Benthic Foraminiferal Shell Weight:
Deglacial Species-Specific Responses from the Santa Barbara Basin

Catherine V. Davis^{1,2*}, Sarah E. Myhre², Tessa M. Hill^{1,2}

1. Department of Earth and Planetary Sciences, University of California Davis,
Davis, United States of America
2. Bodega Marine Laboratory, University of California Davis, Bodega Bay, United
States of America

* Bodega Marine Laboratory, 2099 Westside Road, Bodega Bay, CA, 94923

phone: +1 (707) 875-1972 e-mail: cvdavis@ucdavis.edu

1 **Abstract**

2 Here we present a record of size-normalized shell weight for four species of benthic
3 foraminifera through a period of rapid environmental change during the most recent
4 deglaciation (Santa Barbara Basin, CA). A strong Oxygen Minimum Zone (OMZ), the
5 product of high surface productivity and poor ventilation, characterizes the eastern
6 Pacific; this subsurface zone is mechanistically coupled with high concentrations of
7 dissolved inorganic carbon. The OMZ migrated vertically during warming of the last
8 deglaciation, leading to rapid shifts in the oxygenation and inorganic carbon system of
9 the benthos. The size-normalized weight (SNW) of benthic foraminifers *Uvigerina*
10 *peregrina*, *Bolivina interjuncta*, and *Bolivina tumida* reflect only the broad trends of the
11 vertical migration of the OMZ, and inorganic carbon system, overshadowed by clear
12 species-specific trends. The relative importance of OMZ migrations versus other
13 environmental variables and optimal growth conditions differs across species of benthic
14 foraminifera. In *U. peregrina*, SNW primarily peaks with foraminiferal density and
15 increased abundance of that species, while *B. interjuncta* and *B. tumida* increase in SNW
16 with a shrinking of the OMZ (and carbon maximum) in the late Holocene. *Bolivina*
17 *argentea* shows no long-term trends in SNW potentially due to its ability to migrate
18 through the sediment. Our results suggest that, while inorganic carbon and dissolved
19 oxygen may play a role in determining shell weight across species of benthic
20 foraminifera, neither parameter alone is responsible for changes in benthic foraminiferal
21 shell weight in the fossil record.

22

23

1 **Keywords**

2 Benthic Foraminifera, Size-Normalized Weight, Oxygen Minimum Zone

3

4 **1. Introduction**

5 *1.1 Oxygen Minimum and Carbon Maximum Zones*

6 Oxygen Minimum Zones (OMZs) are subsurface hydrographic zones in which oxygen
7 depletion acts as a biological barrier in both benthic and pelagic environments (Levin,
8 2003; Helly and Levin, 2004; Nameroff et al., 2004; Middelburg and Levin, 2009;
9 Paulmier and Ruiz-Pino, 2009). OMZs form in eastern boundary current subsurface
10 waters with high oxygen utilization and minimal advection (Wyrтки, 1962; Sarmiento et
11 al., 1988; Kamykowski and Zentara, 1990). These waters are enriched in dissolved
12 inorganic carbon (DIC) and depleted in dissolved oxygen (Wyrтки, 1962; Paulmier et al.,
13 2011), driving the development of an OMZ and associated ‘Carbon Maximum Zone’
14 (CMZ) as defined by Paulmier et al. (2011). Co-located with the OMZ are high
15 subsurface DIC concentrations, demonstrated in every major OMZ, including in detailed
16 investigations offshore the Chilean margin, where the OMZ/CMZ are coupled through
17 seasonal shifts (Paulmier et al., 2011). Observations verify the tight relationship between
18 dissolved oxygen and DIC along the California Margin (Figure 1; Talley, 2007), and
19 confirm the co-occurrence of the OMZ and CMZ in the California Current (Paulmier et al.,
20 2011). The mechanistic link between subsurface OMZs and CMZs implies that these
21 regions were likely coupled in past oceans as they are in the modern.

22

23 *1.2 Shell Weight as a Proxy for Oxygenation and Carbonate Ion Concentration*

1 Oxygen has previously been linked to morphologic changes in calcifying foraminifera,
2 with studies suggesting reduced shell weight in planktic foraminifera cultured at low
3 dissolved oxygen (DO) concentrations (Kuroyanagi et al., 2013). In benthic foraminifera,
4 species with smaller shells, larger pores and higher pore densities have been linked with
5 low oxygen environments (Perez-Cruz and Machain-Castillo, 1990; Moodley and Hess,
6 1992; Sen Gupta and Machain-Castillo, 1993; Glock et al., 2011; Kuhnt et al., 2013;
7 Kuhnt et al., 2014). Pore density could potentially account for changes in weight, with a
8 greater number of pores in the same size shell resulting in a lower shell weight, assuming
9 a consistent or increased pore size. Oxygen has repeatedly been shown to be a limiting
10 factor for benthic foraminifera (Murray, 2001; Linshy, 2008) and to have an influence on
11 morphology in terms of shell and pore size (Perez-Cruz and Machain-Castillo, 1990; Sen
12 Gupta and Machain-Castillo, 1993; Kuhnt et al., 2013), although it has not been directly
13 linked to weight variability.

14

15 Planktic foraminiferal shell weight has also been shown to be sensitive to the
16 concentration of carbonate ion ($[\text{CO}_3^{2-}]$) in surrounding waters during calcification
17 (Bijma et al., 1999; Russell et al., 2004) in addition to post-depositional preservation and
18 dissolution (Lohmann, 1995). For comparative purposes, we follow the assumption that
19 $[\text{CO}_3^{2-}]$ or pH decrease is a response to an increase in DIC relative to alkalinity. Culture
20 studies have concluded that planktic foraminifera calcify lighter shells in reduced $[\text{CO}_3^{2-}]$
21 environments (Spero et al., 1997; Bijma et al., 1999; Russell et al., 2004; Lombard et al.,
22 2010), although the magnitude of this relationship appears to be species-specific and
23 sometimes not a driving force in the fossil record (Bijma et al., 2002; Gonzalez-Mora et

al., 2008). Examples from both the fossil record (Barker and Elderfield, 2002; de Moel et al., 2009) and sediment trap collected planktic foraminifera (Moy et al., 2009; Marshall et al., 2013) indicate that shell weight may be controlled by variations in the DIC system through time.

Boltovskoy et al. (1991) reviewed a number of *in situ* studies of benthic foraminifera and noted that authors independently identified thinner shells and/or the development of alternate morphologies under various conditions of low $[\text{CO}_3^{2-}]$. Laboratory culture experiments have since repeatedly demonstrated that most, though not all, benthic foraminifera produce both smaller and lighter shells in response to reduced pH and/or experimental conditions influenced by high $p\text{CO}_2$, with species-specific degrees of susceptibility (Kuroyanagi et al., 2009; Dissard et al., 2010; Fujita et al., 2011; Hikami et al., 2011). The exceptions are some symbiont-bearing species, which exhibit reduced shell weight or growth rate not at all, or only at very high $p\text{CO}_2$ concentrations (those produced by experimental atmospheric conditions $>\sim 970$ ppm), similar to those found in the heart of the modern CMZ ($>1000 \mu\text{atm}$) (Talley, 2007; Fujita et al., 2011; Hikami et al., 2011; Paulmier et al., 2011; McIntyre-Wressnig et al., 2013). A possible influence of $[\text{CO}_3^{2-}]$ on ornamentation has also been identified (Khanna et al., 2013). These previous studies suggest that the shell weight of fossil benthic foraminifera, regardless of species, is influenced by the inorganic carbon system of surrounding waters.

