Community benthic paleoecology from high-resolution climate records: Mollusca and Foraminifera in post-glacial environments of the California Margin

Authors: Sarah E. Myhre^{1,*}, Kristy J. Kroeker², Tessa M. Hill^{1,3}, Peter Roopnarine⁴, James P. Kennett⁵

¹Bodega Marine Laboratory, University of California, 2099 Westside Road, Bodega Bay, CA 94923 USA.

²Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, 95064, USA.

³Department of Earth and Planetary Sciences, One Shields Avenue, University of California, Davis, CA 95616, USA.

⁴Institute of Biodiversity Science and Sustainability, California Academy of Sciences, 55 Music Concourse Drive, San Francisco, CA 94118, USA.

⁵Department of Earth Sciences and Marine Science Institute, University of California, Santa Barbara, CA 93106, USA.

*Correspondence to: semyhre@uw.edu

University of Washington, School of Oceanography 1503 NE Boat Street Seattle, WA 98104

Abstract

Paleoecological reconstructions of past climate are often based on a single taxonomic group with a consistent presence. Less is known about the relationship between multi-taxon community-wide change and climate variability. Here we reconstruct paleoecological change in a Late Quaternary (16.1-3.4 ka) sediment core from the California margin (418 meters below sea level) of Santa Barbara Basin (SBB), USA, using Mollusca (Animalia) and Foraminifera (Rhizaria) microfossils. Building upon previous investigations, we use multivariate ordination and cluster analyses to interpret community-scale changes in these distinctly different taxonomic groups across discrete climate episodes. The strongest differences between seafloor biological communities occurred between glacial (prior to Termination IA, 14.7 ka) and interglacial climate episodes. Holocene communities were well partitioned, indicating that sub-millennial oceanographic variability was recorded by these microfossils. We document strong evidence of chemosynthetic trophic webs and sulfidic environments (from gastropod *Alia permodesta* and bivalve *Lucinoma aequizonata*), which characterized restricted intervals previously interpreted as well oxygenated (such as the Pre-Bølling Warming). Mollusc records indicate first-order trophic energetic shifts between detrital and chemosynthetically-fixed carbon. Molluscs associated with widely different physiological preferences occur here within single, decadal intervals of sediment, and as such mollusc assemblages may reflect significant inter-decadal oceanographic variability. Foraminifera assemblages provide exceptional records of the sequential, chronological progression of the deglacial climatic and oceanographic events, whereas mollusc assemblages reflect non-chronological similarities in reoccurring communities. Foraminifera taxa that drive community similarity here are also independently recognized

as marker species for seafloor hypoxia regimes, which provides support for the idea that oxygenation change is a principal driver of seafloor environmental variability.

1.0 INTRODUCTION

1.1 Deglacial paleoceanography in the California margin

The most recent deglaciation (18-8 ka) was a major global climate shift accompanied by increases of 80-100 ppmv in atmospheric carbon dioxide (CO₂) concentrations (e.g., Sigman and Boyle 2000; Monnin et al. 2001), high and low latitude surface ocean warming (5-8 °C and 1.5-2.5 °C, respectively; e.g., Sonzogni et al. 1998; Elderfield and Ganssen 2000), and sea level rise (by ~110 m; e.g., Fleming et al. 1998; Milne et al. 2005). This event also was marked by significant shifts in ocean circulation (e.g., Keigwin et al. 1992; Schmittner and Galbraith 2008), the pervasive reduction of dissolved oxygen below the thermocline and the expansion of intermediate water Oxygen Minimum Zones (OMZ) across the Eastern Pacific (e.g., Behl and Kennett 1996; Cannariato et al. 1999; Zheng et al. 2000a, Ohkushi et al. 2013, Moffitt et al. 2014; Praetorius et al. 2015).

Oxygen variability in the California margin has been well described in continental margin sedimentary archives, using foraminiferal communities (e.g., Cannariato et al. 1999; Ohkushi et al. 2013, Moffitt et al. 2014), sedimentary laminations (e.g., Behl and Kennett 1996), redox metals (e.g., Zheng et al. 2000b; Nameroff et al. 2002), and $\delta^{15}\text{N}$ records (e.g., Ivanochko and Pedersen 2004). These records demonstrate remarkable synchrony in changes to bottom water dissolved oxygen concentrations through the warming and cooling events of the last deglaciation. The OMZ expanded and intensified at glacial

Terminations IA (14.7 ka) and IB (11.7 ka) and remained expanded during the warm intervals of the Bølling-Allerød and the interglacial warmth of the Preboreal and Holocene. During these rapid warming events, hypoxic waters vertically expanded and compressed upper-ocean oxygenated ecosystems to within <300 meters of the sea surface (Moffitt et al. 2014). Conversely, during the Younger Dryas cool episode (12.7-11.6 ka), the California margin OMZ contracted and the continental margin returned to conditions analogous to the cool, oxygenated oceanic structure of the Last Glacial Maximum (Moffitt et al. 2015a).

1.2 Marine microfossil paleoecology

Marine paleoecological investigations on orbital and millennial timescales have largely been based on foraminifera records (e.g., Jorissen et al. 2007) while metazoan paleoecology has primarily been limited to crustacean (Ostrocodia) records (e.g. Yasuhara et al. 2008; Yasuhara et al. 2012). Ostracod investigations show that seafloor diversity is sensitive to abrupt climate and oceanographic change (Cronin and Raymo 1997). However, the sensitivity of shallow continental margin seafloor biota remains poorly understood despite the taxonomic richness and economic interests associated with margin ecosystems. For example, studies of mollusc assemblages from the last deglaciation have largely been limited to terrestrially accessible sequences, such as those provided by uplifted glaciomarine sediment deposits (e.g., England and Furze 2008). Alternatively, molluscs present in marine sediment records have been used for radiocarbon dating and age model generation (e.g., Pieńkowski et al. 2013). A broader understanding of seafloor community responses to climate change, however, can be obtained through quantitative studies of the complete microfossil assemblage in marine sedimentary sequences, including

underutilized metazoan microfossils (Moffitt et al. 2015b).

1.3 Community paleoecology

Here we expand upon previously published work to investigate high-resolution multiple-taxon records of microfossils from a sediment core from Santa Barbara Basin, California, USA. The archive described here is a complex record of community-scale seafloor ecology, which can be used to analyze a range of relationships between environmental conditions and ecological communities. Parallel reconstruction of mollusc and foraminifera records provides an opportunity to assess the unique considerations of mollusc microfossil proxies in reconstructing environments relative to that of foraminifera. Here we focus on:

1. Reconstructing contemporaneous records of both Foraminifera and Mollusca for detailed comparisons and paleoecological interpretation of the two archives.
2. Reconstructing changes in biological community similarity and composition through climate episodes.
3. Describing the primary taxa that contribute to community similarity within climate episodes.

1.4 Continental margin benthic ecology

The composition of continental margin seafloor communities along the Eastern Pacific is strongly influenced by the OMZ and the presence of “cold seeps” (methane and/or sulfur rich). Chemical gradients (e.g., dissolved oxygen concentrations) produce vertical succession patterns over continental margins (Vaquer-Sunyer and Duarte 2008). OMZ-associated taxa are identifiable and exhibit a suite of adaptive morphological, behavioral,

life history, and symbiotic features. Extensive seafloor mats of filamentous sulfur-oxidizing chemosynthetic microbes thrive at severely hypoxic levels ($[O_2] < 0.3 \text{ ml L}^{-1}$; Levin and Michener 2002). These mats signify major energetic shifts from a community dependent on labile, detrital and photosynthetically-derived carbon to a community supported by chemosynthetically-fixed carbon (Levin and Michener 2002). Cold seep environments produce sediments rich in pore-water sulfide, which is highly toxic to most animals (Grieshaber and Volkel 1998). In such environments, metazoan community members persist through harboring chemoautotrophic prokaryotic symbionts (Bernhard et al. 2000). Importantly, benthic communities in continental margin environments also exhibit sensitive affiliations with cold, oxygenated, and non-sulfidic conditions, and these particular taxa are useful here in detecting the absence of chemically stressful environments (e.g., Coan 2000; Long et al. 2008).

1.5 Environmental associations of taxa

Dominant members of the paleocommunities examined here demonstrate tolerance or fidelity to specific environments with hypoxic or sulfidic conditions. We briefly summarize environmental characteristics of mollusc and foraminifera community members, including molluscs *Lucinoma aequizonata*, *Macoma* sp., *Alia permodesta*, *Lirobittium paganicum*, Gadilidae, and Rhabdidae and foraminifera *Bolivina argentea*, *Pseudoparella pacifica*, *Uvigerina peregrina*, *Nonionella stella*, *Bolivina tumida*, *Quinqueloculina* spp., and *Nonionellina labradorica*.

1.5.1 *Lucinoma aequizonata*

Lucinoma aequizonata, like all members of Family Lucinidae, hosts sulfur-oxidizing chemoautotrophic microbial endosymbionts in gill tissue, and these symbionts metabolize nitrate and respire at the same rate regardless of oxygen concentrations (Hentschel et al. 1993). This small bivalve species is known to colonize the hypoxic-anoxic transition zone within a very narrow depth range (500 ± 10 meters below sea level) in modern Santa Barbara Basin (Cary et al. 1989; Hein et al. 2006). The bivalve is a filter feeder, lives at 3-5 cm depths, and has been collected live from *Vesicomya* spp. clam beds characteristic of cold seep environments (Hein et al. 2006). *L. aequizonata* is also known to tolerate low or patchy sulfide environments (Hentschel et al. 1993).

1.5.2 *Macoma* spp.

Macoma is a genus of infaunal deposit and suspension feeding bivalves (Reid and Reid 1969). There are no prior studies to suggest that *Macoma* species are tolerant of hypoxia or associated with OMZ environments. *Macoma* species are commonly associated with Arctic and circumboreal waters (Coan 2000). *Macoma balthica* buries in shallower sediments when exposed to low oxygen conditions, indicating hypoxic conditions are physiologically marginal for this species (Long et al. 2008).

1.5.3 *Alia permodesta* and *Lirobittium paganicum*

Alia permodesta is a gastropod that occurs in close affiliation with filamentous sulfur-oxidizing chemosynthetic microbial mats (e.g., *Beggiatoa* or *Thioploca*; Bernhard et al. 2003). No evidence exists to indicate this species hosts sulfur-oxidizing endosymbionts (Deming et al. 1997), and the isotopic signatures of *A. permodesta* shells suggest that it

grazes on chemosynthetic microbes and is part of chemosynthetic trophic pathways (Levin and Michener 2002). OMZ sediments on the Peruvian margin (579 m water depth) and within Santa Barbara Basin (590 m water depth) have been shown to host dense concentrations of *A. permodesta* (~900 individuals m⁻²; Bernhard et al, 2003; Mosch et al. 2012). *A. permodesta* tolerates sulfidic environments and is thought to be intolerant to high water flow environments (Mosch et al. 2012). The species has also been found in association with the sulfidic stage of whale carcass decomposition (Smith and Baco 2003). The environmental niche of *Lirobittium paganicum*, a gastropod that co-occurs commonly with *A. permodesta*, is unclear, although it has been collected live from methane seeps and *Vesicomya* spp. clam beds (Sahling et al. 2000).

1.5.4 Scaphopods

Scaphopods are motile predators and detritivores encased in elongate, fang-shaped shells, and are the primary benthic predators represented in the ecosystem reported here. They are known to prey on foraminifera (e.g., Langer et al. 1995; Lichter and Luque 2004) and are associated with elevated seafloor oxygenation ([O₂] > 0.5 ml L⁻¹; Zamorano et al. 2007).

1.5.5 Foraminifera

We follow the approach of Jorissen et al. (2007) and focus on a set of marker species for oxygenation, which have been collected in the modern ocean alongside seawater oxygen concentration measurements. Extensive discussion and citation of paleoxygenation interpretations of these taxa can be found in Moffitt et al. (2014).

Bolivina argentea, *Pseudoparella pacifica*, and *Uvigerina peregrina* are used to mark the presence of OMZ sediments. *B. argentea* is a primary OMZ-indicator species and is associated with $[O_2]$ from 0.3-0.5 ml L⁻¹ (Mullins et al. 1985; Bernhard et al. 1997). *P. pacifica* is also associated with hypoxia ($[O_2]<0.5$ ml L⁻¹; Blake 1976; Quintero and Garner 1987). Species of *Uvigerina* are associated with the upper and lower boundary of open margin OMZ environments ($[O_2]>0.3-0.5$ ml L⁻¹), but not necessarily the core of the hypoxic zone (Mullins et al. 1985). Importantly, both *P. pacifica* and *Uvigerina* spp. are also associated with cold seep environments of continental margins (Bernhard et al. 1997; Bernhard et al. 2001; Hill et al. 2003).

