



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



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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 m 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.

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1. 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

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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 m 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 (Ostracoda) 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 ($[\text{O}_2] < 0.3 \text{ ml L}^{-1}$; 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 ($500 \pm 10 \text{ m}$ 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,

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