Response of seafloor ecosystems to abrupt global climate change

Sarah E. Moffitt, Tessa M. Hill, Peter D. Roopnarine, and James P. Kennett

Anthropogenic climate change is predicted to decrease oceanic oxygen concentrations, with potentially significant effects on marine ecosystems. Geologically recent episodes of abrupt climatic warming provide opportunities to assess the effects of changing oxygenation on marine communities. Thus far, this knowledge has been largely restricted to investigations using Foraminifera, with little being known about ecosystem-scale responses to abrupt, climate-forced deoxygenation. We here present high-resolution records based on the first comprehensive quantitative analysis, to our knowledge, of changes in marine metazoans (Mollusca, Echinodermata, Arthropoda, and Annelida; >5,400 fossils and trace fossils) in response to the global warming associated with the last glacial to interglacial episode. The molluscan archive is dominated by extemepholx taxa, including those containing endosymbiotic sulfur-oxidizing bacteria (Lucinoma aequizonatum) and those that graze on filamentous sulfur-oxidizing benthic bacterial mats (Alia permodesta). This record, from 16,100 to 3,400 y ago, demonstrates that seafloor invertebrate communities are subject to major turnover in response to relatively minor inferred changes in oxygenation (>1.5 to <0.5 mL−1 [O2]) associated with abrupt (<100 y) warming of the eastern Pacific. The benthic turnover and recovery events within the record expand known rates of marine biological recovery by an order of magnitude, from <100 to >1,000 y, and illustrate the crucial role of climate and oceanographic change in driving long-term successional changes in ocean ecosystems.

Oceanic deoxygenation is a predictable, fundamental, and long-lasting property of anthropogenic climate change (1). The global ocean inventory of oxygen is predicted to decline between 1% and 7% by the year 2100, and modeling predictions reveal extensive oceanic deoxygenation, on thousand-year timescales, under “business-as-usual” carbon emission scenarios (2). Modern oceanographic time series already document rapid loss of [O2] in interior ocean waters over the last 4 decades (3, 4), although this trend is complicated in regions where [O2] demand is decreased through the slackening of trade winds (5). As oxygen levels in the ocean decrease and the already extensive oxygen minimum zones (OMZs) expand, the volumetric habitat for aerobic respiration is reduced, presumably resulting in a fundamental reorganization of marine communities. Past events of climate warming and OMZ expansion, including the recent deglaciation from Santa Barbara Basin (SBB), a relatively shallow (600 m) anoxic basin in the eastern boundary current of the northeast Pacific Ocean, exhibit close synchrony to the Greenland Ice Sheet Project 2 (GISP2) Greenland ice core climate records (8, 9). Vertical expansion and intensification of the California Current OMZ are recorded during the last deglacial episode, as well as an episode of expanded subsurface oxygenation (OMZ contraction) during the temporary cooling of the Younger Dryas episode (6, 8, 9).

Paleoecological reconstructions from ocean sedimentary sequences have primarily relied on records of benthic Foraminifera (6, 10, 11) and less so on ostracods (12). Previous studies have not documented changes in a broad spectrum of marine biodiversity, in contrast to those long carried out on the terrestrial realms (e.g., refs. 13 and 14). We present a record of >5,350 microfossils and macrofossils and 51 trace fossils from SBB sediment core MV0811-15JC (418 m water depth; sedimentation rates of 42.2–100.0 cm ky−1; 16.1–3.4 ka), which reveals community-scale responses of continental margin ecosystems to OMZ oscillations. This newly recognized archive exhibits dramatic upper-ocean reorganization of benthic faunal communities in response to abrupt changes in ocean circulation and climate.