Nonionella stella and *Bolivina tumida* are considered the end-member hypoxic marker species. *N. stella* is found at high densities in the near-anoxic sediments (<0.02 ml L⁻¹ O₂) in the deep center of Santa Barbara Basin (Bernhard et al. 1997) and is known to harbor plastids scavenged from detrital algal cells (Bernhard and Bowser 1999). *B. tumida* is a foraminifera associated with shallow active methane seeps in the modern basin (Hill et al. 2003) and with well laminated sediments of the late Pleistocene, which are interpreted to reflect severely hypoxic conditions ($[O_2]<0.1$ ml L⁻¹; Cannariato et al. 1999). *B. tumida* has never been collected alive, so respiratory thresholds for this species are unclear, however its close association with late Pleistocene laminated sediment sequences in the Santa Barbara Basin indicates the species persists in severely hypoxic conditions.

Miliolid (i.e., *Quinqueloculina* spp.) foraminifera are porcelaneous and largely absent from OMZ environments (e.g., Kaiho 1994; Gooday et al. 2000), and the presence of this taxon

typically indicates oxygen concentrations $>3.5 \text{ ml L}^{-1}$. *N. labradorica* has been found in oxygen-depleted sediments and is known to harbor plastids, which is a strategy that potentially connotes physiological plasticity (Alve 1990; Cedhagen 1991). Preferred oxygenation concentrations for *N. labradorica* are essentially undescribed, however we know that this fauna is compositionally dominant in the cold glacial waters of Santa Barbara Basin and co-occurs with Milliolid fauna (Cannariato et al. 1999; Ohkushi et al. 2013).

2.0 METHODS

2.1 Study system: Santa Barbara Basin, California

Santa Barbara Basin is located in the Southern California Borderlands, USA (Fig. 1). The offshore basin is found between the Santa Barbara coastline and the Channel Islands and has eastern (230 m water depth) and western (475 m water depth) sills (Emery 1960). Paleoclimate reconstructions from the deep center ($\sim 600 \text{ m}$) of Santa Barbara Basin have exceptional, sub-millennial ($<100 \text{ year}$) synchrony to Greenland climate records (e.g., Hendy et al. 2002). Prior investigations have shown that this location records vertical oscillations in the upper boundary of the regional California margin OMZ (Moffitt et al. 2014; Moffitt et al. 2015b).

Figure 1. Location of site MV0811-15JC (9.2 m core length; 34.37°N, 120.13°W) within Santa Barbara Basin, California, USA. The core was collected in 2008 from the *R/V Melville* at a water depth of 418 meters.

2.2 Core MV0811-15JC, a deglacial marine sediment archive

A bioturbated jumbo piston core MV0811-15JC (diameter 11.43 cm) was collected from the *R/V Melville* in 2008 (Fig. 1) at 418 meters below sea level on the northwestern margin of Santa Barbara Basin (9.22 m core length; 34.37°N, 120.13°W). Shipboard samples for geochemical and foraminifera analyses were taken at 10-cm intervals and at a sample volume of 2.5-cm³. The core was resampled in 2012 at 1-cm resolution and a 5-cm³ volume, for a total of 922 individual sediment samples. Sediment samples were disaggregated in deionized water, washed over a 150 µm sieve, and oven dried at 50°C. The age model for core MV0811-15JC is based on linear interpolation between radiocarbon dates and oxygen isotopic stratigraphy tie points to ODP Site 893A (Moffitt et al. 2014). The core represents a post-glacial sediment archive from 16.1 to 3.4 ka with rates of sedimentation of 42.9-100

cm kya⁻¹ (Fig. 2). $\delta^{18}\text{O}$ values from the planktonic foraminifera *Globigerina bulloides* provide a proxy for changing sea surface temperature (e.g., Bemis et al. 2002) and global ice volume (e.g., Schrag et al. 2002; Fig. 2). This record captures most of the deglaciation, but does not extend to include a record of the coldest waters of the Last Glacial Maximum from ~20-18 ka.

We follow Hendy et al. (2002), and references therein, in summarizing the deglaciation into established climatic episodes alongside inferred surface water conditions in the Santa Barbara Basin, including Heinrich 1 (16.1-15.8 ka; *cool*), Pre-Bølling Warming (15.8-15 ka; *warm*), Older Dryas (15-14.7 ka; *cool*), Bølling (14.7-14 ka; *warm*), Allerød (14-12.8 ka; *warm*), Younger Dryas (12.8-11.7 ka; *cool*), Preboreal (11.7-10 ka; *warm*), Early Holocene (10-8 ka; *warm*), Middle Holocene (8-5 ka; *warm*), and Late Holocene (5-3.4 ka; *warm*). We also are particularly interested in the two glacial termination events of Termination IA (14.7 ka) and Termination IB (11.7 ka).

2.3 Mollusca and Foraminifera assemblages

Both mollusc and foraminifera assemblages were examined for the >150 μm size fraction. Mollusc communities were assessed at a 1-cm resolution and every mollusc from the core was counted. Foraminifera were assessed at a lower 10-cm resolution and a minimum of 300 individuals were identified in each sediment sample. Molluscs in these assemblages are small (2 cm length) to very small (0.5 cm length) and only intact molluscs were identified; fragments of larger individuals were not identified. Molluscs were identified to the lowest taxonomic resolution possible using comparative voucher specimens from the

California Academy of Sciences. Mollusc diversity, density, and trophic guild associations are previously published (Moffitt et al. 2015a). For foraminifera (and unlike the taxonomic assessment of the mollusc assemblage), rare species (which account for <5% of abundance) are not included in the analyses; foraminifera diversity and density were previously described for this site (Moffitt et al. 2014). Metrics of community structure include density (fossils cm⁻³) and the Shannon diversity index ($H' = -\sum p_i \ln(p_i)$), where p_i is the proportional abundance of a taxon and H' values increase by either the addition of unique species or by greater species evenness. H' values from <1 are associated with low diversity and >2 are associated with high diversity. Mollusc diversity is shown as a running 5-cm calculation of H' .

2.4 Multivariate statistical analyses

The multidimensionality of paleoecological data captures enormous amounts of variation and stochasticity in biological communities (Shi 1993), therefore the use of multivariate statistics allows for a community-scale approach to assessing climate-forced changes. We employ multivariate statistics here to permit the simultaneous analysis of multiple variables with probable correlations, such as species occurrences and abundance in multiple communities (James and McCulloch 1990). Two methods for multivariate ordination were applied here, including non-metric multidimensional scaling (nMDS) and hierarchical clustering (using group-average linking). Separate analyses were performed for the foraminifera and mollusc datasets. Mollusc communities were lumped into discrete 10-cm intervals, which, due to the 9.22 m length of core MV0811-15JC, produced 92 separate community measurements.

Non-metric multidimensional scaling (nMDS) ordinations of data identify relationships among groups or communities on the basis of intra-group similarities or dissimilarities. The product of such analysis is a scatter plot in which distance among data points (groups) represents differences based on multiple variables. Commonly applied to community data, nMDS has no underlying assumptions regarding the linearity or normality of the data and is based on a ranked dissimilarity matrix. Here we used a Bray-Curtis dissimilarity matrix of square-root transformed species abundance. Bray-Curtis dissimilarities account for differences in composition and abundance between samples and square-root transformation was used to account for rare taxa and down-weight more abundant taxa (Clarke and Warwick 2001).

We employ agglomerative hierarchical cluster analysis to pair and nest communities in a hierarchy of increasing dissimilarity (Gordon 1987). This clustering does not necessarily reveal relationships between groups, but rather quantifies the degree of similarity/dissimilarity between the established groups. Cluster analyses were performed for communities within climate episodes, using a Bray-Curtis dissimilarity matrix of square-root transformed fossil species abundance.

Additionally, we concentrate on the species that are principally responsible for determining community groupings in either the nMDS or cluster analysis. Similarity of percentage (SIMPER) analysis was conducted to quantify the average similarity within a climate episode ($\bar{S}_i$), as well as the average contribution of individual taxa to that episode's

similarity (Clarke 1993). Certain taxa will characterize a climatic interval if they are found at consistent abundances and show relatively high contributions to similarity in a suite of samples from that climate interval ($\bar{S}_i$). For consistent and abundant taxa, the standard deviation of similarity would be low, and the ratio of similarity to standard deviation high ($\bar{S}_i/1\sigma$). Interpretation of the contributions of taxa to community similarity in SIMPER analyses were cut off at 50% for foraminifera and 70% for molluscs. Mollusc and foraminifera taxa that contribute to community similarities are superimposed as bubble plots onto community nMDS ordinations.

To test for the simultaneous response of multiple variables to multiple factors, we use permutation-based multivariate analysis of variance (PERMANOVA; McArdle and Anderson 2001). Significance of these tests was based on permutations of the data (Anderson 2001, Anderson and Ter Braak 2003). Additionally, Monte Carlo tests were run simultaneously to account for intervals where only a limited number of permutations can be drawn because of sample sizes (Anderson and Robinson 2003). If permutations were limited to <100, then tests of significance (p values) and t statistics were sourced from the Monte Carlo test. If permutations were >100, then p values and t statistics were sourced from the PERMANOVA. A significance value of $\alpha=0.01$ was used to interpret only the strongest differences between communities. Multivariate ordinations, cluster analyses, SIMPER and PERMANOVA tests were conducted in PRIMER v6 software (Clarke and Gorley 2005).

3.0 RESULTS

3.1 Density and diversity

The mollusc record is a discontinuous, bioturbated biotic archive that was potentially biased toward smaller size classes, and was represented in only 28% of sediment samples in core MV0811-15JC (Fig. 2, Table 1). Mean mollusc density ($\pm 1\sigma$) was 0.14 ± 0.65 fossils cm^{-3} (for the entire record) and 0.52 ± 1.16 fossils cm^{-3} (excluding intervals with no molluscs; Table 1). 584 mollusc fossils were collected from the core, including 291 bivalves, 189 gastropods and 104 scaphopods (Table 2). Twenty-seven taxonomic groups were identified to the lowest resolution possible, ranging from family (34%), subfamily (7%), genus (14%), to species (38%). Communities with the highest densities occurred during the Pre-Bølling Warming (15.3 ka, 18.8 fossils cm^{-3}), Younger Dryas (12.4 ka, 1.2 fossils cm^{-3}) and Middle Holocene (6.7 ka, 2 fossils cm^{-3}) climatic episodes (Fig. 2). Molluscs were at low abundances or absent during the Bølling-Allerød, Preboreal, and Early and Late Holocene climatic episodes. Mean densities for these episodes included Heinrich 1 (0.25 ± 0.06 fossils cm^{-3}), Pre-Bølling Warming (0.55 ± 0.37 fossils cm^{-3}), Oldest Dryas (0.18 ± 0.09 fossils cm^{-3}), Younger Dryas (0.19 ± 0.13 fossils cm^{-3}), and Middle Holocene (0.10 ± 0.15 fossils cm^{-3} ; Table A.1). Peaks in mollusc community diversity occurred in the Pre-Bølling Warming (15.2 ka, $H'=4.5$), the transition between the Allerød and Younger Dryas (12.8 ka, $H'=1.9$), the Younger Dryas (12.1 ka, $H'=3.4$), and the Middle Holocene (6.7 ka; $H'=2.4$).

Figure 2. Sedimentation rates, oxygen isotopes, and foraminifera and mollusc community data for site MV0811-15JC, with shading to differentiate high-resolution deglacial climate intervals. The color bar on the top of the figure represents the current interpretation of surface ocean temperature in Santa Barbara Basin, with orange corresponding to warmer intervals and blue corresponding to cooler intervals (e.g., Hendy et al. 2002). All data are modified from Moffitt et al., 2014 and 2015b. A. Relative frequency changes (5-cm moving average) in mollusc trophic guilds include chemosynthetically-associated, deposit, suspension, deposit/suspension, carnivore/detritivore, carnivore/deposit, detritivore, and unknown (Table 2). B. Sedimentation rates (cm ka^{-1}), C. Planktonic foraminifera *Globigerina bulloides* $\delta^{18}\text{O}$ (‰) values, D. foraminifera diversity (H'), E. Foraminiferal density (individual cm^{-3}), F. Mollusc *log* density (individual cm^{-3}), G. Mollusc diversity (H' , 5-cm moving average).

