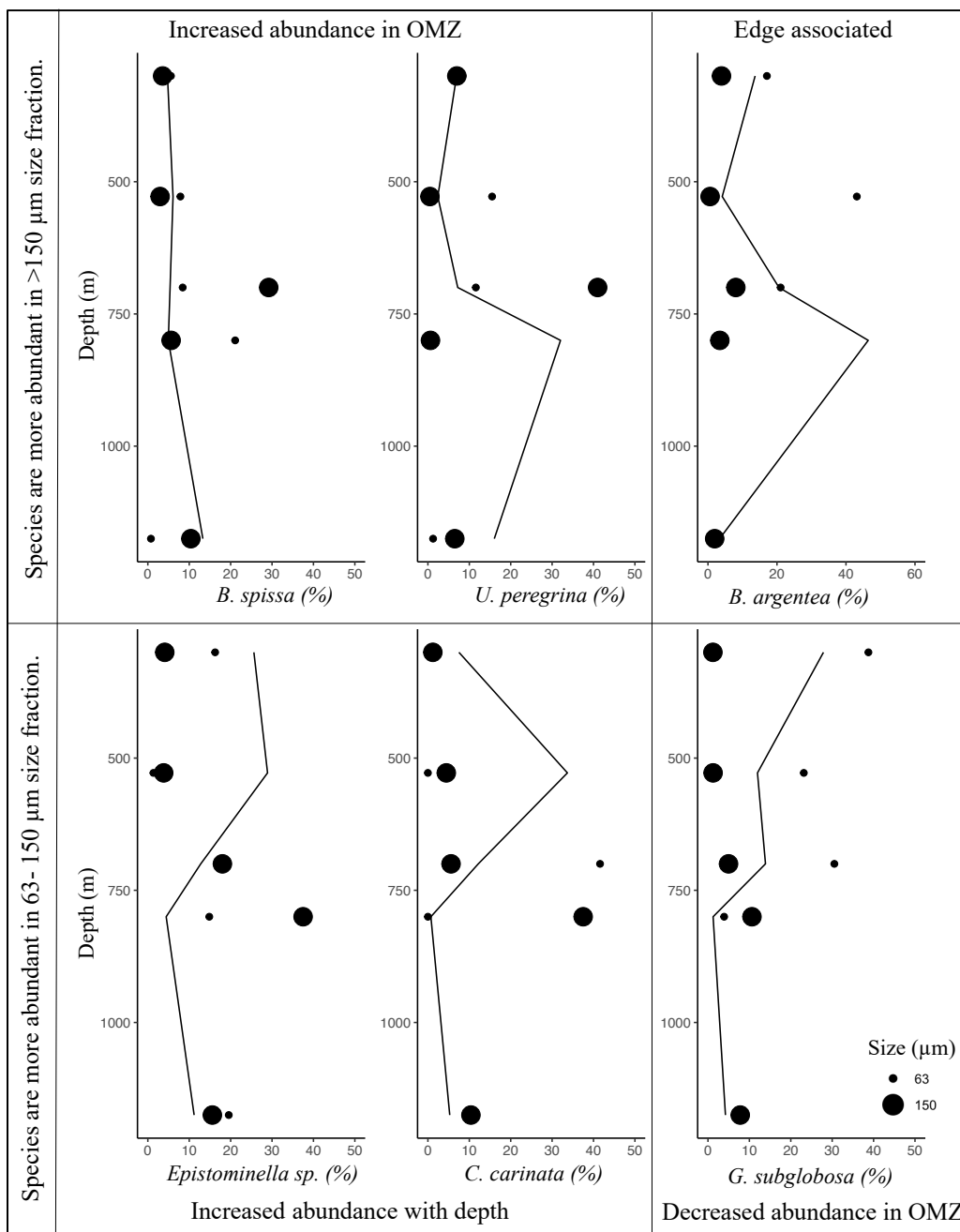
Figure 2. Profiles of temperature (a), dissolved oxygen (b), pH (c), and total organic matter (% by weight) (d) across
depth transect. Foraminiferal abundance (total calcareous foraminifera, (e)) and diversity (Shannon Index, H) are
shown for two size fractions. Large black dots are >150 µm size fraction, small black dots are 63-150 µm and black
line on diversity plot represents trends from the complete assemblage (>63 µm). Gray dashed line shows
approximate boundaries of the oxygen minimum zone.

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Figure 3: Relative abundance of foraminiferal species vs. water depth. Large black dots are >150 µm size fraction, small black dots are 63-150 µm size fraction and black lines represent trends considering the complete assemblage (>63 µm). General observations discussed in the text are noted here, e.g., species that increase in abundance in the OMZ, appear associated with the "edge" of the OMZ, etc. Note difference in x-axis in *B. argentea* plot.