Seafloor Hypoxia Zonation and Indicator Taxa

The diversity of continental margin benthic faunas is, in part, controlled by the distribution and consumption of oxygen (15). This investigation presents the first record to our knowledge of the disturbance and recovery of seafloor ecosystem biodiversity in response to abrupt climate change. Ocean sediments have been extensively studied using geochemical and microfossil (e.g., Foraminifera) analyses; however, these traditional approaches produce limited interpretations of ecological and community-scale responses. We demonstrate here that ocean sediments harbor metazoan fossil material that can be used to reconstruct the response of seafloor biodiversity to global-scale climate events. We show that the last deglaciation, the most recent episode of climate warming, was accompanied by abrupt reorganizations of continental margin seafloor ecosystems through expansions and contractions of the surface low-oxygen zones. This archive reveals that global climate change disturbs seafloor ecosystems on continental margins and commits them to millennia of ecological recovery.
Hypoxia thresholds vary greatly across marine benthic organisms (16), resulting in successional patterns along OMZ gradients. Vertical zonation patterns in diversity, trophic structures, and physiological strategies are driven by the transition from well-oxygenated shallower waters to the hypoxic center of the OMZ (0.5–0.1 mL·L⁻¹). Hypoxic zones are marked by low density, low diversity, and high community dominance in both invertebrate and foraminiferal communities (15, 17).

Foraminifera are well adapted to the extreme chemical environments found on certain continental margins and exhibit associations with specific oxygenation regimes (18). High foraminiferal diversity is generally associated with oxygenated sediments (15, 17). Peak densities of benthic Foraminifera (>1,000 individuals/cm³), however, occur when hypoxic oxygen concentrations range between 0.5 and 0.1 mL·L⁻¹, in response to rich detrital food resources and a scarcity of invertebrate competitors and predators (19). Overall, changes in foraminiferal density, diversity, and relative abundances of hypoxic marker species are sensitive recorders of changes in OMZ strength (20).

Invertebrate communities abruptly decline as dissolved oxygen concentrations fall below a hypoxic threshold (0.5–0.4 mL·L⁻¹) (15). Echinoderms (Spatangoida, Ophiuroidae), arthropods (Ostracoda), and molluscs (Bivalvia, Gastropoda, Scaphopoda) are members of continental margin benthic communities and, in addition to benthic foraminifera, contribute to the fossil assemblages preserved in MV0811-15JC. Ostracod populations are found in seafloor environments with >0.4 mL·L⁻¹ O₂ (21). Molluscs exhibit a wide range of sensitivity to hypoxia, with gastropods associated with a lower lethal oxygen threshold compared with bivalves (17). Gastropods thrive and create high-density bands in the hypoxic center of modern OMZs (15, 22). Respiratory thresholds are unknown for scaphopods; they are, however, motile predators of Foraminifera and detritivores, and their respiration requirements may be analogous to other molluscans. Echinoderms exhibit variable hypoxia thresholds: Spatangoid urchins (heart urchins) are ubiquitous community members of soft sediment continental margins across OMZ gradients (23), whereas ophiuroids (brittle stars) live above and below the hypoxic center of the OMZ (between 1.4 and 4.3 mL·L⁻¹ O₂) (24) to form distinct, high-density depth zones (22). Spatangoid urchins exhibit a threshold of hypoxia sensitivity with in situ data from the abyssal megahalocline, where background oxygenation conditions are <0.1 mL·L⁻¹ O₂ (25). In such extreme hypoxia, along with the cessation of bioturbation (8, 26), and with sufficiently high surface carbon export (27), the preservation of sedimentary laminations can occur. Not all laminations originally formed may be preserved in paleoceanographic records, as laminations can be subject to removal or deterioration when followed by postdepositional intervals of oxygenation, invertebrate settlement, and bioturbation.