Foraminifera completed a continuous archive across the sedimentary sequence and occurred in 100% of the sediment samples (Fig. 2, Table 1). 139,795 foraminifera were counted and 22 taxonomic groups were identified at the level of genera (45%) and species (55%). This assessment of diversity was conservative, as rare taxa (<5% of the assemblage) were not incorporated into the analysis. Mean foraminifera density ($\pm 1\sigma$) was 582.6 ± 497.3 fossils cm^{-3} , which is four orders of magnitude higher than total mollusc density (Table 1). The highest density across all intervals was measured in the Early Holocene ($1,883 \pm 1,168$ fossils cm^{-3}) and the Middle Holocene ($1,645 \pm 1,243$ fossils cm^{-3}) (Table A.1). The lowest density was recorded in Heinrich 1 (338 ± 22 fossils cm^{-3}) and the Younger Dryas (374 ± 256 fossils cm^{-3}) (Table A.1).

Table 1. Mollusc and foraminifera total sampling number, mean density (fossil $\text{cm}^{-3} \pm 1\sigma$), number of taxa, and % of samples containing faunal group for core MV0811-15JC. Mollusc mean density was partitioned into

total mean density (all sediment intervals) and density for only samples with the faunal group (excluding depauperate intervals).

	Number of samples	Mean density (fossil cm ⁻³ ±1σ)	Number of taxa groups	% of total sediment samples with faunal group
Mollusca	922	0.14 ± 0.65 (all sediment intervals) 0.52 ± 1.16 (excluding depauperate intervals absent of molluscs)	28	28.3
Foraminifera	92	582.6 ± 497.3	22	100

Table 2. Mollusc taxa and total counts of fossils recovered from core MV0811-15JC. Trophic guild affiliations shown for each taxa with supporting references. Table is organized by class and abundance within classes.

Adapted from Moffitt et al. 2015b.

Class	Family, Subfamily	Genus, Species	Fossils # of individual valves, shells, tusks	Trophic guilds <i>Chemosynthetically-associated, Deposit, Suspension, Deposit/Suspension Carnivore/Detritivore, Carnivore/Deposit, Detritivore, Unknown</i>	Oxygenation and environmental affiliations
BIVALVIA	Lucinidae, Codakiinae	<i>Lucinoma aequizonata</i> (Stearns, 1890)	199	Chemosynthetically-associated <i>L. aequizonata</i> is associated with low or patchy sulfide environments (Cary et al. 1989) and hosts sulfur-oxidizing chemoautotrophic endosymbiotic bacteria in gill tissue (Brooks et al. 1987; Mosch et al. 2012) that metabolize nitrate and respire at the same rate regardless of oxygen concentrations (Hentschel et al. 1993).	OMZ core associated, form dense mats Colonize the hypoxic-anoxic transition zone at a very narrow depth range (500±10 meters below sea level) in the modern Santa Barbara Basin (Cary et al. 1989; Hein et al. 2006). The infaunal species lives in anaerobic sediments at 3-5 cm depths, and has been collected live from cold seep <i>Vesicomya</i> spp. clam beds (Schweimanns and Felbeck 1985).

	Tellinidae, Macominae	<i>Macoma</i> (Leach, 1819)	36	Deposit/Suspension (Reid and Reid 1969)	Not OMZ-Associated There is no indication in the literature that genus <i>Macoma</i> is tolerant of hypoxia or associated with OMZ environments. <i>Macoma</i> species are commonly associated with Arctic and circumboreal waters (Sander and Allen 1977). Low oxygen conditions induce behavioral changes in one <i>Macoma</i> species, thought to increase vulnerability to predation, wherein the species does not bury as deeply in hypoxic condition (Zamorano et al. 2007).
	Cardiidae	(Lamarck, 1809)	14	Suspension Common observation	
	Lucinidae	(Fleming, 1882)	7	Chemosynthetically-associated Chemosymbiosis with sulphide-oxidizing and methane-oxidizing microbes has been identified in the bivalve family Lucinidae (Oliver et al. 2011).	
	Psammobiidae	(Fleming, 1882)	7	Deposit (Sander and Allen 1977)	
	Cardiidae, Clinocardiinae	<i>Clinocardium nuttalli</i> (Conrad, 1837)	5	Suspension Common observation	
	Cardiidae, Trachycardiinae	<i>Trachycardium</i> (Mörch, 1857)	5	Suspension Common observation	
	Tellinidae, Macominae	(Leach, 1819)	4	Deposit (Sander and Allen 1977)	
	Nuculanidae	(Adams and Adams, 1856)	4	Deposit (Long et al. 2008)	
	Tindariidae	(Verrill and Bush, 1897)	3	Deposit Census of Marine Life	
	Yoldiidae	<i>Portlandia</i> (Mörch, 1857)	2	Deposit (Stanley 1970)	
	Limidae		2	Suspension Common observation	
	Ungulinidae	(Adams and Adams, 1856)	2		
	Manzanellidae	<i>Huxleyia munita</i> (Dall, 1898)	1	Chemosynthetically-associated The presence of chemosynthetic microbes in the gills of Manzanellidae has been demonstrated (Coan 2000; Oliver and Taylor 2012).	
GASTROPODA	Columbellidae, Pyreninae	<i>Alia permodesta</i> (Dall, 1890)	83	Chemosynthetically-associated <i>A. permodesta</i> is a part of chemosynthetic trophic pathways (Bernhard et al. 2003). <i>A. permodesta</i> occurs in tight affiliation with filamentous sulfur-oxidizing chemosynthetic bacterial mats (e.g., <i>Beggiatoa</i> or <i>Thioploca</i>) (Deming et al. 1997).	OMZ core associated, form dense mats Epifaunal gastropod <i>A. permodesta</i> colonizes seafloor environments associated with the Eastern Pacific OMZ (Levin and Michener 2002; Mosch et al. 2012).

				No evidence exists that this species harbors sulfur-oxidizing endosymbionts (Taylor and Glover 2006). Isotopic signatures indicate <i>A. permodesta</i> graze on chemosynthetic bacteria (Bernhard et al. 2003).	
	Cerithiidae, Bittiinae	<i>Lirobittum paganicum</i> (Dall, 1919)	72	Detritivore (Sahling et al. 2002).	Cold seep associated <i>L. paganicum</i> has been collected within methane seeps in association with vesicomyid bivalves (Sahling et al. 2002).
	Cerithiidae, Bittiinae	<i>Lirobittum rugatum</i> (Carpenter, 1896)	30	Detritivore (Richter and Luque 2004)	
	Unknown		4		
	Columbellidae, Pyreninae	(Suter, 1919)	2	Carnivore/Detritivore (Levin et al. 2000)	
	Epitoniidae	<i>Epitonium</i> (Röding, 1798)	1	Carnivore/Deposit (Modica and Holford, 2010)	
	Columbellidae, Pyreninae	<i>Amphissa bicolor</i> (Dall, 1892)	1		
SCAPHOPODA	Gadilidae	(Stoliczka, 1886)	61	Carnivore/Deposit (Langer et al. 1995; Richter and Luque 2004).	OMZ margin associated [O ₂] > 0.5 ml L ⁻¹ (Zamorano et al. 2007).
	Rhabdidae	(Chistikov, 1975)	22	Carnivore/Deposit (Langer et al. 1995; Richter and Luque 2004).	OMZ margin associated [O ₂] > 0.5 ml L ⁻¹ (Zamorano et al. 2007).
	Gadilidae	<i>Siphodentalium quadrifissatum</i> (Pilsbry and Sharp, 1898)	10	Carnivore/Deposit (Langer et al. 1995; Richter and Luque 2004).	OMZ margin associated [O ₂] > 0.5 ml L ⁻¹ (Zamorano et al. 2007).
	Gadilidae	<i>Cadulus tolmiei</i> (Dall, 1897)	7	Carnivore/Deposit (Langer et al. 1995; Richter and Luque 2004).	OMZ margin associated [O ₂] > 0.5 ml L ⁻¹ (Zamorano et al. 2007).
	Unknown		5		
	Rhabdidae	<i>Rhabdus recticus</i> (Carpenter, 1864)	2	Carnivore/Deposit (Langer et al. 1995; Richter and Luque 2004).	OMZ margin associated [O ₂] > 0.5 ml L ⁻¹ (Zamorano et al. 2007).
	Gadilidae	<i>Gadila aberrans</i> (Whiteaves, 1887)	2	Carnivore/Deposit (Langer et al. 1995; Richter and Luque 2004).	OMZ margin associated [O ₂] > 0.5 ml L ⁻¹ (Zamorano et al. 2007).

3.2 Ordinations and cluster analyses

Ordinations visualize the relatedness of communities on a 2-D space for molluscs and foraminifera (Fig. 3, panels a and c). Cluster analyses yielded hierarchical rankings of similarity between climatic intervals (Fig. 3, panels b and d). The 2-D stress values for the community ordinations were >0.1, and this suggested the 2-D visualizations did not

capture all the differences between communities. The coherence between the cluster analyses and nMDS ordinations, however, suggested that the interpretations of the 2D ordinations were robust at the scale of the analysis (Clarke and Warwick 2001).

Foraminifera communities were less similar to one another (>40% similar) and have a more variable community structure than molluscs, for which all post-glacial communities were >58% similar (Fig. 3).

Similar patterns emerged between the taxonomic groups in relation to how related communities are to one another, such as how the Younger Dryas clustered together with communities from the Pre-Bølling Warming and the Older Dryas. A primary difference between the two taxonomic groups was how Heinrich 1 foraminifera communities clustered with the Younger Dryas, whereas Heinrich 1 mollusc communities clustered with the Holocene, Bølling and Allerød. Another difference emerged between the Bølling and Allerød, where Allerød mollusc communities clustered with Early and Middle Holocene, and Bølling communities clustered with the Preboreal and Late Holocene. In contrast, foraminifera communities of the Bølling and Allerød clustered together and post-Termination IB communities (Preboreal and Holocene) clustered together. The ordinations of foraminifera reflected a sequential, chronological progression of the deglacial climatic events, whereas the mollusc ordination reflected a non-chronological grouping of similar communities.

Figure 3. Cluster analyses and nMDS plots of mollusc and foraminifera community data for site MV0811-15JC. These plots can be interpreted as a visualization of the relatedness of mollusc and foraminifera communities and they indicate how communities changed through post-glacial climate transitions. A. Mollusc nMDS ordination with groupings of 60% similarity. B. Mollusc hierarchical cluster. C. Foraminifera nMDS ordinations with groupings of 40% and 60% similarity. D. Foraminifera hierarchical cluster.

3.3 Community similarity

Community similarity ($\bar{S}_i$), or the average similarity among the communities within a climate episode, exhibited variability through the post-glacial sequences (Fig. 4). In general, foraminifera community similarity was high and did not change dramatically from interval to interval, whereas mollusc assemblages exhibited large swings in similarity. Peak similarity occurred in Heinrich 1 for foraminifera ($\bar{S}_i=90.41$) and molluscs ($\bar{S}_i=65.03$) communities, which was followed by declining similarity through the Pre-Bølling Warming and Oldest Dryas. The nadir of foraminifera community similarity occurred during the Oldest Dryas ($\bar{S}_i =55.46$), whereas the nadir in mollusc community similarity occurred in the Bølling ($\bar{S}_i =1.85$).

Figure 4. Intra climate interval average community similarity ($\bar{S}_i$) produced from SIMPER analyses.

Associated data table shown. These data can be interpreted as a record of the sequential, post-glacial changes in climate interval community similarity where foraminifera document incremental differences and mollusc communities document large swings.

3.4 Dominant mollusc taxa

Community similarity ($\bar{S}_i$) through each climate episode was primarily dominated by seven molluscan taxa, including bivalves (*Macoma* sp., Cardiidae, *Lucinoma aequizonata*), gastropods (*Alia permodesta*, *Lirobittum paganicum*) and scaphopods (Gadilidae, Rhabdidae) (Fig. 5; Table 3). Bivalve taxa did not consistently co-occur through the post-glacial climate events, whereas gastropods occurred together in the Allerød, Younger Dryas and Middle Holocene and scaphopods occurred together during the Pre-Bølling Warming, Oldest Dryas, and Younger Dryas (Fig. 5).