1.3 Ecology of Benthic Foraminifera

1 Here we present a benthic foraminiferal record from Santa Barbara Basin (California,
2 USA) to test whether fossil foraminiferal SNW responds to known changes in the
3 OMZ/CMZ for the past 15,000 years. We focus on four species of benthic foraminifera:
4 *Uvigerina peregrina*, *Bolivina argentea*, *Bolivina interjuncta* and *Bolivina tumida*. All of
5 these species are associated with low oxygen environments to varying degrees. *Bolivina*
6 *argentea*, *B. interjuncta*, and *U. peregrina* are associated with intermediate to strong
7 hypoxia (Quinterno and Gardner, 1987; Mackensen and Douglas, 1989; Sen Gupta and
8 Machain-Castillo, 1993; Altenbach et al., 2011; Moffitt et al., 2014). *Bolivina tumida*,
9 sometimes associated with methane seeps (Hill et al., 2003), is found concurrent with
10 sediment laminations, which form only in conditions of $O_2 < 0.1 \text{ ml L}^{-1}$ and is therefore
11 interpreted as an indicator species of severe hypoxia (Behl and Kennett, 1996; Ohkushi et
12 al., 2013; Moffitt et al., 2014). Foraminifera from low-oxygen environments, including
13 Santa Barbara Basin, have also been associated with symbiotic protozoa (Bernhard and
14 Bowser, 1996; Bernhard et al., 2000) and nitrogen respiration (Risgaard-Peterson et al.,
15 2006; Bernhard et al., 2012).

16

17 *Uvigerina peregrina*, though somewhat variable in depth distribution, prefers a shallow
18 infaunal habitat (Corliss and Emerson, 1990; Ernst and van der Zwaan, 2004). *Bolivina*
19 *argentea* has an overlapping epifaunal or shallow infaunal distribution in the modern
20 North Pacific (Stott et al., 2000; Holsten et al., 2004), while $\delta^{13}\text{C}$ values from Santa
21 Barbara fossil shells are interpreted as showing a slightly deeper habitat relative to *U.*
22 *peregrina* (Kennett, 1995). Less is known about the microhabitat of *B. interjuncta*, while
23 *B. tumida* is thought to be the deepest dwelling of the species investigated here (Kennett,

1995). Moreover, some low oxygen benthic species, including *U. peregrina* and many other benthic foraminifera have been observed to migrate to shallower habitats within the sediment under low oxygen conditions (Alve and Bernhard, 1995; Moodley et al., 1998; Gross, 2000; Geslin et al., 2004; Fontanier et al., 2006); $\delta^{13}\text{C}$ values support similar behavior in the fossil record (Kennett, 1995). Examinations of living specimens have linked depth distribution in *U. peregrina* to macrofauna-influenced microhabitat such as zones containing biotic structures (Loubere et al., 1995), and in *B. argentea* to differing microhabitat preferences in the megalospheric and microspheric generations (Douglas and Staines-Urias, 2007; Staines-Urias and Douglas, 2009). Thus, the benthic foraminiferal record does not provide a consistent record of a single depth interval, but rather a record of environmental changes that permeate the sediment-water interface and the surficial sediment layers.

We present a multispecies record of benthic shell weight in order to test if: (1) variations in SNW have occurred during the dramatic OMZ/CMZ shifts in Santa Barbara, (2) SNW and size trends are consistent across species or species-specific; (3) changes in shell wall thickness are responsible for observed changes in SNW in *U. peregrina* and finally, (4) whether trends in individual species records covary with other environmental parameters.

2. Methods

2.1 Santa Barbara Basin and Core MV0811-15JC

Climate, oceanographic, and ecological records from Santa Barbara Basin exhibit remarkable, sub-millennial synchrony with Greenland ice core records (GISP2) (e.g.,

Grootes and Stuvier, 1997; Kennett and Ingram, 1995; Behl and Kennett, 1996; Cannariato et al., 1999; Hendy et al., 2002; Ivanochko and Pedersen, 2004; Moffitt et al., 2014). Biotic proxy reconstructions from Santa Barbara Basin sediment archives are of very high quality, due to high sedimentation rates and superb microfossil preservation (e.g., Kennett and Ingram, 1995; Behl and Kennett, 1996; Cannariato et al., 1999; Hendy et al., 2002).

Sediment was acquired from piston core MV0811-15JC (34.37°N, -120.13°W; 418 m water depth; 9.22 m in length), located at the northwestern edge of Santa Barbara Basin (Figure 2). Santa Barbara Basin is a restricted basin with a maximum depth of 590 m, a 230 m sill to the east and a 476 m sill to the west (42-100 cm ky⁻¹ sedimentation rate in core MV0811-15JC; Moffitt et al., 2014). The core was divided shipboard at a 10-cm resolution; sediment intervals were washed and sieved at 63 µm. We follow a previously published chronology (Moffitt et al., 2014) based upon two radiocarbon dates and three oxygen isotope tie-points to the well-dated Santa Barbara Basin core ODP 893A (Kennett, 1995; Hendy and Kennett, 2000). Foraminiferal community relative abundance, oxygenation marker species interpretations and δ¹⁸O stratigraphy for core MV0811-15JC are previously published (Moffitt et al., 2014). Core MV0811-15JC biotic proxies reflect both a regional signal of California Current OMZ intensity and local-scale basin-specific hypoxia (Cannariato et al., 1999; Ohkushi et al., 2013; Moffitt et al., 2014).

2.2 Shell Weight and Size-Normalization

1 All specimens of four benthic foraminifera (*Uvigerina peregrina*, *Bolivina argentea*,
2 *Bolivina interjuncta*, and *Bolivina tumida*) were picked from the washed >150 µm size
3 fraction. In the case of *Uvigerina peregrina*, with known morphologic plasticity and
4 subtypes (Schweizer et al., 2005; Schönfeld, 2006), only the characteristic elongate type
5 was selected and measured, although multiple morphotypes were present (See
6 Supplementary Figure fs01). Individuals with a combination of ridges and spines on the
7 final chamber were included. In the case of *B. argentea* and *B. interjuncta*, where strong
8 dimorphism is present, individuals of both the megalospheric and microspheric
9 generations were included in our analysis. A broad size fraction (>150 µm) was chosen in
10 order to ensure the inclusion of at least 7 individuals from each sediment interval.
11 *Uvigerina peregrina* specimens were cleaned by sonication for 20 seconds in methanol;
12 other species proved too fragile to be subjected to cleaning, but were generally
13 translucent enough for potential infilling to have been identified and avoided by light
14 microscopy. Foraminifers were weighed in groups on a Mettler Toledo XP2U balance
15 with group sizes ranging from 7 to 50 individuals. A subset of *U. peregrina* was also
16 weighed individually. Each sample was photographed and individual shells measured
17 using ImageJ (Abramoff, 2004). The abundance of the four species of interest did not
18 allow for a multispecies record prior to 13 ka, although *U. peregrina* appears back to 14.7
19 ka.

20
21 Size normalized weight (SNW) was calculated following previously published
22 methodologies (Barker and Elderfield, 2002; Alderidge et al., 2009; Beer et al., 2010;
23 Marshall et al., 2013), by normalizing a sample weight to both the average area of the

1 shell as well as the overall average area of all shells of that species across all samples. We
2 traced the 2-D silhouette of photographed foraminifera (see Supplementary Figure fs01)
3 and calculated SNW as:

$$\text{SNW}_{\text{Sample}} = (\text{AverageArea}_{\text{AllSamples}} / \text{AverageArea}_{\text{Sample}}) * \text{Weight}_{\text{Sample}} \quad (1)$$

4
5
6
7 This method was chosen as opposed to the area-density method used by Marshall et al.
8 (2013) due to the use of sample averages instead of individual weights. Normalization by
9 2-D surface area was chosen as the most straightforward shell measurement given the
10 shape of these species and known dimorphism in the length/width ratio of *B. argentea*
11 and *B. interjuncta* (Smith, 1963), and will be referred to hereafter as SNW. The best
12 approach to size normalization may differ in foraminifera with different shell geometries.
13 Samples were weighed in groups and thus no standard deviation is defined for individual
14 sample SNWs.

16 2.3 Morphologic Measurements

17 Shell length was measured in all species as the distance from proloculus to aperture.
18 Shell area was measured as the total 2-Dimensional area visible from above. Shell wall
19 thickness was determined by SEM imaging of epoxy-mounted and cross-sectioned *U.*
20 *peregrina* individuals (Figure 3). The total cross sectional area of calcite shell visible in
21 8-10 individuals from 8 samples was measured in ImageJ (Abramoff, 2004) by
22 subtracting the cross sectional areas, composed of empty internal space, from the total
23 cross sectional area of the shell.