**MV0811-15JC: A Shallow, Bioturbated Northeast Pacific Record**

Core MV0811-15JC is a short (922 cm) deglacial archive with an independent age model constructed using radiocarbon dates and oxygen isotopic tie-points to ODP Site 893A (9, 20). Core MV0811-15JC exhibits a “two-step” record of planktonic foraminiferal oxygen isotopic shifts during the last deglaciation with a relatively indistinct, highly variable cooling episode representing the Younger Dryas; similar characteristics to this episode are exhibited at nearby ODP 893A (9, 28) (Fig. 1 and Fig. S1). Sedimentation rates for core MV0811-15JC range from 100.0 cm·ky⁻¹ during the deglaciation to 42.2 cm·ky⁻¹ during the Holocene (Fig. S1). Core MV0811-15JC is bioturbated and exhibits lower sedimentation rates than in the very high resolution (140 cm·ky⁻¹) and intermittently laminated ODP Site 893A recovered from near the center of SBB. At Termination 1A (14.7 ka), core MV0811-15JC was at ∼300 m water depth, with sea level ∼110 m below that of the present day (29). At this shallow water depth, the foraminiferal biotic archive of core MV0811-15JC recorded vertical changes in the upper boundary of the regional California Current OMZ (20).

Core MV0811-15JC is a nonlaminated sediment sequence, and the presence of bioturbating spatangoid urchin test and spine material is continuous throughout the core (Table S1). Estimates for bioturbation depth disturbance in deep-sea sediments are commonly assumed to be ∼10 cm, although shallower (2–5 cm) (30, 31) and deeper (20 cm) depths are reported (32). Very high sediment volumes are displaced as a result of spatangoid movement (33), and these physical changes produce complex biogeochemical interactions in sediments associated with changes in primary productivity and nutrient flux (34). This sedimentary, microfossil, and spatangoid evidence indicates this is a bioturbated deglacial archive, which is a critical factor in interpreting rates of change in this record. For the purposes of this investigation, interpreting the “abrupt” nature of community change is especially relevant in the context of sediment bioturbation, which can vertically smear an event horizon across 5–20 cm of sediment. Transitions in metazoan community diversity and abundance are prominent features of this record; biological transitions recorded across <20 cm of preserved sediment may therefore have taken place even more abruptly than suggested by rates of sediment accumulation, over very short intervals of time, rather than being paced on decadal or centennial timescales.

**MV0811-15JC Biotic Record**

Seafloor invertebrate communities underwent major oscillations during the last ∼16,000 y along the continental margin of the Eastern Pacific (Figs. 1 and 2 and Figs. S2 and S3). The high degree of sensitivity of seafloor ecosystem structure to climate change is revealed by changes in benthic communities both within and between each climatic interval of the last deglaciation (Fig. 1). We document changes in the abundance of seafloor metazoans, including ostracods, ophiuroids, and molluscs (Fig. 1), as well as metrics of community diversity (Shannon’s Index of diversity, H’) and functional guilds in both Mollusca and Foraminifera (Fig. 2). Ostracod valves were observed in 32.1% of sediment intervals, and ophiuroid vertebral ossicles were observed in 20% of sediment intervals (Table S1).

The molluscan record is dominated by chemosynthetically associated symbiotic sulfur-oxidizing bacteria within their tissues (Lucinoma aequizonatum, unidentified Lucinidae, Manzanellidae) and those that graze on filamentous sulfur-oxidizing benthic bacterial mats (Alla permodesta; Fig. 2 and Table S1). These forms are metazoan extremophiles and are characteristic of the most sulfide-rich, methane-rich, and oxygen-poor environments of modern continental margins (35–37). Many of these extremophiles are opportunistic, weedy species and appear in high-density (∼900 individuals/m²) zonations on modern continental margins (22, 38–40). Deposit feeding, suspension feeding, and detritivorous and carnivorous trophic guilds are also present within the molluscan assemblage. The presence of additional trophic guilds, particularly the motile guilds associated with carnivory and detritivory, indicate seafloor ecosystems marked by both the absence of free sulfide and elevated (O₂ > 0.5 mL·L⁻¹) oxygen concentrations (41).