L. aequizonata was present at moderately high densities (0.2-1.8 fossils cm⁻³) prior to Termination IA, and was also recorded in the Younger Dryas (0.4-2.0 fossils cm⁻³). *L. aequizonata* contributed to community similarity during Heinrich 1 ($\bar{S}_i$ =65.03), Pre-Bølling Warming ($\bar{S}_i$ =22.14) and Younger Dryas ($\bar{S}_i$ =4.83; Table 3). The highest density for the entire mollusc record was found at 15.3 ka in the Pre-Bølling Warming, from which 40 individual shells of the bivalve *L. aequizonata* were recovered from a 1-cm interval (Fig. 5). This layer also included scaphopods *Gadila aberrans* and *Cadulus tolmiei* and two bivalves from Cardiidae (Trachycardiinae and species *Clinocardium nuttalli*). High *Macoma* spp. densities were found in the Younger Dryas (0.2-1.0 fossils cm⁻³). The Younger Dryas was the only interval in which *Macoma* spp. was found to contribute to community similarity ($\bar{S}_i$ =9.22) (Table 3). Cardiidae was found primarily in the Pre-Bølling Warming, Oldest Dryas, and Bølling and was the only mollusc to contribute to community similarity in the Bølling (Fig. 5; Table 3).

Alia permodesta was present in high densities in the Middle Holocene (0.2-1.2 fossils cm⁻³), in moderate densities at the Allerød-Younger Dryas transition (0.2-0.6 fossils cm⁻³), and in low densities in the Pre-Bølling Warming and Oldest Dryas (0.2-0.4 fossils cm⁻³; Fig. 5). *A. permodesta* contributed to community similarity in the Allerød ($\bar{S}_i=15.22$) and to a lesser extent in the Pre-Bølling Warming, Oldest Dryas, Younger Dryas and Middle Holocene (Table 3). *L. paganicum* was present at high densities in the Allerød and Younger Dryas (0.2-0.4 fossils cm⁻³), and Middle Holocene (0.2-0.8 fossils cm⁻³; Fig. 5), and contributed to community similarity in the Allerød ($\bar{S}_i=15.22$) and the Middle Holocene ($\bar{S}_i=16.41$; Table 3).

Gadilidae and Rhabdidae were present during the Pre-Bølling Warming (Gadilidae 0.2-0.8 fossils cm⁻³; Rhabdidae 0.2 fossils cm⁻³), Oldest Dryas (Gadilidae, 0.4 fossils cm⁻³; Rhabdidae 0.2 fossils cm⁻³), and Younger Dryas (Gadilidae, 0.2-0.6 fossils cm⁻³; Rhabdidae 0.2-0.4 fossils cm⁻³) (Fig. 5). Gadilidae contributed to community similarity during the Pre-Bølling Warming ($\bar{S}_i=9.86$), Oldest Dryas ($\bar{S}_i=4.44$), and Younger Dryas ($\bar{S}_i=10.51$), whereas Rhabdidae contributed during the Oldest Dryas ($\bar{S}_i=4.44$; Table 3).

Bubble plots of *L. aequizonata*, *A. permodesta* (Fig. 6) and *L. paganicum*, Cardidae, *Macoma* sp., Gadilidae, and Rhabdidae visualize the density distribution of respective species across the community ordination space (Fig. 7). The highest densities of *L. aequizonata* and *A. permodesta* grouped at opposite sides of the ordination, although *A. permodesta* occurred at low densities in communities with dense assemblages of *L. aequizonata*. *A. permodesta*

tightly grouped on one side of the ordination (Fig. 6) in association with Allerød and Middle Holocene communities (Fig. 3) and also with high *L. paganicum* densities (Fig. 7). The highest densities of *L. aequizonata* occurred in two Pre-Bølling Warming communities (Fig. 3) and represent acme (i.e., the highest point) events in the mollusc archive. High scaphopod densities were associated with communities dominated by *L. aequizonata* (Fig. 6, 7). Bivalve taxa *Macoma* sp. were distributed across the center and Cardiidae were distributed horizontally across the ordination (Fig. 7).

Figure 5. Mollusc density (tusks, shells or valves cm^{-3}) for taxa that drove intra-interval community similarity for site MV0811-15JC, including three bivalves (A. *Macoma* sp., B. *Cardiidae*, C. *Lucinoma aequizonata*), two

gastropods (D. *Alia permodesta*, E. *Lirobittum paganicum*) and two scaphopods (F. Gadilidae, G. Rhabdidae). The color bar on the top of the figure represents the current interpretation of surface ocean temperature in Santa Barbara Basin, with orange corresponding to warmer intervals and blue corresponding to cooler intervals (e.g. Hendy et al. 2002).

Table 3. Mollusc taxa that contribute to community similarity within climate episodes (SIMPER analyses), with up to a 70% contribution point. Average similarity contributions ($\bar{S}_i$) for each taxon and the ratio of average similarity by the standard deviation (1σ) is calculated from Bray-Curtis similarities. Depauperate intervals of the Preboreal and Late Holocene are not included.

Climate Interval	N, 10-cm samples	Species	Average Similarity ($\bar{S}_i$)	$\bar{S}_i/1\sigma$
Heinrich 1	3	<i>Lucinoma aequizonata</i>	65.03	2.31
Pre-Bølling Warming	8	<i>Lucinoma aequizonata</i>	22.14	3.28
		Gadilidae	9.86	1.29
		<i>Alia permodesta</i>	4.80	1.00
Oldest Dryas	3	<i>Alia permodesta</i>	4.44	0.58
		Gadilidae	4.44	0.58
		Rhabdidae	4.44	0.58
Bølling	7	Cardiidae	1.85	0.22
Allerød	11	<i>Alia permodesta</i>	15.22	0.73
		<i>Lirobittum paganicum</i>	5.65	0.47
Younger Dryas	12	Gadilidae	10.51	0.98
		<i>Macoma spp.</i>	9.22	0.74
		<i>Lucinoma aequizonata</i>	4.83	0.62
		<i>Alia permodesta</i>	3.76	0.52
Early Holocene	8	Gastropod, Unknown	11.02	0.35
Middle Holocene	20	<i>Lirobittum paganicum</i>	16.41	0.83
		<i>Alia permodesta</i>	4.42	0.43

Figure 6. Bubble plots of gastropod *Alia permodesta* (green bubbles) and bivalve *Lucinoma aequizonata* (blue bubble); sediment intervals with no *A. permodesta* or *L. aequizonata* are shown as black circles.

Bubble size approximates relative density of each respective species at each individual sampling interval, and the bubbles are superimposed on the mollusc community ordination from Fig. 3. The figure visualizes the relative abundance of these two fauna in relationship to community similarity and demonstrates how the fauna do not consistently co-occur. The highest abundances of *A. permodesta* and *L. aequizonata* occur in assemblages that are the least similar to one another.

Figure 7. Bubble plots of scaphopod, bivalve and gastropod taxa. Sediment intervals absent of each individual fauna groups(a-e) are shown as black circles. Bubble size approximates relative density of each respective species at each individual sampling interval, and the bubbles are superimposed on the mollusc community ordination from Fig. 3. The figure visualizes the relative abundance of these faunal groups in relationship to community similarity and demonstrates that in some cases these fauna co-occur and in others they do not. Taxa include Gadilidae, Rhabdidae, *Macoma* sp., *Lirobittum paganicum* and Cardiidae.

3.5 Dominant foraminifera taxa

Ten taxonomic groups provide the highest average contributions to group similarity, including *Quinqueloculina* spp., *Nonionellina labradorica*, *Uvigerina* spp., *U. peregrina*, *Bolivina argentea*, *B. spissa*, *B. pseudobeyrichi*, *Buliminella* spp., *Pseudoparella pacifica*, and *Nonionella stella* (Table 4). These taxonomic groups oscillate in compositional dominance and abundance across the post-glacial climate episodes (Fig. 8). *Quinqueloculina* spp. and *N. labradorica* occurred prior to Termination IA and contributed to similarity in Heinrich 1, the Pre-Bølling Warming and the Oldest Dryas (Fig. 8). *P. pacifica*, *N. stella*, and *U. peregrina* contributed to community similarity in the Bølling and Allerød. *N. labradorica* contributed to community similarity in the Younger Dryas. Preboreal and Holocene episodes were compositionally dominated by species from genera *Bolivina*, *Uvigerina*, and *Buliminella*.

Bubble plots (Fig. 9) show how densities of prominent taxa, including *Quinqueloculina* spp., *N. labradorica*, *U. peregrina*, *B. argentea*, *P. pacifica*, and *N. stella*, clustered together across the community ordination (Fig. 3). The highest densities of *N. labradorica* and *Quinqueloculina* spp. clustered together in Heinrich 1, Pre-Bølling warming, Oldest Dryas, and the Younger Dryas. The highest densities of *N. stella* and *B. tumida* clustered together in the Bølling, Allerød and Preboreal, and the highest densities of *P. pacifica* were found in the Bølling and Allerød. *B. argentea* densities were very high in the Early, Middle and Late Holocene, as well as the Preboreal. The highest densities of *U. peregrina* occurred in the Holocene, and moderate to low densities occurred in the Bølling, Allerød, and the Younger Dryas.

Table 4. Foraminifera taxa that contributed to community similarity within climate episodes (SIMPER analyses), with up to a 50% contribution point. Average similarity ($\bar{S}_i$) for each contributing taxon and the ratio of average similarity by the standard deviation (1σ) is calculated from Bray-Curtis similarities.

Climate Interval,	N, 10-cm samples	Species	Average Similarity ($\bar{S}_i$)	$\bar{S}_i/1\sigma$
Heinrich 1	3	<i>Nonionellina labradorica</i>	30.76	20.37
		<i>Bolivina argentea</i>	13.22	19.7
		<i>Quinqueloculina</i> spp.	12.47	43.18
Pre-Bølling Warming	8	<i>Nonionellina labradorica</i>	31.86	8.51
		<i>Quinqueloculina</i> spp.	12.86	3.34
Oldest Dryas	3	<i>Nonionellina labradorica</i>	19.45	1.35
		<i>Pseudoparella pacifica</i>	7.3	1.52
		<i>Quinqueloculina</i> spp.	6.42	1.75
Bølling	7	<i>Pseudoparella pacifica</i>	19.43	2.22
		<i>Uvigerina peregrina</i>	11.49	5.62
		<i>Nonionella stella</i>	8.21	3.7
Allerød	11	<i>Pseudoparella pacifica</i>	16.55	2.84
		<i>Nonionella stella</i>	10.11	2.96
		<i>Uvigerina peregrina</i>	7.33	4.29
Younger Dryas	12	<i>Uvigerina</i> spp.	12.31	4.77
		<i>Nonionellina labradorica</i>	8.07	1.8
		<i>Pseudoparella pacifica</i>	7.83	2.53
		<i>Uvigerina peregrina</i>	7.35	3.9
Preboreal	7	<i>Bolivina argentea</i>	19.14	3.22
		<i>Uvigerina peregrina</i>	9.71	3.7
		<i>Buliminella</i> spp.	6.56	1.84
Early Holocene	8	<i>Bolivina argentea</i>	18.03	6.16
		<i>Bolivina spissa</i>	12.25	4.16
		<i>Buliminella</i> spp.	5.76	3.18
Middle Holocene	20	<i>Bolivina argentea</i>	14.13	2.92
		<i>Uvigerina peregrina</i>	10.53	3.83
		<i>Bolivina spissa</i>	9.18	3.43
		<i>Bolivina pseudobeyrichi</i>	8.74	5.08
Late Holocene	13	<i>Bolivina argentea</i>	21.29	5.16
		<i>Uvigerina peregrina</i>	16.84	5.79
		<i>Uvigerina</i> spp.	8.91	2.93

Figure 8. Foraminifera density (fossils cm^{-3}) for primary taxa influencing community similarity at site MV0811-15JC, including A. *Quinqueloculina* spp., B. *Nonionellina labradorica*, C. *Uvigerina peregrina*, D. *Bolivina argentea*, E. *Pseudoparella pacifica*, and F. *Nonionella stella*. The color bar on the top of the figure represents the current interpretation of surface ocean temperature in Santa Barbara Basin, with orange corresponding to warmer intervals and blue corresponding to cooler intervals (e.g. Hendy et al. 2002).