1

2 **3. Results**

3 *3.1 Record of SNW in MV0811-15JC*

4 The range of values for non-normalized and normalized weights varied, with non-
5 normalized sample weights per individual ranging from 7-74 μg in *U. peregrina*, 4-26 μg
6 in *B. argentea*, 4-17 μg in *B. interjuncta*, and 5-20 μg in *B. tumida*. Sample average
7 lengths per individual ranged from 604-1433 μm in *U. peregrina*, 308-595 μm in *B.*
8 *argentea*, 246-472 μm in *B. interjuncta*, and 291-409 μm in *B. tumida*. When weights
9 were area-normalized, the range of weight values per individual were 8-64 μg in *U.*
10 *peregrina*, 11-35 μg in *B. argentea*, 4-17 μg in *B. interjuncta* and 7-16 μg in *B. tumida*
11 (Table 1). By any measure, *U. peregrina* is the most heavily calcified foraminifer. No
12 upper limits were imposed on the size fraction of foraminifera weighed (Table 1);
13 however all species except *U. peregrina* fall within the range of size fractions previously
14 utilized for SNW and compared in Marshall et al. (2013).

15

16 *U. peregrina* demonstrates high SNW in the Bølling-Allerød, from 14.7 to 12.9 ka
17 (Figure 4). *Bolivina interjuncta* exhibits stable SNWs when present in both the Bølling-
18 Allerød and Younger Dryas, while neither *B. argentea* or *B. tumida* is present in large
19 numbers through this interval. Bolivinid species are poorly represented in the Younger
20 Dryas (12.9-11.7 ka) and when present do not show extremes in SNW. In *U. peregrina*,
21 SNW is low during the Younger Dryas, with the exception of apparent high SNW just
22 prior to Termination IB. This generally correlates to an ephemeral change in assemblage
23 from hypoxic to oxic marker species. Species investigated here are more abundant in the

1 Holocene, providing a more consistent record of long-term variability. A distinct interval
2 of increased SNW in *U. peregrina* occurred during the mid-Holocene, along with
3 increased relative abundance in *B. tumida* and *B. interjuncta* between 7.5 and 5 ka.
4 *Bolivina argentea* does not show this increase (Figure 4).

5

6 3.2 Record of Size in MV0811-15JC

7 The average length of shells, highly influenced by both the size and total number of
8 chambers, is most variable in *U. peregrina*. There is a marked increase in overall size at
9 10-6 ka, with very short lengths previous to this peak and averages around 350 μm
10 subsequently (Figure 5; see Supplementary Table). Average length in *B. argentea* is
11 variable but shows no distinct trends through the Holocene. Length peaks in *B.*
12 *interjuncta* between 7-6 ka. In *B. tumida* there is a slight increase in size from its first
13 appearance in the early Holocene to a stable average of 390 μm after 7 ka. Data are sparse
14 prior to the Holocene due to low abundance of these species and are difficult to interpret.
15 However, average lengths of bolivinids in the Bølling-Allerød and Younger Dryas are not
16 markedly different from those in the Holocene. Shell thickness as measured by cross-
17 sectional area measurements of shell calcite correlated well with non-normalized weight
18 ($r^2 = 0.70$; p-value < 0.0005 ; n = 73)(see Supplementary Figure fs02 and fs03), but not
19 sample average SNW ($r^2 = 0.02$; p-value = 0.77; n = 8).

20

21 4. Discussion

22 4.1 Deglacial Climate and Morphometric Trends

1 Post-glacial climate variability in Santa Barbara Basin was accompanied by changes in
2 SNW in multiple species of benthic foraminifera, although these trends were not coherent
3 across species (Figure 4). Established changes in sea surface temperature (SST) as
4 interpreted from planktic foraminiferal $\delta^{18}\text{O}$ as well as seafloor oxygenation (Figure 4;
5 Kennett and Ingram, 1995; Cannariato et al., 1999; Cannariato and Kennett, 1999;
6 Ohkushi et al., 2013; Moffitt et al., 2014) can be compared to species-specific
7 morphometric changes in benthic foraminifera. Our results indicate that benthic faunal
8 calcification and morphology is variable on the timescales of deglacial and post-glacial
9 environmental change, and that complex and species-specific trends are present.
10 Additionally, we find that although shell wall thickness, assessed here by measurement of
11 cross sectional calcite area, correlates with *individual* shell SNW, it does not show a
12 strong correlation with sample *average* SNW in the samples measured.

13

14 4.1.1 Deglacial Intervals: Bølling-Allerød and Younger Dryas

15 Foraminiferal assemblages at site MV0811-15JC indicate that the Bølling-Allerød was
16 anomalously and severely hypoxic (Figure 4), with an expanded OMZ <300 m from the
17 ocean surface (Zheng et al., 2004; Moffitt et al., 2014). The Younger Dryas initiated a
18 return to regional oxygenated conditions (Cannariato et al., 1999; Zheng et al., 2004;
19 Ohkushi et al., 2013; Moffitt et al., 2014). The mid-Younger Dryas is marked at this site
20 by an ephemeral oscillation of OMZ associated fauna (Kennett and Ingram, 1995;
21 Ohkushi et al., 2013; Moffitt et al., 2014). *Uvigerina peregrina* was in high abundance
22 through these oscillations, whereas other species were discontinuous in the post-glacial
23 biotic archive. Broadly, *U. peregrina* SNWs were higher through the Bølling-Allerød

1 than the Younger Dryas, mirroring foraminiferal density while SNW in *B. interjuncta* and
2 *B. argentea* from 14-11 ka were comparable to those seen in the early Holocene.
3 *Uvigerina peregrina* SNWs through the deglaciation are higher during hypoxic intervals.
4 Neither *B. argentea* nor *B. interjuncta* show dramatic weight fluctuations through the
5 Bølling-Allerød and Younger Dryas.

6

7 4.1.2 Holocene

8 The OMZ remained relatively stable through much of the Holocene, as interpreted from
9 the hypoxic deep basin laminated sequences and OMZ-associated fauna in shallower
10 MV0811-15JC, where subtle shifts are also apparent (Ohkushi et al., 2013; Moffitt et al.,
11 2014). At the onset of the Holocene and through the pre-Boreal (between 11.4 and 10 ka),
12 low SNWs are observed briefly in both *U. peregrina* and *B. interjuncta*, coincident with a
13 return to severely hypoxic bottom waters, while *B. tumida* is absent from the early
14 Holocene (Figure 4; Ohkushi et al., 2013; Moffitt et al., 2014). An overall increase in
15 SNW is seen in *B. interjuncta* at 6.5 ka. *Bolivina tumida* SNW also increases beginning at
16 6.5 ka coincident with an increased stability in length (Figure 5). There is no clear trend
17 in *B. argentea* SNW, which remains stable throughout the Holocene; *B. argentea* length
18 is also stable with the exception of a slight increase at 4 ka. *Uvigerina peregrina* shows a
19 period of increased SNW during the mid Holocene, starting around 10 ka, prior to that in
20 the Bolivinids. The increase in *U. peregrina* is closely associated with the development
21 of an OMZ-fauna dominated by that species and a foraminiferal density peak (Figure 4).
22 *Uvigerina peregrina* is the most abundant species during this interval of high SNW, and
23 reaches greatest average length, indicative of a link between large SNW and optimal

1 conditions for this species. However, SNW of *U. peregrina* declines and plateaus after 6
2 ka while the species continues as a dominant component of the assemblage. It is possible
3 that such shifts are indicative of subtypes not identified by external shell appearance.

4 5 *4.2 Post-Depositional and Environmental Influences on SNW*

6 Inorganic carbon system mediated controls on foraminiferal calcite can occur not only
7 during growth (Spero et al., 1997; Bijma et al., 2002; Russell et al., 2004; Lombard et al.,
8 2010), but also upon deposition (Bijma et al., 2002) and during burial processes (de
9 Villiers, 2005), potentially resulting in either dissolution or calcite overgrowth of fossil
10 shells. In this depositional system, the primary controls on preservation are the intensity
11 of the CMZ and the production of bicarbonate in anoxic bottom waters and sediment
12 (Boudreau, 1987; Reimers et al., 1996). Previous *in situ* measurements of pore-water pH
13 and alkalinity in the deep, anoxic Santa Barbara Basin record an increase in calcite
14 saturation within sediments as shallow as 0.25 mm, in contrast to the undersaturated
15 sediment-water interface (Reimers et al., 1996). These measurements suggest that post
16 depositional burial for shallow infaunal species could result in greater SNW, whereas
17 SNW of epifaunal species exposed to low-[CO₃⁻²] bottom waters could decrease due to
18 dissolution. However, shell textures indicative of post-depositional dissolution,
19 recrystallization, pyritization or diagenetic overgrowth are not evident in any of the
20 individuals in this record. Post-depositional overgrowth as an explanation for SNW
21 changes is also inconsistent with the observed differences between individual species
22 documented here.