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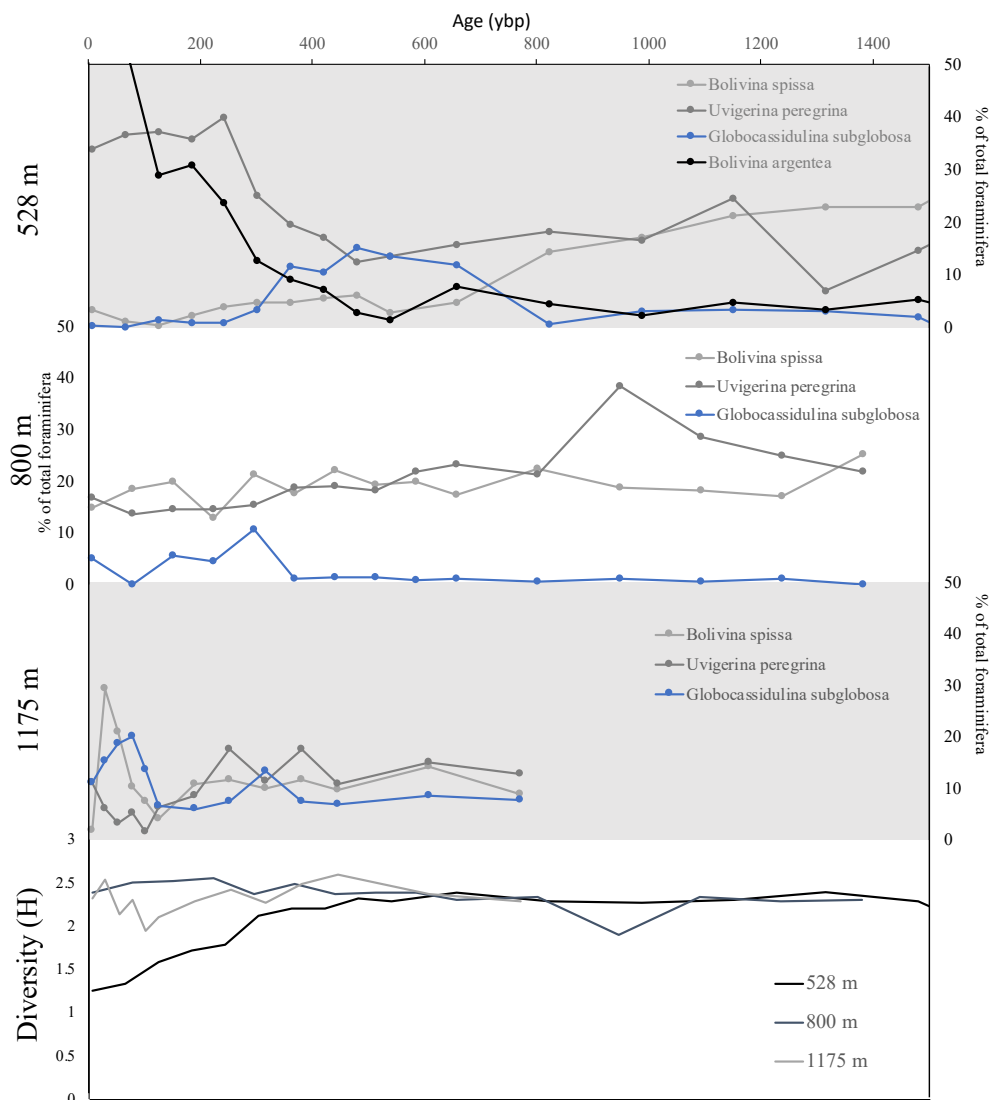
Figure 4: Top 3 panels show relative abundance of two species of low-oxygen foraminifera (*B. spissa* and *U. peregrina*, gray lines) and one species of oxic foraminifera (*G. subglobosa*, blue lines) from the >150 μm size fraction downcore through time, in years before present for cores from 3 water depths (528 m, 800 m, 1175 m). Top panel also includes relative abundance of *B. argentea*. Bottom panel shows diversity (Shannon's Index, H) through time for 3 cores)

Tables

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Core Name	Water Depth (m)	Latitude	Longitude	Length (cm)	Temperature (ºC)	Dissolved Oxygen (mL/L)	pH	TOM (% wt)
MV1217-5-2	300	32.8100166	117.4681	16	8.6137	1.54	7.65	6.8
MV1217-2-3	528	32.8100333	117.416583	26	6.6217	0.35	7.57	11.7
MV1217-3-3	700	32.8099666	117.450966	20	5.8975	0.26	7.56	13.9
MV1217-1-3	800	32.8095166	117.506933	20	5.0491	0.29	7.56	14.2
MV1217-4-3	1175	32.6333333	117.499883	16	3.8231	0.58	7.59	14.7

Table 1: Cores used in this study.

Core	Sample Interval	Age (14C years)	±	1 Sigma Maximum Calendar Age Range	1 Sigma Minimum Calendar Age Range	Age in Calendar Years	Sedimentation Rate (cm/ka)	±
MV1217-2-3	11-12 cm	1230	30	1403	1319	1361	16.9	1.0
MV1217-2-3	16-17 cm	2085	30	602	474	538	6.1	0.2
MV1217-2-3	25-26 cm	2405	35	237	107	172	24.6	0.1
MV1217-4-3	5-6 cm	670	35	1950	1837	1893.5	42.2	11.3
MV1217-4-1	10-11 cm	960	30	1630	1518	1574	15.6	0.2
MV1217-4-1	20-21 cm	1840	35	817	698	757.5	12.3	0.4

Table 2. Radiocarbon ages of bulk mixed planktonic foraminifera from MV1217-2-3 (528 m water depth), MV1217-4-3 (1175 m water depth) and MV1217-4-1 (1175 m water depth).

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