Figure 9. Bubble plots of foraminifera taxa. Sediment intervals absent of each faunal group are indicated as black circles. Bubble size approximates relative density of each respective species at each individual sampling

interval, and the bubbles are superimposed on the foraminifera community ordination in Fig. 3. The figure visualizes the relative abundance of these faunal groups in relationship to community similarity and demonstrates that in some cases these fauna co-occur and in other they do not. Note scale changes due to differences in density of each species. Taxa include *Quinqueloculina* spp., *Nonionella stella*, *Bolivina tumida*, *Nonionellina labradorica*, *Uvigerina peregrina*, *Pseudoparella pacifica*, and *Bolivina argentea*.

3.6 Testing community similarity across climate episodes

Pair-wise comparisons of faunal assemblages (with PERMANOVA analyses) were produced, and all pairwise test of significance (p values) and t statistics are listed for molluscs (Table A.2) and foraminifera (Table A.3). Heinrich 1, Pre-Bølling Warming and Oldest Dryas faunal assemblages were all similar to one another (Table A.2, A.3). Oldest Dryas fauna were also similar to those found in the Younger Dryas. Bølling and Allerød assemblages were also similar to one another. For molluscs, Allerød and Middle Holocene assemblages were similar to one another. And for foraminifera, assemblages after Termination IB continued to change and exhibited differences through the Holocene.

4.0 DISCUSSION

Biotic archives presented here allow for reconstructions of California continental margin seafloor paleoecological change between 16.1 and 3.4 ka (Fig. 1). Mollusc and foraminifera assemblages exhibited sensitive responses to the millennial-scale climatic and oceanographic episodes that marked the post-glacial interval of the late Pleistocene (Fig. 2). We note that there were differences in sampling and identification protocol between molluscs and foraminifera, as well as identification (rare species of foraminifera representing <5% of assemblage were not considered, whereas all molluscs were identified

to species-level where possible). There is likely a bias towards overrepresentation of small mollusc fauna in this record, although this should not be interpreted as a direct bias towards age classes, because for adult bivalves, as well as many gastropods, adult body size is more sensitive to environmental conditions than to age. Additionally, small body size is one of the principal morphologies of animals in OMZs (Levin 2002), and we therefore expect this to be a primary characteristic of the assemblages in core MV0811-15JC.

Multivariate statistics are used here (at 10 cm resolution) to produce new interpretive benchmarks for paleoecological reconstructions. These include nMDS, cluster analyses (Fig. 3), and bubble plots (Fig. 6, 7, 9) to visualize hierarchy and similarity, as well as analyses to identify taxa which contribute most to intra-episode similarity (Fig. 4, Table 3, 4). We also tested pairwise difference between climate episodes (Table A.2, A.3).

Sediment winnowing and bioturbation are potential mechanisms that may influence the integrity of the environmental record, although these processes can occur without significantly altering stratigraphy (François et al. 2004). These caveats have been previously examined for core MV0811-15JC (Moffitt et al. 2014; Moffitt et al. 2015b). Sedimentation rates for MV0811-15JC are lower ($42.9\text{--}100\text{ cm kyr}^{-1}$) than published rates for deeper cores located within the center of Santa Barbara Basin ($\sim 130\text{ cm kyr}^{-1}$) (Ohkushi et al. 2013); this difference is attributed to postdepositional downslope transport or sediment winnowing (Moffitt et al. 2014). Despite these factors, when compared to deeper independently-dated cores from the Santa Barbara Basin, core MV0811-15JC recorded synchronous deglacial changes across foraminifera communities and lamination

preservation with the deeper sites (Cannariato et al. 1999; Ohkushi et al. 2013; Moffitt et al. 2014).

Down-slope transport of microfossils can potentially complicate interpretations of microfossil diversity and abundance. This is especially critical for shallow continental margin settings that express distinctly different chemical and physical water column gradients. Foraminifera would logically be impacted by downslope transport. However, we have identified significant differences ($p < 0.001$) in foraminifera communities between almost all pairwise comparisons between deglacial climate intervals (Table A.3), demonstrating these assemblages have clear relationships to deglacial climate episodes. These results sufficiently demonstrate that down-slope transport has not obscured the capacity of the microfossil record to partition changes in seafloor ecology.

In addition, sediments are clearly bioturbated and spatangoid urchin spines (a ubiquitous seafloor bioturbating invertebrate) are identified through the entire core (Moffitt et al, 2015b). For context, estimates for bioturbation depth disturbance in deep-sea sediments are commonly assumed to be ~10 cm, although shallower (2–5 cm) (Kirstensen et al, 2010; Thompson and Riddle 2005) and deeper (20 cm) depths are reported (Bromley 1996). Based on such bioturbation depths, the depositional rate of the first and last disappearances of metazoans (including mollusc classes, ostracods, and ophuroids) were examined across the rapid oxygen-loss events of Termination IA (12 cm of sediment, 130 years) and IB (18 cm of sediment, 170 years; Moffitt et al. 2015b). In short, the first and last disappearances across all metazoan taxa occur in <20 cm for both termination events. The

homogenizing, vertical mixing effect of bioturbation suggests that the over-estimation of the duration of these ecological transitions may be occurring – such that an abrupt event reconstructed to take centuries may have only taken decades.

4.1 Ecosystem history

4.1.1 Heinrich 1, Pre-Bølling Warming and the Oldest Dryas

Pre-Termination IA mollusc (Table A.2) and foraminifera (Table A.3) assemblages are statistically similar to one another, indicating that similar environmental regimes were present during these climatic episodes. These intervals precede the abrupt Northern Hemisphere warming of Termination IA. Heinrich 1 and the Oldest Dryas have cool, glacial-like sea surface temperatures, whereas the Pre-Bølling Warming is marked by increasing sea surface temperatures (e.g., Hendy et al. 2002; Hill et al. 2006). In overlapping fashion, *L. aequizonata* characterizes Heinrich 1 and the Pre-Bølling Warming, whereas *A. permodesta* and Gadilidae scaphopods mark the Pre-Bølling Warming and Oldest Dryas (Table 3). Foraminifera *N. labradorica* and *Quinqueloculina* spp. both contribute to community similarity during Heinrich 1, Pre-Bølling Warming, and Oldest Dryas (Table 4). These foraminifera also occurred in the deeper Santa Barbara Basin during Pre-Termination IA episodes (and in the Younger Dryas), and they indicate elevated oxygen concentrations at these depths (Cannariato et al. 1999; Ohkushi et al. 2013; Moffitt et al. 2014).

The presence of *Quinqueloculina* spp., high mollusc diversity and abundance, and previously reported ophuroid and ostracod assemblages (Moffitt et al. 2015b) in the Pre-Termination IA intervals clearly indicate elevated seafloor oxygenation concentrations

($[O_2] > 0.5 \text{ ml L}^{-1}$). However, this interpretation directly conflicts with the presence of mollusc fauna dominated by *L. aequizonata* and *A. permodesta*, indicative of chemosynthetic and microbial communities. Both of these taxa are found in dense conspecific zonations, and are considered opportunistic, OMZ-associated fauna (Levin and Michener 2002; Mosch et al. 2012). However, they are not associated with identical margin environments, and we see this clearly in the ordination of the fauna through the post-glacial climate intervals; at their most dense, these communities do not co-occur (Fig. 6). This suggests pre-Termination IA communities were at times punctuated by intermittent hypoxic ($[O_2] < 0.5 \text{ ml L}^{-1}$), and/or sulfidic conditions.

A broad range of environmental affiliations in Mollusc taxa are associated with discrete 1-cm sediment intervals. For example, the 15.3 ka high-density peak of *L. aequizonata* occurred in the same 1-cm sampling interval as scaphopods (motile, oxic predators), cardiid bivalves, and oxic foraminifera marker species (*Quinqueloculina* spp.). The assemblages in this 1-cm sample, representing about 10 years of sedimentation (Moffitt et al. 2014), indicate that a wide range of biological communities colonized the margin during a single decade, in association with environments that ranged from well-oxygenated to hypoxic, sulfidic, and chemosynthetic. This range of life history and trophic strategies demonstrates that the mollusc assemblages may be reflecting significant inter-decadal oceanographic variability, likely associated with the vertical movements of the upper boundary of the regional OMZ.

4.1.2 Bølling and Allerød

Termination IA (14.7 ka) initiates the transition to the mid-deglacial climate episodes and is associated with abrupt warming in the Northern Hemisphere and changes deep ocean circulation (e.g., Keigwin et al. 1992; Schmittner and Galbraith 2008). The warming of Termination IA co-occurred with an abrupt, basin-wide expansion of the Eastern Pacific OMZ (e.g., Cannariato et al. 1999; Zheng et al. 2000a; Moffitt et al. 2015a,b; Praetorius et al. 2015). The Bølling interval immediately follows Termination IA, and is a depauperate, hypoxic interval that lacks a consortium of invertebrate fauna, including ostracods, asteroides, and most molluscs, including *L. aequizonata* and *A. permodesta*. The absence of even sulfidic, chemosynthetic fauna during the Bølling may mean that conditions along the continental margin were so unique that we are lacking a modern ecological analogue for comparison. These faunal changes demonstrate that glacial-to-interstadial change, such as seen across Termination IA, comes with significant ecological shifts to a non-analogous metazoan community at this location on the California Margin.

The Allerød seafloor was colonized by the gastropods *A. permodesta* and *L. paganicum* and both appear in the record at 13.5 ka (Fig. 5), and community similarity at this time was influenced by these two species (Table 3). The presence of these taxa likely indicate hypoxic, sulfidic conditions occurred, and may indicate the presence of chemosynthetic microbial mats. Importantly, mollusc communities are similar between the Allerød and the Middle Holocene (Table S.2), and this represents unique evidence that compositionally-similar chemosynthetic ecosystems occurred non-sequentially (i.e., between different millennial-scale climate intervals) in the post-glacial California Margin.

Foraminifera assemblages of the Bølling and Allerød are interpretable in the context of both the natural history of the dominant fauna and their compositional similarity to existing published microfossil records from the California Margin (e.g., Cannariato and Kennett 1999; Cannariato et al. 1999; Ohkushi et al. 2014). Bølling and Allerød foraminifera communities are similar to one another (Table A.3, Fig. 3). Two primary species contribute to community similarity and are associated with strong hypoxia (*N. stella*, $[O_2] < 0.02 \text{ ml L}^{-1}$; Bernhard et al. 1997), intermediate hypoxia (*P. pacifica*, $[O_2] < 0.5 \text{ ml L}^{-1}$; Blake 1976; Quintero and Garner 1987) and methane-enriched seep environments (*P. pacifica*; Bernhard et al. 2001; Hill et al. 2003). Importantly, a significant shift in the densities of the dominant taxa proceeded Termination IA in the Oldest Dryas, when oxic fauna including *Quinqueloculina* spp. (Kaiho 1994) rapidly decreased as the density of *P. pacifica* and *N. stella* increased.

4.1.3 Younger Dryas

The Younger Dryas event in both sea surface and bottom water temperatures in Santa Barbara Basin is described as a mild cooling compared with other records (e.g., Kennett and Ingram 1995; Hill et al. 2006). Yet, a unique mollusc community occurred in the Younger Dryas. Faunal changes at the onset of the Younger Dryas (12.8-11.7 ka) indicate that sulfidic, chemosynthetic communities were abruptly replaced by increasing oxygenation ($[O_2] > 0.5 \text{ ml L}^{-1}$) and non-sulfidic conditions (Fig. 5). Dominant molluscs include gadilid scaphopods, *Macoma* spp., *L. aequizonata* and *A. permodesta* (Table 3). *A. permodesta* and *L. paganicum*, both of which are abundant over the Allerød/Younger Dryas boundary declined by the middle to late Younger Dryas. Scaphopod densities (Gadilidae,

Rhabdidae) increase in the middle to late Younger Dryas (Figure 5). *Macoma* spp. (a taxa associated with more oxygenated, subpolar environments) dominated the mollusc community in the Younger Dryas, and this mid-deglacial anomaly may reflect seafloor conditions most-similar to the Last Glacial Maximum (Fig. 5). The Younger Dryas also marks the return of foraminifera communities exhibiting similarity with communities before Termination IA. These communities included increased densities of oxic marker species (Figure 8) . Thus, although sea surface temperatures do not reflect a major cooling during the Younger Dryas, foraminifera and mollusc assemblages are distinctive.