1 Although SEM images of *U. peregrina* cross-sections reveal what appear to be clay
2 particles infilling some shells even after cleaning (potentially adding to the weight), this
3 condition was neither common nor does this process appear preferentially concentrated in
4 any particular sample. Furthermore, none of the climatic conditions under consideration
5 in Santa Barbara Basin are associated with changes in either the proportion of sediment
6 comprised of clays or clay mineral composition (Stein, 1995). Infilling is a likely source
7 of variability in this weight record but is a process that would not impose patterns
8 associated with broad scale climatic trends.

10 4.3 Species-Specific Interpretations

11 The disparity between SNW through the deglacial and Holocene intervals indicate the
12 influence of species-specific factors. We consider several factors that may influence
13 SNW against the backdrop of large-scale changes in benthic oxygenation and $[\text{CO}_3^{2-}]$,
14 including depth habitat, natural history, response to stressful/optimal environmental
15 conditions and species-specific weight/ $[\text{CO}_3^{2-}]$ relationships. First, differences in depth
16 habitat subject species to different porewater alkalinity, which drives variability on
17 shorter time-scales than in bottom water and could therefore be markedly different in the
18 habitats of a deeper dwelling species (e.g., Reimers et al., 1996; Zheng et al., 2000;
19 Fontanier et al., 2006; Zeebe, 2007). However, from what is known of the depth habitats
20 of these species, this alone is not enough to explain the species-specific trends. *Uvigerina*
21 *peregrina* and *B. argentea* in particular are thought to have similar microhabitat depth
22 distribution (1-4 cm) (Corliss and Emerson, 1990; Kennett, 1995; Stott et al., 2000; Ernst
23 and van der Zwaan, 2004; Holsten et al., 2004), yet these two species exhibit no

1 similarity in SNW trends. *Uvigerina peregrina* and *B. argentea* migrate vertically within
2 the sediments in response to benthic oxygenation (Alve and Bernhard, 1995; Moodley et
3 al., 1998; Gross, 2000; Geslin et al., 2004; Fontanier et al., 2006). Intergenerational
4 changes in microhabitats in some bolivinids (Douglas and Staines-Urias, 2007; Staines-
5 Urias and Douglas, 2009), may additionally contribute to a muted response to deglacial
6 climate oscillations, especially within *B. argentea*, which shows the least variability.

7
8 Ecology and natural history of the species investigated here may also influence SNW and
9 shell morphology, including the presence of symbionts (Bernhard and Bowser, 1996;
10 Bernhard et al., 2000; Bernhard, 2003), denitrification in the foraminifera (Risgaard-
11 Peterson et al., 2006; Bernhard et al., 2012), biasing due to selective predation on certain
12 size-classes, genetic variability and the potential for undifferentiated cryptic species or
13 subspecies in the fossil record. Such ecological, physiological and genetic differences
14 could drive size and weight trends in either direction, as well as bias the
15 preservation of a representative community in the sedimentary record. We suggest
16 that some combination of these factors provides the most probable explanation for the
17 disparity between SNW of *U. peregrina*, the stable record of *B. argentea* and the late
18 Holocene increase in the other two bolivinids.

19
20 SNW in planktic foraminifera has been linked to “optimal growth” conditions, as high
21 SNW co-occurs with the highest abundance of that species (de Villiers, 2004). In benthic
22 foraminifera, without time-cued reproduction, this may be linked with environmentally-
23 driven variability in life span as well. Here we find that SNW in *U. peregrina* does

1 broadly correlate to peaks in foraminiferal density, indicating that in this species,
2 conditions optimal for growth may be reflected in increased calcification. In *U. peregrina*,
3 increased SNW is observed during intermediate hypoxic intervals (13-14 and 6-8 ka)
4 when the species is also compositionally dominant.

5
6 By contrast, SNW in the bolivinids does not follow peaks in abundance. *Bolivina tumida*
7 and *B. interjuncta* both appear to increase in SNW in the Middle Holocene, concurrent
8 with a sub-millennial shift in structure of the coastal OMZ to foraminifera dense,
9 *Uvigerina*-dominated communities that more closely resemble the ecology of the modern
10 OMZ (Ohkushi et al., 2013; Moffitt et al., 2014). In addition, this middle Holocene event
11 also coincided with the ephemeral development of sulfur-oxidizing seafloor bacterial
12 communities (Moffitt et al., 2015). While we cannot rule out the direct influence of
13 oxygen concentrations on SNW here, the known association of these two species with
14 low oxygen environments suggests that benthic $[\text{CO}_3^{2-}]$ may be more important for SNW
15 in these two species.

16 17 *4.4 Impacts of environmental variability on SNW*

18 The greatest source of benthic variability at MV0811-15JC is the climate-driven
19 migration of the OMZ and associated CMZ, as described above and by others (Ohkushi
20 et al., 2013; Moffitt et al., 2014; Moffitt et al., 2015). Previous studies linking low
21 oxygen and low $[\text{CO}_3^{2-}]$ to reduced shell weight/size would lead to a prediction of low
22 SNW associated with periods of OMZ/CMZ expansion and intensity at the site (e. g.
23 Spero et al., 1997; Bijma et al., 1999; Barker and Elderfield, 2002; Russell et al., 2004;

1 de Moel et al., 2009; Kuroyanagi et al., 2009; Moy et al., 2009; Lombard et al., 2010;
2 Marshall et al., 2013). The anticipated response is present only broadly in *U. peregrina*
3 SNW which reflects the migration of the OMZ through the Bølling-Allerød and Younger
4 Dryas, while *B. interjuncta* and *B. tumida* SNW increases with increasing oxygenation
5 beginning in the mid-Holocene. Even taking into account the potential for species-
6 specific weight/[CO₃²⁻] relationships (Bijma et al., 2002; Gonzalez-Mora et al., 2008),
7 OMZ/CMZ variability alone is not sufficient to explain the full range of SNW observed
8 through the deglaciation.
9
10 The inorganic carbon system is the most likely determinant of benthic foraminiferal
11 weight as has been repeatedly demonstrated under culture (Kuroyanagi et al., 2009;
12 Dissard et al., 2010; Fujita et al., 2011; Hikami et al., 2011), yet other fluctuating
13 environmental variables could impact foraminiferal morphology, including temperature
14 and nutrient flux. Temperature is a known contributor to both the size and growth rate of
15 planktic foraminifera (Be et al., 1973; Hecht, 1976; Schmidt et al., 2004; Lombard et al.,
16 2009) and potentially SNW as well (Aldridge et al., 2012). While SST has varied in Santa
17 Barbara Basin through the last deglaciation (6-8°C), changes in benthic foraminiferal
18 δ¹⁸O suggest significantly less change (~2°C) in temperature at Intermediate Water
19 depths (e.g. Kennett et al., 1995; Kennett and Ingram, 1996, Hill et al., 2006). We note
20 that benthic SNW does not correlate well with the deglacial temperature curve, and thus
21 come to the conclusion that the temperature is not a driving factor in SNW.

22

Carbon export is a major determinant of benthic foraminiferal abundance and habitat preferences (Murray, 2001; Linshy, 2008 and references therein). Of the four species, *U. peregrina*, particularly of the morphotype measured here, has been associated with high organic matter flux (Koho et al., 2008). Extensive analysis of deglacial productivity from nearby ODP Site 893A indicates variable Total Organic Carbon (TOC) in the Bølling-Allerød, a peak in the mid-Younger Dryas, and a return to lower, stable levels through much of the Holocene until ~2 kya (Nederbragt et al., 2008). No significant increase in glacial/interglacial TOC fluxes was observed in neighboring cores MD02-2503 and MD02-2504 (Ohkushi et al., 2013). All of these records indicate that export productivity has been relatively high throughout the deglaciation and Holocene and therefore, not likely a limiting factor for either foraminiferal abundance or growth. A slight increase in productivity occurs in the late Holocene at around 6 ka (Nederbragt et al., 2008; Ohkushi et al., 2013). This increase is too late to account for the mid-Holocene increase in SNWs and size in *U. peregrina* but may coincide with the late plateau in both size and SNW in the species. Taken together with an increase in abundance, an increase in export could also be a contributing factor in the continued increase in *B. tumida* and *B. interjuncta* SNWs in the Holocene.