**Termination 1A: Abrupt Seafloor Disturbance**

During the glacial episode, before Termination 1A, metazoan communities were diverse and dense; the bioturbated seafloor was colonized by ostracods, ophiuroids, molluscs, and oxic–mildly hypoxic foraminiferal assemblages (>1.5 mL·L⁻¹ O₂; Figs. 1 and 2). The molluscan community was dominated by taxa associated assemblages, including elements that harbor endosymbiotic sulfur-oxidizing bacteria within their tissues (L. aequizonatum, unidentified Lucinidae, Manzanellidae) and those that graze on filamentous sulfur-oxidizing benthic bacterial mats (Alla permodesta; Fig. 2 and Table S1). These forms are metazoan extremophiles and are characteristic of the most sulfide-rich, methane-rich, and oxygen-poor environments of modern continental margins (35–37). Many of these extremophiles are opportunistic, weedy species and appear in high-density (∼900 individuals/m²) zonations on modern continental margins (22, 38–40). Deposit feeding, suspension feeding, and detritivorous and carnivorous trophic guilds are also present within the molluscan assemblage. The presence of additional trophic guilds, particularly the motile guilds associated with carnivory and detritivory, indicate seafloor ecosystems marked by both the absence of free sulfide and elevated (O₂ > 0.5 mL·L⁻¹) oxygen concentrations (41).
Fig. 1. Core MV0811-15JC’s (SBB; 418 m water depth; 9.2 m core length; 34.37°N, 120.13°W) oxygen isotopic, foraminiferal, and metazoan deglacial record of the latest Quaternary. Timescale (ka) is in thousands of years before present, and major climatic events include the Last Glacial Maximum (LGM), the Bølling and Allerød (B/A), the Younger Dryas (YD), and the Holocene. (A) GISP2 ice core δ¹⁸O values (46). (B) Planktonic Foraminifera *Globigerina bulloides* δ¹⁸O values for core MV0811-15JC, which reflects both deglacial temperature changes in Eastern Pacific surface waters and changes in global ice volume. (C) Benthic foraminiferal density (individuals/cm³). (D) Relative frequency (%) of benthic Foraminifera with faunal oxygen-tolerance categories including oxic–mildly hypoxic (>1.5 mL·L⁻¹ O₂; *N. labradorica, Quinqueloculina* spp., *Pyrgo* spp.), intermediate hypoxia (1.5–0.5 mL·L⁻¹ O₂; *Epistominella* spp., *Bolivina* spp., *Uvigerina* spp.), and severe hypoxia (<0.5 mL·L⁻¹ O₂; *N. stella, B. tumida*) (19). (E) Log mollusc density (individuals/cm³) and 5-cm moving average. (F) Ophiuroids (brittle star) presence (presence = 1, absence = 0, 5-cm moving average). (G) Ostracod valve density (circles, valves/cm³) and 5-cm moving average. Data from ref. 20.
as secondary elements. The most pronounced high molluscan density event at 15.3 ka was found to contain 40 individual shells of the bivalve _L. aequizonatum_ in 1-cm-thick intervals in addition to scaphopods _Gadila aberrans_ and _Cadulus tolmiei_, and bivalves from Cardiidae (_Trachycardiinae_ and _Clinocardium nuttalli_).

Termination 1A (14.7 ka) is marked by dramatic and rapid changes in metazoan and foraminiferal assemblages, including an abrupt decline in the density and diversity of metazoan faunas. These major changes in the ecosystem, involving density and presence/absence shifts in molluscan classes, ostracods, and ophiuroids, are limited to just 12 cm of sediment (Fig. S4). Higher trophic level processes (involving worms, crustaceans, and predatory gastropods; Fig. S3) also exhibit high sensitivity to the environmental changes associated with climate transitions. Within 130 y (12 cm of sediment), the invertebrate community collapsed and was replaced by low-density communities primarily composed of foraminifera associated with intermediate (1.5–0.5 mL·L⁻¹ O₂) and severe (<0.5 mL·L⁻¹ O₂) hypoxia.