4.1.4 Preboreal and Holocene

Termination IB (11.7 ka), the transition into the Preboreal climate interval, is marked with abrupt warming in the Northern Hemisphere and the vertical expansion of the OMZ in the Eastern Pacific, which has been extensively documented with continental margin sediment records (e.g., Zheng et al. 2000a; Praetorius et al. 2015; Moffitt et al. 2015a, Moffitt et al. 2015b). At 11.7 ka, all molluscs, ostracods, and asteroids abruptly disappeared from the faunal record (Moffitt et al. 2015b). We interpret these data to be capturing the vertical expansion of the California Margin OMZ and an environmental transition to extreme conditions that were prohibitive to seafloor invertebrate communities (Moffitt et al. 2015b; Fig. 2).

The strongest statistical differences between communities were found between Holocene and Pre-Termination IA communities, and these results indicate large differences between glacial and interglacial continental margin ecosystems (Table S.3). Preboreal and Early

Holocene foraminifera document an increase in total community density and increases in OMZ-associated fauna *B. argentea* and *U. peregrina* (Fig. 8). Holocene foraminifera communities are all distinct from one another, despite the predominance of *B. argentea* and *U. peregrina*, and this indicates that foraminifera communities continued to experience oceanographic change through these episodes (Table 4).

Dense assemblages of the gastropods *A. permodesta* and *L. paganicum* occurred during the Middle Holocene, and these assemblages are similar to those from the Allerød (Fig. 5; Table A.2). The presence of *A. permodesta* ~7.5 to 5.5 ka indicates the seafloor was likely characterized by microbial mats, chemosynthetic trophic webs, and sulfidic environments. Foraminifera were found in extremely high densities during the Middle Holocene (Fig. 2), which indicates that these communities were released from metazoan predation pressure. Similar to the Allerød, bivalve *L. aequinozata* (also a member of chemosynthetic trophic webs) is absent in the Middle Holocene. Such differences in the biostratigraphy of chemosynthetic fauna illustrate again that chemosynthetic assemblages can be non-overlapping and do not necessarily co-occur. They also serve to illustrate how mollusc archives can reveal seafloor trophic processes and the presence of microbially-mediated environments that were previously undiscernible with only foraminifera assemblages.

4.2 Community similarity through warming and OMZ expansion

Comparisons of the compositional similarity of communities within climate intervals provide a basis for hypotheses regarding the relative differences in environmental stability between climate intervals (Fig. 4; Table 4). Highly similar communities within a single

climatic episode may be attributed to communities with either low environmental disturbance (and therefore competitive dominance and climax communities) or high environmental disturbance (and therefore depauperate, early successional stage communities; Connell, 1978). Communities exhibiting low similarity and high diversity within a climate episode may be attributed to intermediate disturbance regimes, wherein successional change is captured within individual climate episodes (Connell, 1978). Highest community similarity, in both molluscs and foraminifera, is exhibited during Heinrich 1, and is followed by abrupt declines in stability during the Pre-Bølling Warming and the Oldest Dryas episode (Fig. 4). During the major oceanographic transitions of Termination IA and IB, marked by increased warming and deoxygenation, molluscs and foraminifera exhibit temporal variability in compositional stability, likely in response to increasing strength of the OMZ (e.g., van Geen et al. 1996, Gardner et al. 1997, Zheng et al. 2000a, Moffitt et al. 2014).

An additional key difference between mollusc and foraminifera assemblages is the higher degree of assemblage dissimilarity in foraminifera (Fig. 3). Indeed, foraminifera assemblages were all different from one another through the post-glacial intervals, yet with key similarities between Pre-Termination IA assemblages and between the Bølling and Allerød. Even Holocene communities were well partitioned, indicating that sub-orbital through sub-millennial oceanographic variability produces detectable environmental change during interglacial climate episodes. Importantly, no similarities are exhibited between Allerød and Holocene foraminifera communities, and no community-scale foraminifera evidence were present to indicate the presence of chemosynthetic trophic

webs. Foraminifera communities reflected, at high-resolution, the well-known progression of climate and oceanographic events since the Last Glacial Maximum. Importantly, the foraminifera which drive interval similarity (including *Quinqueloculina* spp., *Nonionellina labradorica*, *U. peregrina*, *Bolivina argentea*, *Pseudoparella pacifica*, and *Nonionella stella*) are also broadly used as marker species for Eastern Pacific hypoxia reconstructions (see Moffitt et al. 2014). The significance of these species in driving community similarity is an ideal confirmation that OMZ hydrographic structure is a principal driver of environmental variability on the seafloor, and that the existing environmental interpretative paradigms for foraminifera communities are well-supported.

4.3 Mollusc assemblages in paleoenvironmental reconstructions

Mollusc assemblages potentially represent a unique tool for reconstructing specific environments and high-resolution timescales in marine ecosystems. Some mollusc species exhibit high sensitivity to narrow physical or chemical gradients, and they may have unique physiological or trophic adaptations in order to persist in marginal environments (Crame 2000; Taylor et al. 2014). In continental margin environments, where the chemical gradient of dissolved oxygen produces steep zonation gradients in biological communities, some parts of that gradient are prohibitive to mollusc communities. Certain mollusc species (here *L. aequizonata* and *A. permodesta*) can dominate the community structure, because they are competitively dominant and occur in dense con-specific assemblages.

Interpretations of mollusc assemblages must assess the role opportunistic species play in compositionally skewing reconstructions towards over-representing marginal

environments. Additionally, molluscs may be a naturally discontinuous biotic archive, and as such the absence of molluscs also provides important environmental evidence.

5.0 CONCLUSIONS

Here we demonstrate the strong differences between glacial and interglacial seafloor ecosystems of the continental margin of the Northeast Pacific Ocean. We provide strong evidence for the intermittent presence of chemosynthesis in the seafloor environment, which represents a first-order energetic shift in benthic metabolisms and trophic structures. Molluscs provide evidence for the presence of hypoxic, sulfidic, and chemosynthetic environments, and also provide evidence that fauna associated with chemosynthetic trophic webs do not necessarily co-occur. Mollusc assemblages demonstrate that taxa associated with widely different physiological preferences can occur within a single interval of sediment (in this case associated with decadal sedimentation rates), and such assemblages can range from associations with oxygenated environments to hypoxic, sulfidic, and chemosynthetic conditions. We conclude that mollusc assemblages may be reflecting significant inter-decadal oceanographic variability. Foraminifera assemblages display sequential, chronological associations with post-glacial climate episodes, whereas the mollusc produce non-chronological groupings of similar communities. Foraminifera taxa responsible for community similarity here are also largely recognized as OMZ marker species, providing support for the observations that oxygenation change is a principal driver of environmental variability on the post-glacial seafloor.

ACKNOWLEDGEMENTS

We wish to thank H. Spero, R. Mooi, K. Thompson, D. Winter, J. Hosfelt, C. Replogle, and L. Jacobs for sample preparation, analytical assistance, and constructive comments. We thank Craig Nicholson for his efforts and effective leadership associated with our *R/V Melville* coring expeditions in Santa Barbara Basin. We also thank two anonymous reviewers who significantly improved this manuscript. Support was provided by the National Science Foundation (OCE-0825322 and OCE 1255194 TMH), the UC Multicampus Research Programs and Initiatives (to TMH), UC Davis REACH IGERT (to SEM), Mia Tegner Historical Ecology Grant (to SEM), the EPA STAR Fellowship (to SEM) and Switzer Environmental Fellowship (to SEM). This is a contribution of the Bodega Marine Laboratory.

Appendices

Table A.1. Mean density (fossils $\text{cm}^{-3} \pm 1\sigma$) and diversity ($H' \pm 1\sigma$) for both molluscs and foraminifera within climate episodes. Mollusc density is calculated for all sediment samples (including depauperate intervals) within a climate interval.

Climate Interval	Mean mollusc density (fossils $\text{cm}^{-3} \pm 1\sigma$)	Mean foraminifera density (fossils $\text{cm}^{-3} \pm 1\sigma$)	Mean mollusc diversity ($H' \pm 1\sigma$)	Mean foraminifera diversity ($H' \pm 1\sigma$)
Late Holocene	0.00 ± 0.01	577 ± 155	0.00 ± 0.00	1.67 ± 0.25
Middle Holocene	0.10 ± 0.15	$1,645 \pm 1,243$	0.22 ± 0.54	1.77 ± 0.16
Early Holocene	0.01 ± 0.01	$1,883 \pm 1,168$	0.00 ± 0.00	1.69 ± 0.12
Preboreal	0.01 ± 0.01	992 ± 359	0.00 ± 0.00	1.69 ± 0.21
Younger Dryas	0.19 ± 0.13	374 ± 256	0.75 ± 0.89	2.01 ± 0.21
Allerød	0.07 ± 0.10	755 ± 623	0.25 ± 0.47	1.66 ± 0.26
Bølling	0.03 ± 0.02	741 ± 543	0.04 ± 0.16	1.56 ± 0.38
Oldest Dryas	0.18 ± 0.09	773 ± 562	0.53 ± 0.51	1.39 ± 0.40
Pre-Bølling Warming	0.55 ± 0.37	405 ± 153	1.88 ± 0.85	1.15 ± 0.13
Heinrich 1	0.25 ± 0.06	338 ± 22	0.11 ± 0.24	1.37 ± 0.09

Table A.2 Pair-wise PERMANOVA and Monte Carlo tests reveal statistical similarity of post-glacial mollusc communities of core MV0811-15JC. Tests of significance (p values), t statistics and degrees of freedom (v) from PERMANOVA and Monte Carlo tests are listed. If statistical permutations numbered >100, then p statistics were sourced from the PERMANOVA ($p_{perm, v}$). If statistical permutations numbered <100, then p statistics were sourced from the Monte Carlo test ($p_{MC, v}$). Significance is indicated in red ($p < 0.001$) and blue ($p < 0.01$) text. Climate intervals are abbreviated and include the Late Holocene (LH), Middle Holocene (MH), Early Holocene (EH), Preboreal (PB), Younger Dryas (YD), Allerød (A), Bølling (B), Oldest Dryas (OD), Pre-Bølling Warming (PW), and Heinrich 1 (H1).

	LH	MH	EH	PB	YD	A	B	OD	PW
MH	t=3.00 $p_{perm, 31}$ <0.01								
EH	t=0.800 $p_{MC, 19}$ =0.57	t=2.616 $p_{perm, 26}$ <0.01							
PB	t=1.165 $p_{MC, 18}$ =0.28	t=2.391 $p_{perm, 25}$ <0.01	t=0.990 $p_{MC, 13}$ =0.42						
YD	t=3.774 $p_{perm, 23}$ <0.001	t=3.540 $p_{perm, 30}$ <0.001	t=2.881 $p_{perm, 18}$ <0.001	t=2.777 $p_{perm, 17}$ <0.001					
A	t=2.780 $p_{perm, 22}$ <0.001	t=1.087 $p_{perm, 29}$ =0.27	t=2.554 $p_{perm, 17}$ <0.01	t=2.335 $p_{perm, 16}$ <0.1	t=2.744 $p_{perm, 21}$ <0.001				
B	t=0.259 $p_{MC, 18}$ =0.94	t=2.380 $p_{perm, 25}$ <0.01	t=1.439 $p_{perm, 13}$ =0.09	t=0.914 $p_{MC, 12}$ =0.48	t=2.681 $p_{perm, 17}$ <0.001	t=2.055 $p_{perm, 16}$ =0.015			
OD	t=2.746 $p_{MC, 14}$ <0.01	t=2.10 $p_{perm, 21}$ <0.01	t=1.811 $p_{MC, 9}$ =0.05	t=1.997 $p_{MC, 8}$ =0.04	t=1.111 $p_{perm, 13}$ =0.30	t=1.701 $p_{perm, 12}$ =0.050	t=1.641 $p_{MC, 8}$ =0.08		
PW	t=5.710 $p_{perm, 19}$ <0.001	t=5.096 $p_{perm, 26}$ <0.001	t=4.301 $p_{perm, 14}$ <0.001	t=4.127 $p_{perm, 13}$ <0.001	t=2.240 $p_{perm, 18}$ <0.01	t=4.165 $p_{perm, 17}$ <0.001	t=3.688 $p_{perm, 13}$ <0.001	t=1.249 $p_{perm, 9}$ =0.19	
H1	t=6.523 $p_{MC, 14}$ <0.001	t=3.330 $p_{perm, 21}$ <0.001	t=4.401 $p_{MC, 9}$ <0.001	t=4.815 $p_{MC, 8}$ <0.001	t=1.848 $p_{perm, 13}$ <0.01	t=3.423 $p_{perm, 12}$ <0.001	t=3.191 $p_{perm, 8}$ <0.01	t=1.228 $p_{MC, 4}$ =0.27	t=1.194 $p_{perm, 9}$ =0.23

Table A.3 Pair-wise PERMANOVA and Monte Carlo tests reveal statistical similarity of post-glacial foraminifera communities of core MV0811-15JC. Tests of significance (p values), t statistics and degrees of freedom (ν) from PERMANOVA and Monte Carlo tests are listed. If statistical permutations were >100, then P statistics were sourced from the PERMANOVA ($p_{perm, \nu}$). If statistical permutations were <100, then p statistics were sourced from the Monte Carlo test ($p_{MC, \nu}$). Significance is indicated in red ($p < 0.001$) and blue ($p < 0.01$) text. Climate intervals are abbreviated and include the Late Holocene (LH), Middle Holocene (MH), Early Holocene (EH), Preboreal (PB), Younger Dryas (YD), Allerød (A), Bølling (B), Oldest Dryas (OD), Pre-Bølling Warming (PW), and Heinrich 1 (H1).