5. Conclusions

We find that the morphology of populations is governed by a complex suite of environmental variables, including but not limited to, dissolved oxygen and inorganic carbon, and appears to be highly species-specific even amongst species sharing a similar benthic habitat. In *U. peregrina*, the highest SNWs and greatest shell lengths coincide

1 with peaks in foraminiferal density and increased compositional dominance but are not
2 clearly linked to changes in shell wall thickness. For *B. interjuncta* and *B. tumida*, an
3 increase in SNW occurs with a weakening of the OMZ/CMZ in the late Holocene.
4 *Bolivina argentea* is the only species that shows no long-term trends in SNW. We find
5 that the SNW differences across species are indicative of a complex suite of factors,
6 requiring interpretation on a species-specific level. Experimental investigations with
7 modern species are needed to conclusively link species records to benthic conditions,
8 however the species-specific nature of these relationships is a promising avenue for
9 ecological reconstructions using multispecies records.

11 **Acknowledgements**

12 We would like to acknowledge and thank S. Downing (NSF supported REU) for a
13 preliminary dataset that prompted further investigation and G. Baxter for assistance in the
14 mounting and thin sectioning samples. Support was provided by UC Davis Durrell Fund
15 (C. Davis) and NSF (T. Hill; OCE 0825322 and OCE 1255194). We acknowledge H.
16 Spero, A. Russell, and two reviewers for suggestions that improved the manuscript. We
17 thank the Captain, crew, and scientific party of the *R/V Melville* for acquisition of the
18 piston core. All data will be made available at the NOAA National Climatic Data Center
19 for Paleoclimate.

1 **References**

- 2 Alve, E., Bernhard, J.M. 1995. Vertical Migratory Response of Benthic Foraminifera
3 to Controlled Oxygen Concentrations in an Experimental Mesocosm. *Mar. Ecol.*
4 *Progress Series*. 116. <http://dx.doi.org/10.3354/meps116137>.
- 5 Abramoff, M.D., Magalhaes, P.J., Ram, S.J. 2004. Image Processing with ImageJ.
6 *Biophotonics International*. 11(7), 36-42.
- 7 Aldridge, D., Beer, C.J., Purdie, D.A. 2012. Calcification in the planktonic
8 foraminifera *Globigerina bulloides* linked to phosphate concentrations in surface
9 waters of the North Atlantic Ocean. *Biogeosci.* 9, 1725-1739.
10 <http://dx.doi.org/10.5194/bg-9-1725-2012>.
- 11 Altenbach, A.V., Bernhard, J.M., Seckbach, J. 2011. Anoxia: Evidence for
12 Eukaryote Survival and Paleontological Strategies. *Cellular Origin, Life in*
13 *Extreme Habitats and Astrobiology*. Vol. 21, Springer.
- 14 Alvarez-Borrego, S., Gordon, L., Jones, L., Park, P.K., Pytkowicz R. 1972.
15 Oxygen-carbon dioxide-nutrients relationships in the Southeastern Region of the
16 Bering Sea. *J. Oceanogr. Soc. Jpn.* 28(2), 71-93.
- 17 Barker, S., Elderfield, H. 2002. Foraminiferal calcification response to glacial-
18 interglacial changes in atmospheric CO₂. *Science*. 297, 833-836.
- 19 Bé, A. W.H., Harrison, S.M., Lott, L. 1973. *Orbulina universa* d'Orbigny in the
20 Indian Ocean. *Micropal.* 19(2), 150-192.
- 21 Beer, C.J., Schiebel, R., Wilson, P.A. 2010. Testing planktic foraminiferal shell weight as
22 a surface water [CO₃⁻²] proxy using plankton net samples. *Geology*. 38(2), 103–
23 106.

1 Behl, R.J. 1995. Sedimentary Facies and Sedimentology of the Late Quaternary, *in*
2 Kennett, J. P., Baldauf, J.G., Lyle, M, ed., Proceedings of the Ocean Drilling
3 Program, Scientific Results. 146, 295-308.

4 Behl, R.J., Kennett, J.P. 1996. Brief interstadial events in the Santa Barbara basin,
5 NE Pacific, during the past 60 kyr. *Nature*. 379, 243-246.

6 Ben-Yaakov, S. 1972. On the CO₂/O₂ system in the Northeastern Pacific. *Mar. Chem.*
7 1(1), 3-26.

8 Bernhard, J.M., Bowser, S.S. 1996. Benthic foraminifera of dysoxic sediments:
9 chloroplast sequestration and functional morphology. *Earth Sci. Rev.* 24, 149-165.
10 [http://dx.doi.org/10.1016/S0012-8252\(99\)00017-3](http://dx.doi.org/10.1016/S0012-8252(99)00017-3).

11 Bernhard, J.M., Buck, K.R., Farmer, M.A., Bowser, S.S. 2000. The Santa Barbara
12 Basin is a symbiosis oasis. *Nature*, 403, 77-80. <http://dx.doi.org/10.1038/47476>.

13 Bernhard, J.M. 2003. Potential Symbionts in Bathyal Foraminifera. *Science*. 299(5608).
14 <http://dx.doi.org/10.1126/science.1077314>.

15 Bernhard, J.M., Casciotti, K.L., McIlvin, M.R., Beaudoin, D.J., Visscher, P.T.,
16 Edgcomb, V.P. 2012. Potential importance of physiologically diverse benthic
17 foraminifera in sedimentary nitrate storage and respiration. *J. Geophys. Res.*
18 117(3). <http://dx.doi.org/10.1029/2012JG001949>

19 Bijma, J., Barbel, H., Zeebe, R.E. 2002. Impact of the ocean carbonate chemistry on
20 living foraminiferal shell weight: Comment on ‘carbonate ion concentration in
21 glacial-age deep waters of the Caribbean Sea’ by W.S. Broecker and E. Clark.
22 *Geochem., Geophys., Geosyst.* 3(11), 1-7.
23 <http://dx.doi.org/10.1029/2002GC000388>.

- 1 Boltovskoy, E., Scott, D.B., Medioli, F.S. 1991. Morphological Variations of
2 Benthic Foraminiferal Tests in Response to Changes in Ecological Parameters: A
3 Review. *J. Paleontol.* 65(2), 175-185.
- 4 Boudreau, B.P. 1987. A steady-state diagenetic model for dissolved carbonate species
5 and pH in the porewaters of oxic and suboxic sediments. *Geochim. Cosmochim.*
6 *Acta.* 51(7), 1985-1996.
- 7 Bray, N.A., Keyes, A., Morawitz, W.M.L. 1999. The California Current system in
8 the Southern California Bight and the Santa Barbara Channel. *J. Geophys. Res.:*
9 *Oceans.* 104(4), 7695-7714.
- 10 Cannariato, K.G., Kennett, J.P. 1999. Climatically related millennial-scale
11 fluctuations in strength of California margin oxygen-minimum zone during the
12 past 60 k.y. *Geology.* 27(11), 975-978.
- 13 Cannariato, K.G., Kennett, J.P., Behl, R.J. 1999. Biotic response to late
14 Quaternary rapid climate switches in Santa Barbara Basin : Ecological and
15 evolutionary implications. *Geology.* 27, 63-66.
- 16 Corliss, B.H., Emerson, S. 1990. Distribution of rose bengal stained deep-sea
17 benthic foraminifera from the Nova Scotian continental margin and Gulf of Maine.
18 *Deep-Sea Res. Part I.* 37(3), 381-400.
- 19 de Moel, H., Ganssen, G.M., Peeters, F.J.C., Jung, S.J.A., Kroon, D., Brummer, G.J. A.,
20 Zeebe, R.E. 2009 Planktic foraminiferal shell thinning in the Arabian Sea due to
21 anthropogenic ocean acidification? *Biogeosciences.* 6, 1917-1925.
22 <http://dx.doi.org/10.5194/bg-6-1917-2009>.
- 23 de Villiers, S. 2004. Optimum growth conditions as opposed to calcite saturation as a