There was not a total loss of the metazoans at Termination 1A, as rare individuals of molluscs, ophiuroids, and ostracods persisted into the Bølling warm episode. Nevertheless, the change at Termination IA represents an ecosystem-scale shift from the dense metazoan communities of the last glacial episode to an assemblage dominated by foraminiferal extremophiles (_Nonionella stella_, _Bolivina tumida_) during the Bølling (Fig. 2). This comprehensive loss of invertebrate biodiversity at the onset of the warm Bølling episode (14.7 ka) is a product of regional hydrographic change associated with the vertical expansion of the OMZ and compression of the oxygenated upper ocean. The faunal changes of the Bølling are particularly revealing of how extreme this hydrographic interval was: It was so intense, even metazoan extremophiles did not settle or colonize the continental margin. The major faunal change at the onset of the Bølling warming is confined to <20 cm sediment. Therefore, because of the presence of bioturbation, our assessment of decadal–centennial timescales for this biotic turnover is likely conservative; instead, it could have been nearly instantaneous.

**Allerød-Younger Dryas: >1,000-y Seafloor Recovery**

Chemosynthetically associated mollusc (particularly gastropod) densities increased during the Allerød, beginning at 13.5 ka (Fig. 2). The biotic changes indicate seafloor ecosystem recovery after the major disturbance of the Bølling began during the Allerød and was initiated by the colonization of the seafloor by filamentous sulfur-oxidizing benthic bacterial mats and bacterial mat grazers (_A. permodesta_). During the late Allerød-Younger Dryas from 13.5 to 12.5 ka, the metazoan biotic community gradually recovered taxonomic diversity and density (Fig. S4). A full recovery of seafloor biodiversity to pre-Termination 1A levels occurred from 12.5 to 11.7 ka, wherein deposit feeding, suspension feeding, and carnivorous molluscan trophic guilds became dominant (Fig. 2); ostracods recovered to high densities (Fig. 1); and ophiuroid vertebral ossicles were continuously present (Fig. 1). Trace fossils on Younger Dryas molluscs indicate...
Variability may have altered mid-Holocene OMZ structure and intermediate water oxygenation. Such climate and oceanographic Subtropical Pacific (43), could create mid-Holocene variability in nature and solar variability records resolved from the eastern foraminiferan assemblage to be consistent with a hypoxic, sulfidic most similar to the successional colonization and recovery of the apatated fauna (20). Interestingly, the mid-Holocene community is nifera are extremely abundant and dominated by OMZ-associ-
ated fauna (15, 17). Simultaneously, foraminiferan communities surged at Termination 1B to high densities and dominance by Bolivina spp. Metazoan absence, extremely high foraminiferal densities, and dominance of Bolivina spp. are indicative of intermediate hypoxia at the ocean floor (1.5–0.5 mL L−1 O2) throughout the Holocene (20).

**Termination 1B: Abrupt Seafloor Disturbance**

Termination 1B (~1.7 ka) is marked by another abrupt and acute ecological disturbance wherein all metazoans disappeared from the sediment record within 18 cm of sediment, equivalent to ~170 y (Figs. 1 and 2 and Fig. S4). Termination 1B is an extremely abrupt event in the biotic record of core MV0811-15JC; the disappearance of metazoan taxa occurred in <20 cm, and therefore the event may have been relatively instantaneous but subsequently smeared as a result of bioturbation. Unlike Termination 1A, metazoans did not recover from the disturbance of Termination 1B and remained absent in the record for >4,000 y. Foraminiferan communities only after the sedimentary record of core MV0811-15JC was collected aboard the R/V *Melville* in 2008 and is the shallowest deglacial sediment record (418 m water depth; 3.4–16.1 ka) reconstructed from both SB and the broader northeastern Pacific Ocean continental margin. At the time of collection, the core was sampled at 10-cm intervals (92 samples, 2.5 cm3) for benthic foraminifera, invertebrate assemblages, and isotopic analyses. The core was resampled for invertebrate analysis in 2010 at 1-cm intervals (922 samples, 5 cm3). MV0811-15JC’s planktonic and benthic δ18O records and benthic foraminiferal communities are previously published (19), and the age model is based on two radiocarbon dates and three nearby points to ODP Site 1255 (418 m water depth) in the tem-