	LH	MH	EH	PB	YD	A	B	OD	PW
MH	t=3.633 $p_{perm, 31}$ <0.001								
EH	t=4.522 $p_{perm, 22}$ <0.001	t=1.983 $p_{perm, 27}$ <0.01							
PB	t=3.537 $p_{perm, 19}$ <0.001	t=3.144 $p_{perm, 24}$ <0.001	t=2.319 $p_{perm, 15}$ <0.01						
YD	t=7.552 $p_{perm, 24}$ <0.001	t=7.129 $p_{perm, 29}$ <0.001	t=5.849 $p_{perm, 20}$ <0.001	t=4.158 $p_{perm, 17}$ <0.001					
A	t=5.896 $p_{perm, 23}$ <0.001	t=5.681 $p_{perm, 28}$ <0.001	t=4.481 $p_{perm, 19}$ <0.001	t=3.067 $p_{perm, 16}$ <0.001	t=3.561 $p_{perm, 21}$ <0.001				
B	t=6.183 $p_{perm, 19}$ <0.001	t=5.595 $p_{perm, 24}$ <0.001	t=4.870 $p_{perm, 15}$ <0.001	t=3.616 $p_{perm, 12}$ <0.001	t=3.997 $p_{perm, 17}$ <0.001	t=1.534 $p_{perm, 16}$ =0.05			
OD	t=5.867 $p_{perm, 15}$ <0.001	t=4.759 $p_{perm, 20}$ <0.001	t=4.071 $p_{perm, 11}$ <0.001	t=3.266 $p_{perm, 8}$ <0.01	t=1.866 $p_{perm, 13}$ =0.013	t=2.502 $p_{perm, 12}$ <0.01	t=2.668 $p_{perm, 8}$ <0.01		
PW	t=9.748 $p_{perm, 20}$ <0.001	t=8.235 $p_{perm, 25}$ <0.001	t=7.185 $p_{perm, 16}$ <0.001	t=5.880 $p_{perm, 13}$ <0.001	t=3.771 $p_{perm, 18}$ <0.001	t=5.359 $p_{perm, 17}$ <0.001	t=5.694 $p_{perm, 13}$ <0.001	t=1.234 $p_{perm, 9}$ =0.22	
H1	t=8.230 $p_{perm, 15}$ <0.001	t=5.807 $p_{perm, 20}$ <0.001	t=5.563 $p_{perm, 11}$ <0.001	t=4.714 $p_{perm, 8}$ <0.001	t=2.605 $p_{perm, 13}$ <0.001	t=3.888 $p_{perm, 12}$ <0.001	t=4.822 $p_{perm, 8}$ <0.001	t=1.429 $p_{mc, 4}$ =0.19	t=1.117 $p_{perm, 9}$ =0.30

LITERATURE CITED

- Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* **26**:32-46.
- Anderson, M. J., and J. Robinson. 2003. Generalized discriminant analysis based on distances. *Australian & New Zealand Journal of Statistics* **45**:301-318.
- Anderson, M. J., and C. J. F. Ter Braak. 2003. Permutation tests for multi-factorial analysis of variance. *Journal of Statistical Computation and Simulation* **73**:85-113.
- Alve, E. 1990. Variations in estuarine foraminifera biofacies with diminishing oxygen conditions in Drammensfjord, SE Norway. Hemleben et al., (Eds.), *Paleoecology, Biostratigraphy, Paleooceanography and Taxonomy of Agglutinated Foraminifera*. Kluwer Academic, Amsterdam, pp. 661-694.
- Behl, R. J., and J. P. Kennett. 1996. Brief interstadial events in the Santa Barbara basin, NE Pacific, during the past 60 kyr. *Nature* **379**:243-246.
- Bemis, B. E., H. J. Spero, and R. C. Thunell. 2002. Using species-specific paleotemperature equations with foraminifera: a case study in the Southern California Bight. *Marine Micropaleontology* **46**:405-430.
- Bernhard, J. M., B. K. Sen Gupta, and P. F. Borne. 1997. Benthic foraminifera proxy to estimate dysoxic bottom-water oxygen concentrations: Santa Barbara Basin, U.S. Pacific continental margin. *Journal of Foraminifera Research* **27**:301-310.
- Bernhard, J. M., and S. S. Bowser. 1999. Benthic foraminifera of dysoxic sediments: Chloroplast sequestration and functional morphology. *Earth Science Reviews* **46**: 149-165.

- Bernhard, J. M., K. R. Buck, M. A. Farmer, and S. S. Bowser. 2000. The Santa Barbara Basin is a symbiosis oasis. *Nature* **403**:77-80.
- Bernhard, J. M., K. R. Buck, and J. P. Barry. 2001. Monterey Bay cold-seep biota: Assemblages, abundance and ultrastructure of living foraminifera. *Deep Sea Research Part I* **48**:2233-2249.
- Bernhard, J. M., P. T. Visscher, and S. S. Bowser. 2003. Submillimeter life positions of bacteria, protists, and metazoans in laminated sediments of the Santa Barbara Basin. *Limnology and Oceanography* **48**:813-828.
- Pieńkowski, A. J., J. H. England, M. F. A. Furze, S. Blasco, P.J. Mudie, and B. MacLean. 2013. 11,000 yrs of environmental change in the Northwest Passage: A multiproxy core record from central Parry Channel, Canadian High Arctic. *Marine Geology* **341**:68-85.
- Blake, G. H. 1976. The distribution of benthic foraminifera in the outer borderland and its relationship to Pleistocene facies, MS thesis, Univ. of Southern California, Los Angeles, USA.
- Brooks, J. M., M. C. Kennicutt, C. R. Fisher, S. A. Macko, K. Cole, J. J. Childress, R. R. Bidigare, and R. D. Vetter. 1987. Deep-sea hydrocarbon seep communities - evidence for energy and nutritional-carbon sources. *Science* **238**:1138-1142.
- Bromley, R. G. 1996. *Trace Fossils: Biology, Taphonomy and Applications*. Chapman & Hall, London.
- Cannariato, K. G., and J. P. Kennett. 1999. Climatically related millennial-scale fluctuations in strength of California margin oxygen-minimum zone during the past 60 k.y. *Geology* **27**:975-987.

- Cannariato, K. G., J. P. Kennett, and R. J. Behl. 1999. Biotic response to late Quaternary rapid climate switches in Santa Barbara Basin: Ecological and evolutionary implications. *Geology* **27**:63-66.
- Cary, S. C., R. D. Vetter, and H. Felbeck. 1989. Habitat characterization and nutritional strategies of the endosymbiont-bearing bivalve *Lucinoma aequizonata*. *Marine Ecology Progress Series* **55**:31-45.
- Census of Marine Life. Available from <http://coml.org>. Accessed 15 November 2014.
- Cedhagen, T. 1991. Retention of chloroplasts and bathymetric distribution in the sublittoral foraminiferan *Nonionellina labradorica*. *Ophelia* **33**:17-30.
- Clarke, K. R. and R. M. Warwick. 2001. A further biodiversity index applicable to species lists: variation in taxonomic distinctness. *Marine Ecology Progress Series* **216**:265-278.
- Clarke, K. R. 1993. Nonparametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**:117-143.
- Clarke, K. R., and R. N. Gorley. 2005. PRIMER v.6: User Manual/Tutorial. PRIMER-E Ltda. Primer, Plymouth, UK.
- Coan, E. V. 2000. The eastern Pacific recent species of the bivalve genus *Gari* (Tellinoidea: Psammobiidae), with notes on western Atlantic and fossil taxa. *Malacologia* **42**:1-29.
- Crame, J. A. 2000. Evolution of taxonomic diversity gradients in the marine realm: evidence from the composition of recent bivalve faunas. *Paleobiology* **26**:188-214.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* **199**: 1302-1013.
- Cronin, T. M., and M. E. Raymo. 1997. Orbital forcing of deep-sea benthic species diversity. *Nature* **385**:624-627.

- Deming, J. W., A. L. Reysenbach, S. A. Macko, and C. R. Smith. 1997. Evidence for the microbial basis of a chemoautotrophic invertebrate community at a whale fall on the deep seafloor: Bone-colonizing bacteria and invertebrate endosymbionts. *Microscopy Research and Technique* **37**:162-170.
- Emery, K. O. 1960. Basin plains and aprons off Southern California. *Journal of Geology* **68**:464-479.
- Elderfield, H., and G. Ganssen. 2000. Past temperature and $\delta^{18}\text{O}$ of surface ocean waters inferred from foraminiferal Mg/Ca ratios. *Nature* **405**: 442-445.
- England, J. H., and M. F. A. Furze. 2008. New evidence from the western Canadian Arctic Archipelago for the resubmergence of Bering Strait. *Quaternary Research* **70**:60-67.
- Fleming, K., P. Johnston, D. Zwart, Y. Yokoyama, K. Lambeck, and J. Chappell. 1998. Refining the eustatic sea-level curve since the Last Glacial Maximum using far- and intermediate-field sites. *Earth and Planetary Science Letters* **163**:327-342.
- François, R., M. Frank, M. M. R. van der Loeff, and M. P. Bacon. 2004. ^{230}Th normalization: An essential tool for interpreting sedimentary fluxes during the late Quaternary, *Paleoceanography* **19**: PA1018, doi:10.1029/2003PA000939.
- Gardner, J. V., W. E. Dean, and P. Dartnell. 1997. Biogenic sedimentation beneath the California Current system for the past 30 kyr and its paleoceanographic significance. *Paleoceanography* **12**:207-225.
- Gooday, A. J., J. M. Bernhard, L. A. Levin, and S. B. Suhr. 2000. Foraminifera in the Arabian Sea oxygen minimum zone and other oxygen-deficient settings: taxonomic composition, diversity, and relation to metazoan faunas. *Deep-Sea Research Part I-Topical Studies in Oceanography* **47**:25-54.

- Gordon, A. D. 1987. A review of hierarchical-classification. *Journal of the Royal Statistical Society Series a-Statistics in Society* **150**:119-137.
- Grieshaber, M. K., and S. Volkel. 1998. Animal adaptations for tolerance and exploitation of poisonous sulfide. *Annual Review of Physiology* **60**:33-53.
- Hein, J. R., W. R. Normark, B. R. McIntyre, T. D. Lorenson, and C. L. Powell. 2006. Methanogenic calcite, C¹³-depleted bivalve shells, and gas hydrate from a mud volcano offshore southern California. *Geology* **34**:109-112.
- Hendy, I. L., J. P. Kennett, E. P. Roark, and B. L. Ingram. 2002. Apparent synchronicity of submillennial scale climate events between Greenland and Santa Barbara Basin, California from 30–10 ka. *Quaternary Science Reviews* **21**:1167-1184.
- Hentschel, U., S. C. Cary, and H. Felbeck. 1993. Nitrate respiration in chemoautotrophic symbionts of the bivalve *Lucinoma aequizonata* Marine Ecology Progress Series **94**:35-41.
- Hill, T. M., J. P. Kennett, and H. J. Spero. 2003. Foraminifera as indicators of methane-rich environments: A study of modern methane seeps in Santa Barbara Channel, California. *Marine Micropaleontology* **49**:123-138.
- Hill, T. M., J. P. Kennett, D. K. Pak, R. J. Behl, C. Robert, and L. Beaufort. 2006. Pre-Bølling warming in Santa Barbara Basin, California: Surface and intermediate water records of early deglacial warmth. *Quaternary Science Reviews* **25**:2835-2845.
- Ivanochko, T. S., and T. F. Pedersen. 2004. Determining the influences of Late Quaternary ventilation and productivity variations on Santa Barbara Basin sedimentary oxygenation: a multi-proxy approach. *Quaternary Science Reviews* **23**:467-480.