- 1 control on the calcification rate and shell-weight of marine foraminifera. *Mar. Bio.*
2 144(1), 45-49.
- 3 de Villiers, S. 2005. Foraminiferal shell-weight evidence for sedimentary calcite
4 dissolution above the lysocline. *Deep-Sea Res. Part I.* 52(5), 671-680.
5 <http://dx.doi.org/10.1016/j.dsr.2004>.
- 6 Dissard, D., Nehrke, G., Reichart, G.J., Bijma, J. 2010. Impact of seawater pCO₂
7 on calcification and Mg/Ca and Sr/Ca ratios in benthic foraminifera calcite:
8 results from culturing experiments with *Ammonia tepida*. *Biogeosciences*. 7(1),
9 81-93. <http://dx.doi.org/10.5194/bg-7-81-2010>.
- 10 Douglas, R., Staines-Urias, F. 2007. Dimorphism, Shell Mg/Ca Ratios and stable isotope
11 content in species of *Bolivina* (Benthic Foraminifera) in the Gulf of California,
12 Mexico. *J Foraminiferal Res.* 37(3), 189-203.
13 <http://dx.doi.org/10.2113/gsjfr.37.3.189>
- 14 Ernst, S., van der Zwaan, B. 2004 Effects of experimentally induced raised levels
15 of organic flux and oxygen depletion on a continental slope benthic foraminiferal
16 community. *Deep-Sea Res. Part I.* 51(11), 1709-1739.
- 17 Fontanier, C., Mackensen, A., Jorissen, F.J., Anschutz, P., Licari, L., Griveaud, C.
18 2006. Stable oxygen and carbon isotopes of live benthic foraminifera from the
19 Bay of Biscay: Microhabitat impact and seasonal variability. *Mar. Micropaleontol.*
20 58(3), 159-183.
- 21 Fujita, K., Hikami, M., Suzuki, A., Kuroyanagi, A., Sakai, K., Kawahata, H.,

1 Nojiri, Y. 2011. Effects of ocean acidification on calcification of symbiont-
2 bearing reef foraminifers. *Biogeosciences*. 8(8), 2089-2098.
3 <http://dx.doi.org/10.5194/bg-8-2089-2011>.

4 Geslin, E., Heinz, P., Jorissen, F., Hemleben, C. 2004. Migratory responses of deep-
5 sea benthic foraminifera to variable oxygen conditions: laboratory investigations.
6 *Mar. Micropaleontol.* 53(3), 227-243.
7 <http://dx.doi.org/10.1016/j.marmicro.2004.05.010>.

8 Glock, N., Eisenhauer, A., Milker, Y., Liebetrau, V., Schonfeld, J., Mallon, J., Sommer,
9 S., Hensen C. 2011. Environmental influences on the pore density of *Bolivina*
10 *spissa* (Cushman). *J. Foraminiferal Res.* 41(1), 22-32.
11 <http://dx.doi.org/10.2113/gsjfr.41.1.22>.

12 Gonzalez-Mora, B., Sierro, F.J., Flores, J.A. 2008. Controls of shell calcification in
13 planktonic foraminifers. *Quat. Sci. Rev.* 27(9), 956-961.
14 <http://dx.doi.org/10.1016/j.quascirev.2008.01.008>.

15 Grootes, P.M., Stuiver, M. 1997. $^{18}\text{O}/^{16}\text{O}$ variability in Greenland snow and ice with
16 103 to 105-year time resolution. *J. Geophys. Res.* 26, 455-470.

17 Gross, O. 2000. Influence of temperature, oxygen and food availability on the
18 migrational activity of bathyal benthic foraminifera: evidence by microcosm
19 experiments. *Hydrobiologia*. 426(1).
20 <http://dx.doi.org/10.1023/A%3A1003930831220>.

21 Hecht, A.D. 1976. An ecologic model for test size variation in Recent planktonic
22 foraminifera; applications to the fossil record. *J. Foraminiferal Res.* 6(4), 295-311.

23 Helly, J.J., Levin, L.A. 2004. Global distribution of naturally occurring marine

1 hypoxia on continental margins. *Deep-Sea Res. Part I.* 51(9), 1159-1168.

2 Hendy, I.L., Kennett, J.P., Roark, E.B., Ingram, B.L. 2002. Apparent
3 synchronicity of submillennial scale climate events between Greenland and Santa
4 Barbara Basin, California from 30–10ka. *Quat. Sci. Rev.* 21(10), 1167-1184.

5 Hikami, M., Ushie, H., Irie, T., Fujita, K., Kuroyanagi, A., Sakai, K., Nojiri, Y., Suzuki,
6 A., Kawahata, H. 2011. Contrasting calcification responses to ocean acidification
7 between two reef foraminifers harboring different algal symbionts. *Geophys. Res.*
8 *Lett.* 38(19), <http://dx.doi.org/10.1029/2011GL048501>.

9 Hill, T.M., Kennett, J.P., Pak, D.K., Behl, R.J., Robert, C., Beaufort., L. 2006.
10 Pre-Bølling warming in Santa Barbara Basin, California: surface and intermediate
11 water records of early deglacial warmth. *Quat. Sci. Rev.* 25(21), 2835-2845.
12 <http://dx.doi.org/10.1016/j.quascirev.2006.03.012>.

13 Hill, T.M., Kennett, J.P., Spero, H.J. 2003. Foraminifera as indicators of methane-
14 rich environments: A study of modern methane seeps in Santa Barbara Channel,
15 California. *Mar. Micropaleontol.* 49(1), 123-138.

16 Holsten, J., Stott, L., Berelson, W. 2004. Reconstructing benthic carbon oxidation
17 rates using $\delta^{13}\text{C}$ of benthic foraminifers. *Mar. Micropaleontol.* 53(1), 117-132.
18 <http://dx.doi.org/10.1016/j.marmicro.2004.05.006>.

19 Ivanochko, T.S., Pedersen, T.F. 2004. Determining the influences of Late
20 Quaternary ventilation and productivity variations on Santa Barbara Basin
21 sedimentary oxygenation: a multi-proxy approach. *Quat. Sci. Rev.* 23(3), 467-480.
22 <http://dx.doi.org/10.1016/j.quascirev.2003.06.006>.

23 Kamykowski, D., Zentara, S.J. 1990. Hypoxia in the world ocean as recorded in the

1 historical data set. *Deep-Sea Res. Part I.* 37(12), 1861-1874.

2 Kennett, J.P. 1995. Latest Quaternary benthic oxygen and carbon isotope stratigraphy:
3 Hole 893A, Santa Barbara Basin, California. Proceedings of the Ocean Drilling
4 Program, Scientific Results, 146.

5 Kennett, J.P., Ingram, B.L. 1995. A 20,000-year record of ocean circulation and
6 climate change from the Santa Barbara basin. *Nature.* 377, 510-514.

7 Keul, N., Langer, G., de Nooijer, L.J., Bijma, J. 2013. Effect of ocean acidification
8 on the benthic foraminifera *Ammonia* sp. Is caused by a decrease in carbonate ion
9 concentration. *Biogeosciences.* 10(1), 6185-6198. [http://dx.doi.org/10.5194/bg-](http://dx.doi.org/10.5194/bg-10-6185-2013)
10 [10-6185-2013](http://dx.doi.org/10.5194/bg-10-6185-2013).

11 Khanna, N, Godbold, J.A., Austin, W.E.N., Paterson, D.M. 2013. The Impact of
12 Ocean Acidification on the Functional Morphology of Foraminifera. *PLoS*
13 *ONE.* 8(12), e83118. <http://dx.doi.org/10.1371/journal.pone.0083118>.

14 Koho, K.A., Garia, R., de Stiger, H.C., Epping, E., Koning, E., Kouwenhoven, T.J., van
15 der Zwaan, G.J. 2008. Sedimentary labile organic carbon and pore water redox
16 control on species distribution of benthic foraminifera: A case study from Lisbon-
17 Setubal Canyon (southern Portugal). *Prog. Oceanography.* 79, 55-82.
18 <http://dx.doi.org/10.1016/j.pocean.2008.07.004>

19 Kuhnt, T., Friedrich, O., Schmiedl, G., Milker, Y., Mackensen, A., Lückge, A.
20 2013. Relationship between pore density in benthic foraminifera and bottom-
21 water oxygen content. *Deep-Sea Res. Part I.* 76, 85-95.
22 <http://dx.doi.org/10.1016/j.dsr.2012.11.013>.

23 Kuhnt, T., Schiebel, R., Schmiedl, G., Milker, Y., Mackensen, A., Friedrich, O. 2014.

1 Automated and manual analyses of the pore density-to-oxygen relationship in
2 *Globobulimina turgida*. *J. Foraminiferal Res.* 44(1), 5-16.
3 <http://dx.doi.org/10.2113/gsjfr.44.1.5>

4 Kuroyanagi, A., Kawahata, H., Suzuki, A., Fujita, K., Irie, T. 2009. Impacts of
5 ocean acidification on large benthic foraminifers: Results from laboratory
6 experiments *Mar. Micropaleontol.* 73(3), 190-195.
7 <http://dx.doi.org/10.1016/j.marmicro.2009.09.003>.

8 Kuroyanagi, A., da Rocha, R.E., Bijma, J., Spero, H.J., Russell, A.D., Eggins, S.M.,
9 Kawahata, H. 2013. Effect of dissolved oxygen concentration on planktonic
10 foraminifera through laboratory culture experiments and implications for oceanic
11 anoxic events. *Mar. Micropaleontol.* 101, 28-32.
12 <http://dx.doi.org/10.1016/j.marmicro.2013.04.005>.

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

15 Linshy, V.N. 2008. Appraisal of laboratory culture experiments on benthic
16 foraminifera to assess/develop paleoceanographic proxies, *Indian J. Mar. Sci.* 36,
17 301-321.

18 Lohmann, G.P. 1995. A model for variation in the chemistry of planktonic foraminifera
19 due to secondary calcification and selective dissolution. *Paleoceanography.* 10(3),
20 445-457.

21 Lombard, F., Labeyrie, L., Michel, E., Spero, H.J., and D. W. Lea (2009), Modelling the
22 temperature dependent growth rates of planktic foraminifera, *Mar.*
23 *Micropaleontol.*, 70(1), 1-7, doi: 10.1016/j.marmicro.2008.09.004.

- 1 Lombard, F., da Rocha, R. E., Bijma, J., Gattuso, J.P. 2010. Effect of carbonate ion
2 concentration and irradiance on calcification in planktonic foraminifera.
3 *Biogeosciences*. 7(1), 247-255. <http://dx.doi.org/10.5194/bg-7-247-2010>.
- 4 Loubere, P., Meyers, P., Gary, A. 1995. Benthic foraminiferal microhabitat
5 selection, carbon isotope values, and association with larger animals; a test with
6 *Uvigerina peregrina*. *J. Foraminiferal Res.* 25(1), 83-95.
7 <http://dx.doi.org/10.2113/gsjfr.25.1.83>
- 8 Mackensen, A., Douglas, R.G. 1989. Down-core distribution of live and dead deep-
9 water benthic foraminifera in box cores from the Weddell Sea and the California
10 continental borderland. *Deep-Sea Res. Part I*. 36(6), 879-900.
- 11 Marshall, B.J., Thunell, R.C., Henehan, M.J., Astor, Y., Wejnert, K.E. 2013.
12 Planktonic foraminiferal area density as a proxy for carbonate ion concentration:
13 A calibration study using the Cariaco Basin Ocean Time Series.
14 *Paleoceanography*. 28, 363–376. <http://dx.doi.org/10.1002/palo.20034>.
- 15 McIntyre-Wressnig, A., Bernhard, J.M., McCorkle, D.C., Hallock, P. 2013. Non-lethal
16 effects of ocean acidification on the symbionts-bearing benthic foraminifera
17 *Amphistegine gibbosa*. *Mar. Ecol. Prog. Ser.* 472, 45-60.
- 18 Middelburg, J.J., Levin, L.A. 2009. Coastal hypoxia and sediment
19 Biogeochemistry. *Biogeosciences*. 6, 1273-1293.
20 <http://dx.doi.org/10.5194/bg-6-1273-2009>.
- 21 Moffitt, S.E., Hill, T.M., Ohkushi, K., Kennett, J.P., Behl, R.J. 2014. Vertical

- 1 oxygen minimum zone oscillations since 20 ka in Santa Barbara Basin: A benthic
2 foraminiferal community perspective. *Paleoceanography*.
3 <http://dx.doi.org/10.1002/2013PA002483>.
- 4 Moodley, L., Hess, C. 1992. Tolerance of Infaunal Benthic Foraminifera for Low
5 and High Oxygen Concentrations. *Bio. Bull.* 183(1), 94-98.
6 <http://dx.doi.org/10.2307/1542410>
- 7 Moodley, L., van der Zwaan, G.J., Rutten, G.M.W., Boom, R.C.E., Kempers, A.J.
8 1998. Subsurface activity of benthic foraminifera in relation to porewater oxygen
9 content: laboratory experiments. *Mar. Micropaleontol.* 34(1), 91-106.
10 [http://dx.doi.org/10.1016/S0377-8398\(97\)00044-3](http://dx.doi.org/10.1016/S0377-8398(97)00044-3).
- 11 Moy, A.D., Howard, W.R., Bray, S.G., Trull, T.W. 2009. Reduced calcification in
12 modern Southern Ocean planktonic foraminifera. *Nat. Geosci.* 2, 276-280.
- 13 Murray, J.W. 2001. The niche of benthic foraminifera, critical thresholds and proxies.
14 *Mar. Micropaleontol.* 41(1), 1-7 <http://dx.doi.org/10.1038/ngeo460>.
- 15 Nameroff, T.J., Calvert, S.E., Murray, J.W. 2004. Glacial-interglacial variability
16 in the eastern tropical North Pacific oxygen minimum zone recorded by redox-
17 sensitive trace metals. *Paleoceanography*. 19(1).
18 <http://dx.doi.org/10.1029/2003PA000912>.
- 19 Nederbragt, A.J., Thurow, J.W., Bown, P.R. 2008. Paleoproductivity, ventilation,
20 and organic carbon burial in the Santa Barbara Basin (ODP Site 893, off
21 California) since the last glacial. *Paleoceanography*. 23(1).
22 <http://dx.doi.org/10.1029/2007PA001501>.
- 23 Ohkushi, K., Kennett, J.P., Zeleshi, C.M., Moffitt, S.E., Hill, T.M., Robert, C.,

- 1 Beaufort, L., Behl, R.J. 2013. Quantified intermediate water oxygenation history
2 of the NE Pacific: A new benthic foraminiferal record from Santa Barbara basin.
3 *Paleoceanography*. 28(3), 453-467. <http://dx.doi.org/10.1002/pale.20043>.
- 4 Paulmier, A., Ruiz-Pino, D. 2009. Oxygen minimum zones (OMZs) in the modern
5 Ocean. *Prog. Oceanogr.* 80(3), 113-128.
6 <http://dx.doi.org/10.1016/j.pocean.2008.08.001>.
- 7 Paulmier, A., Ruiz-Pino, D., Garçon, V. 2011. CO₂ maximum in the oxygen
8 minimum zone (OMZ). *Biogeosciences*. 8(2), 239-252.
9 <http://dx.doi.org/10.5194/bg-8-239-2011>.
- 10 Perez-Cruz, L.L., Machain-Castillo, M.L. 1990. Benthic foraminifera of the
11 oxygen minimum zone, continental shelf of the Gulf of Tehuantepec, Mexico. *J.*
12 *Foraminiferal Res.* 20(4), 312-325.
- 13 Quinterno, P.J., Gardner, J.V. 1987. Benthic foraminifers on the continental shelf
14 and upper slope, Russian River area, Northern California. *J. Foraminiferal Res.*
15 17, 132-152.
- 16 Reimers, C.E., Lange, C.B., Tabak, M., Bernhard, J.M. 1990. Seasonal
17 Spillover and varve foraminifera in the Santa Barbara Basin, California. *Limnol.*
18 *Oceanogr.* 37(7), 1577-1585.
- 19 Reimers, C.E., Rittenberg, K.C., Canfield, D.E., Christiansen, M.B., Martin, J.B. 1996.
20 Porewater pH and authigenic phases formed in the uppermost sediments of the
21 Santa Barbara Basin. *Geochim. Cosmochim. Acta*. 60(21), 4037-4057.
- 22 Risgaard-Petersen, N., Langezaal, A.M., Ingvarsdén, S., Schmid, M.C., Jetten, M.S.M.