- James, F. C., and C. E. McCulloch. 1990. Multivariate-analysis in ecology and systematics - panacea or pandora box. *Annual Review of Ecology and Systematics* **21**:129-166.
- Jorissen, F. J., C. Fontanier, and E. Thomas. 2007. Paleoceanographical proxies based on deep-sea benthic foraminiferal assemblage characteristics. Pages 263-326 in C. Hillaire-Marcel and A. de Vernal, editors. *Proxies in Late Cenozoic Paleoceanography: Pt. 2: Biological tracers and biomarkers*. Elsevier, Amsterdam.
- Kaiho, K. 1994. Benthic foraminiferal dissolved-oxygen index and dissolved-oxygen levels in the modern ocean. *Geology* **22**:719.
- Keigwin, L. D, G. A. Jones, and P. N. Froelich. 1992. A 15,000 year paleoenvironmental record from Meiji Seamount, far northwestern Pacific. *Earth and Planetary Science Letters* **111**: 425-440.
- Kennett, J. P. and B. L. Ingram. 1995. A 20,000-year record of ocean circulation and climate change from the Santa Barbara Basin. *Nature* **377**: 510-514.
- Kristensen, E., G. Penha-Lopes, M. Delefosse, T. Valdemarsen, C. O. Qunitana, and G. T. Banta. 2012. What is bioturbation? The need for a precise definition for fauna in aquatic sciences. *Marine Ecology Progress Series* **446**:285–302.
- Langer, M. R., J. H. Lipps, and G. Moreno. 1995. Predation on foraminifera by the Dentalid deep-sea scaphopod *Fissidentalium megathyris*. *Deep-Sea Research Part I-Oceanographic Research Papers* **42**:849-857.
- Levin, L. 2002. Deep-ocean life where oxygen is scarce. *American Scientist* **90**:436-444.
- Levin, L. A., D. W. James, C. M. Martin, A. E. Rathburn, L. H. Harris, and R. H. Michener. 2000. Do methane seeps support distinct macrofaunal assemblages? Observations on

- community structure and nutrition from the northern California slope and shelf. Marine Ecology Progress Series **208**:21-39.
- Levin, L. A., and R. H. Michener. 2002. Isotopic evidence for chemosynthesis-based nutrition of macrobenthos: The lightness of being at Pacific methane seeps. Limnology and Oceanography **47**:1336-1345.
- Long, W. C., B. J. Brylawski, and R. D. Seitz. 2008. Behavioral effects of low dissolved oxygen on the bivalve *Macoma balthica*. Journal of Experimental Marine Biology and Ecology **359**:34-39.
- McArdle, B. H., and M. J. Anderson. 2001. Fitting multivariate models to community data: A comment on distance-based redundancy analysis. Ecology **82**:290-297.
- Milne, G. A., A. J. Long, and S. E. Bassett. 2005. Modelling Holocene relative sea-level observations from the Caribbean and South America. Quaternary Science Reviews **24**:1183-1202.
- Modica, M. V., and M. Holford. 2010. The Neogastropoda: Evolutionary innovations of predatory marine snails with remarkable pharmacological potential, in: P. Pontarotti (Ed), Evolutionary Biology – Concepts, Molecular and Morphological Evolution. Springer, Heidelberg, pp. 249-270.
- Moffitt, S. E., T. M. Hill, K. Ohkushi, J. P. Kennett, and R. J. Behl. 2014. Vertical oxygen minimum zone oscillations since 20 ka in Santa Barbara Basin: A benthic foraminiferal community perspective. Paleoceanography **29**:44-57.
- Moffitt, S. E., R. Moffitt, W. Sauthoff, C. V. Davis, K. Hewett, and T. M. Hill. 2015a. Paleoceanographic insights on recent oxygen minimum zone expansion: Lessons for modern oceanography. PLOS ONE **10**:e0115246.

- Moffitt, S. E., T. M. Hill, P. Roopnarine, and J. P. Kennett. 2015b. Response of seafloor ecosystems to abrupt global change. *Proceedings of the National Academy of Sciences of the United States of America* **112**:4684-4689.
- Monnin, E., A. Indermuhle, A. Dallenbach, J. Fluckiger, B. Stauffer, T. F. Stocker, D. Raynaud, and J. M. Barnola. 2001. Atmospheric CO₂ concentrations over the last glacial termination. *Science* **291**:112-114.
- Mosch, T., S. Sommer, M. Dengler, A. Noffke, L. Bohlen, O. Pfannkuche, V. Liebetrau, and K. Wallmann. 2012. Factors influencing the distribution of epibenthic megafauna across the Peruvian oxygen minimum zone. *Deep-Sea Research Part I-Oceanographic Research Papers* **68**:123-135.
- Mullins, H. T., J. B. Thompson, K. McDougall, and T. L. Vercoutere. 1985. Oxygen-minimum zone edge effects - evidence from the central California coastal upwelling system. *Geology* **13**:491-494.
- Nameroff, T. J., L. S. Balistrier, and J. W. Murray. 2002. Suboxic trace metal geochemistry in the eastern tropical North Pacific. *Geochimica et Cosmochimica Acta* **66**:1139-1158.
- Ohkushi, K., J. P. Kennett, C. M. Zeleski, S. E. Moffitt, T. M. Hill, C. Robert, L. Beaufort, and R. J. Behl. 2013. Quantified intermediate water oxygenation history of the NE Pacific: A new benthic foraminiferal record from Santa Barbara basin. *Paleoceanography* **28**:453-467.
- Oliver, G., C. F. Rodrigues, and M. R. Cunha. 2011. Chemosymbiotic bivalves from the mud volcanoes of the Gulf of Cadiz, NE Atlantic, with descriptions of new species of Solemyidae, Lucinidae and Vesicomidae. *Zookeys* **113**:1-38.

- Oliver, P. G., and J. D. Taylor. 2012. Bacterial symbiosis in the Nucinelidae (Bivalvia: Solemyida) with descriptions of two new species. *Journal of Molluscan Studies* **78**:81-91.
- Pienkowski, A. J., J. H. England, M. F. A. Furze, S. Blasco, P. J. Mudie, and B. MacLean. 2013. 11,000 yrs of environmental change in the Northwest Passage: A multiproxy core record from central Parry Channel, Canadian High Arctic. *Marine Geology* **341**:68-85.
- Praetorius, S. K., A. C. Mix, M. H. Walczak, M. D. Wilhowe, J. A. Addison and F. G. Prahl. 2015. North Pacific deglacial hypoxic events linked to abrupt ocean warming. *Nature* **527**:362-366.
- Quinterno, P. J., and J. V. Gardner. 1987. Benthic foraminifers on the continental-shelf and upper slope, Russian River area, Northern California. *Journal of Foraminiferal Research* **17**:132-152.
- Reid, R. G. B., and A. Reid. 1969. Feeding processes of members of the genus *Macoma* (Mollusca:Bivalvia). *Canadian Journal of Zoology* **47**:647-657.
- Richter, A., and A. A. Luque. 2004. *Epitonium dendrophylliae* (Gastropoda : Epitoniidae) feeding on *Astroides calycularis* (Anthozoa, Scleractinia). *Journal of Molluscan Studies* **70**:99-101.
- Sahling H., D. Rickert, R. W. Lee, P. Linke, and E. Suess. 2002. Macrofaunal community structure and sulfide flux at gas hydrate deposits from the Cascadia convergent margin, NE Pacific. *Marine Ecology Progress Series* **231**:121-138.
- Sanders, H. L., and J. A. Allen. 1977. Studies on the Deep Sea Protobranchia (Bivalvia), the Family Tindariidae, and the Genus *Pseudotindaria*. *Bulletin of the Museum of Comparative Zoology* **28**:23-59.

- Schmittner, A., and E. D. Galbraith. 2008. Glacial greenhouse-gas fluctuations controlled by ocean circulation changes. *Nature* **456**:373-376.
- Schrag, D. P., J. F. Adkins, K. McIntyre, J. L. Alexander, D. A. Hodell, C. D. Charles, and J. F. McManus. 2002. The oxygen isotopic composition of seawater during the Last Glacial Maximum. *Quaternary Science Reviews* **21**:331-342.
- Schweimanns, M., and H. Felbeck. 1985. Significance of the occurrence of chemoautotrophic bacterial endosymbionts in Lucinid clams from Bermuda. *Marine Ecology Progress Series* **24**:113-120.
- Shi, G. R. 1993. Multivariate data-analysis in paleoecology and paleobiogeography - a review. *Palaeogeography Palaeoclimatology Palaeoecology* **105**:199-234.
- Sigman, D. M., and E. A. Boyle. 2000. Glacial/interglacial variations in atmospheric carbon dioxide. *Nature* **407**:859-869.
- Smith, C. R., and A. R. Baco. 2003. Ecology of whale falls at the deep-sea floor. *Oceanography and Marine Biology* **41**:311-354.
- Sonzogni, C., E. Bard, and F. Rostek. 1998. Tropical sea-surface temperatures during the last glacial period: a view based on alkenones in Indian ocean sediments. *Quaternary Science Reviews* **17**:1185-1201.
- Stanley, S. M. 1970. Relation of shell form to life habits of the *Bivalvia* (Mollusca). *Geological Society of America Bulletin* **125**:1-296
- Taylor, J. D., and E. A. Glover EA. 2006. *Lucinidae* (Bivalvia) - the most diverse group of chemosymbiotic molluscs. *Zoological Journal of the Linnean Society* **148**:421-438.

- Taylor, J. D., E. A. Glover, and S. T. Williams. 2014. Diversification of chemosymbiotic bivalves: origins and relationships of deeper water Lucinidae. *Biological Journal of the Linnean Society* **111**:410-420.
- Thompson, B. A. W., and M. J. Riddle MJ. 2005. Bioturbation behavior of the spatangoid urchin *Abatus ingens* in Antarctic marine sediments. *Marine Ecology Progress Series* **290**:135–143.
- van Geen, A., R. G. Fairbanks, P. Dartnell, M. McGann, J. V. Gardner, and M. Kashgarian. 1996. Ventilation changes in the northeast Pacific during the last deglaciation. *Paleoceanography* **11**:519-528.
- Vaquier-Sunyer, R., and C. M. Duarte. 2008. Thresholds of hypoxia for marine biodiversity. *Proceedings of the National Academy of Sciences of the United States of America* **105**:15452-15457.
- Yasuhara, M., T. M. Cronin, and P. M. Arbizu. 2008. Abyssal ostracods from the south and equatorial Atlantic Ocean: Biological and paleoceanographic implications. *Deep-Sea Research Part I-Oceanographic Research Papers* **55**:490-497.
- Yasuhara, M., G. Hunt, T. M. Cronin, N. Hokanishi, H. Kawahata, A. Tsujimoto, and M. Ishitake. 2012. Climate forcing of Quaternary deep-sea benthic communities in the North Pacific Ocean. *Paleobiology* **38**:162-179.
- Zamorano, P., M. E. Hendrickx, and A. Toledano-Granados. 2007. Distribution and ecology of deep-water mollusks from the continental slope, southeastern Gulf of California, Mexico. *Marine Biology* **150**:883-892.

Zheng, Y., A. van Geen, R. F. Anderson, J. V. Gardner, and W. E. Dean. 2000a. Intensification of the northeast Pacific oxygen minimum zone during the Bølling-Allerød warm period. *Paleoceanography* **15**:528-536.

Zheng, Y., R. F. Anderson, A. van Geen, and J. Kuwabara. 2000b. Authigenic molybdenum formation in marine sediments: A link to pore water sulfide in the Santa Barbara Basin. *Geochimica et Cosmochimica Acta* **64**:4165-4178.