- 1 Opden Camp, H.J.M., Derksen, J.W.M., Piña-Ochoa, E., Eriksson, S.P., Nielsen,
2 L.P. Revsbech, N.P., Cedhagen, T., van der Zwaan, G.J. 2006. Evidence for
3 complete denitrification in a benthic foraminifer. *Nature*. 443(7107) 93-96.
4 <http://dx.doi.org/10.1038/nature05070>
- 5 Russell, A.D., Honisch, B., Spero, H.J., Lea, D.W. 2004. Effects of seawater
6 carbonate ion concentration and temperature on shell U, Mg, and Sr in cultured
7 planktonic foraminifera. *Geochim. Cosmochim. Acta*. 68(21), 4347-4361.
8 <http://dx.doi.org/10.1016/j.gca.2004.03.013>.
- 9 Sarmiento, J.L., Herbert, T.D., Toggweiler, J.R. 1988. Causes of anoxia in the
10 world ocean. *Global Biogeochem. Cycles*. 2(2), 115-128.
- 11 Schmidt, D.N., Renaud, S., Bollmann, J., Schiebel, R., Thierstein, H.R. 2004. Size
12 distribution of Holocene planktic foraminifer assemblages: biogeography, ecology
13 and adaptation. *Mar. Micropaleontol.* 50(3), 319-338.
14 [http://dx.doi.org/10.1016/S0377-8398\(03\)00098-7](http://dx.doi.org/10.1016/S0377-8398(03)00098-7).
- 15 Schönfeld, J. 2006. Taxonomy and distribution of the *Uvigerina peregrina* plexus in the
16 tropical and northeastern Atlantic. *J. Foraminiferal Res.* 36, 355-367.
17 <http://dx.doi.org/10.2113/gsjfr.36.4.355>.
- 18 Schweizer, M., Pawlowski, J., Duijnste, I. A.P., Kouwenhoven, T.J., van der
19 Zwann, G.J. 2005. Molecular phylogeny of the foraminiferal genus *Uvigerina*
20 based on ribosomal DNA sequences. *Mar. Micropaleontol.* 57(3), 51-67.
21 <http://dx.doi.org/10.1016/j.marmicro.2005.07.001>.
- 22 Sen Gupta, B.K., Machain-Castillo, M.L. 1993. Benthic foraminifera in oxygen-
23 poor habitats. *Mar. Micropaleontol.* 20(3), 183-201.

- 1 Spero, H.J., Bijma, J., Lea, D.W., Bemis, B.E. 1997. Effect of seawater carbonate
2 concentration on foraminiferal carbon and oxygen isotopes. *Nature*. 390, 497-500.
- 3 Smith, P.B. 1963 *Quantitative and Qualitative Analysis of the Family Boliviniidae*:
4 U.S. Government Printing Office.
- 5 Staines-Urias, F., Douglas, R.G. 2009. Environmental and intraspecific dimorphism
6 effects on the stable isotope composition of deep-sea benthic foraminifera from
7 the Southern Gulf of California, Mexico. *Mar. Micropaleontol.* 71(1–2), 80-95.
8 <http://dx.doi.org/10.1016/j.marmicro.2009.01.007>
- 9 Stein, R. 1995. Clay and Bulk Mineralogy of Late Quaternary Sediments at Site 893A,
10 Santa Barbara Basin. *Proceedings of the Ocean Drilling Program, Scientific*
11 *Results*, Vol 146.
- 12 Stott, L.D., Berelson, W., Douglas, R., Gorsline, D. 2000. Increased dissolved
13 oxygen in Pacific intermediate waters due to lower rates of carbon oxidation in
14 sediments. *Nature*. 407, 367-370.
- 15 Talley, L.D. 2007. Hydrographic Atlas of the World Ocean Circulation Experiment
16 (WOCE). Southampton, U.K. International WOCE Project Office.
- 17 Wyrski, K. 1962. The oxygen minima in relation to ocean circulation. *Deep-Sea Res.*
18 *and Oceanographic Abstracts*. 9(1), 11-23.
- 19 Zeebe, R.E. 2007. Modeling the CO₂ chemistry $\delta^{13}\text{C}$, and oxidation of organic carbon
20 and methane in sediment porewater: Implications for paleo-proxies in benthic
21 foraminifera. *Geochim. Cosmochim. Acta*. 71(13), 3238-3256.
22 <http://dx.doi.org/10.1016/j.gca.2007.05.004>.

Zheng, Y., Anderson, R. F., van Geen, A., Kuwabara, J. 2000. Authigenic molybdenum formation in marine sediments: A link to pore water sulfide in the Santa Barbara Basin. *Geochim. Cosmochim. Acta*. 64(24), 4165-4178.

Figure Captions

Figure 1. Dissolved Oxygen (DO; green) and Dissolved Inorganic Carbon (DIC; red) values compiled from the National Oceanographic Data Center database, Cruises US-8488 and US-8489 along the Southern California Margin (Talley, 2007).

Figure 2. MV0811-15JC (°34.37, - °120.13; 418 m water depth) located on the Northern edge of Santa Barbara Basin.

Figure 3. SEM image of *Uvigerina peregrina* in cross section (imaged at x120), demonstrating the area of calcite measured for wall thickness (in blue) by the subtraction of internal space (in red).

Figure 4. A comparison of a) $\delta^{18}\text{O}$ of planktic foraminiferal calcite (black) (Moffitt et al. 2014); b) Foraminiferal density (Moffitt et al., 2014); c) Relative frequency (%) of benthic foraminifera with faunal categories modified from Moffitt et al., (2014) including: oxia-mild hypoxia ($>1.5 \text{ ml l}^{-1} \text{ O}_2$; *Nonionella labradorica*, *Quinqueloculina* spp., *Pyrgo* spp.) represented by gradations of blue to purple, intermediate hypoxia ($1.5\text{-}0.5 \text{ ml l}^{-1} \text{ O}_2$; *Epistominella* spp., *Bolivina* spp., *Uvigerina* spp.) and severe hypoxia (<0.5

1 ml l⁻¹ O₂; *Nonionella stella*, *Bolivina tumida*); d) a 3 point moving average of *Uvigerina*
2 *peregrina* SNW (blue); e) *Bolivina argentea* SNW (red squares); f) *Bolivina interjuncta*
3 SNW (red diamonds); and g) *Bolivina tumida* SNW (red triangles) at MV0811-15JC. *U.*
4 *peregrina* SNW data are bounded by an envelope showing 25% SE; no SE values are
5 available for other species.

6

7 Figure 5. Mean length of a) *Uvigerina peregrina* (blue); b) *Bolivina argentea* (red
8 squares); c) *Bolivina interjuncta* (red diamonds); and d) *Bolivina tumida* (red triangles) at
9 MV0811-15JC. All data are bounded by a standard deviation envelope.

10

11 Table 1. Table of the number of individuals broken down by species, used in each
12 analysis, along with maximum and minimum values per individual of unnormalized,
13 length and SNW, as well as the number of sediment intervals considered for each
14 analysis.

Figure 1 Oxygen (mmol L^{-1})

Figure 2

Figure 3

500 μm

Figure 4

Figure 5

Table

	# Per Sample		Raw Weights (µg)		Length (µm)		SNW (µg)	
	Min	Max	Min	Max	Min	Max	Min	Max
<i>U. peregrina</i>	7	37	7	74	604	1433	8	64
<i>B. argentea</i>	7	42	4	26	308	595	11	35
<i>B. interjuncta</i>	7	50	4	17	246	472	4	17
<i>B. tumida</i>	7	49	5	20	291	409	7	16
<i>U. peregrina</i> embedded and cross- sectioned	8	10						