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**Novel, Mid-Holocene Seafloor Communities**

A novel mid-Holocene seafloor community developed between 7.5 and 5.0 ka that is not analogous to earlier communities and is indicative of a sulfide-rich chemosynthetic ecosystem. Invertebrate diversity and abundance are lower in this ephemeral ecosystem: Gastropods [specifically the sulfidic and hypoxic bacterial grazer *A. permodesta* (38)] are the only molluscan group to appear (Fig. 2), ophiuroid fossils are absent, ostracod occurrences are rare (Fig. 1), and there is a high frequency of annelid predation (Fig. S3). Evidence for elevated annelid predation pressure (Fig. S3) is consistent with an environment similar to the core of the modern OMZ (15, 17). Simultaneously, foraminiferan communities surged at Termination 1B to high densities and dominance by OMZ-associated fauna (20). Interestingly, the mid-Holocene community is most similar to the successional colonization and recovery of the late Allerød. We interpret the mid-Holocene metazoan and foraminiferan assemblage to be consistent with a hypoxic, sulfidic seafloor environment. Suborbital, millennial environmental oscillations, for example, those reflected by sea surface temperature and solar variability records resolved from the eastern Subtropical Pacific (43), could create mid-Holocene variability in intermediate water oxygenation. Such climate and oceanographic variability may have altered mid-Holocene OMZ structure and changed vertical ecosystem zonation on the continental margin. This anomalous community abruptly disappeared at 5 ka, and all younger sediments lack metazoans.

**Continental Margins Ecosystems and Climate Change**

Shallow seafloor ecosystems (~300 m water depth) in the temperate northeast Pacific Ocean were dramatically altered during the climatic and oceanographic changes of glacial Termination 1A (duration 130 y) and 1B (duration 170 y) (Figs. 1 and 2 and Fig. S4). During this time, ocean and climate changes led to abrupt reorganization of the vertical zonation of ecosystems on the continental margin through the expansion of the OMZ (20, 44, 45). Long-term (>1,000 y) ecosystem recovery is demonstrated in the Younger Dryas oxygenation reversal, wherein differences in trophic structures and physiological adaptations, from chemosynthetically extremophiles to mobile carnivores and deposit feeders, determine the successional process and its timing. The dominance of chemosynthetically associated mollusc assemblages is striking; even deglacial intervals considered to be more oxygenated can still contain extremophile metazoan communities, and thus, by comparison, the depauperate intervals (Bolling and Holocene) were truly extreme, inhospitable biochemical regimes. The biodiversity record presented here reveals that benthic ecosystems can be rapidly influenced and disturbed by abrupt global climate change and related reorganization of ocean circulation.

Past changes in OMZ intensity (45) and the resulting effects on seafloor benthic biodiversity provide an interpretive precedent to understand the capacity for substantial and long-term ecosystem disturbance to accompany future oceanic oxygen loss (1, 2). Previous deoxygenation events dwarf modern scales of ecological disturbance (42) and illustrate the nonanalogue nature of marine life on continental margins and that this disturbance can commit upper ocean ecosystems to millennia of ecological recovery.

**Methods**

MV0811-15JC was collected aboard the R/V *Melville* in 2008 and is the shallowest deglacial sediment record (418 m water depth; 3.4–16.1 ka) reconstructed from both SB and the broader northeastern Pacific Ocean continental margin. At the time of collection, the core was sampled at 10-cm intervals (92 samples, 2.5 cm3) for benthic foraminifera, invertebrate assemblages, and isotopic analyses. The core was resampled for invertebrate analysis in 2010 at 1-cm intervals (922 samples, 5 cm3). MV0811-15JC’s planktonic and benthic δ18O records and benthic foraminiferal communities are previously published (19), and the age model is based on two radiocarbon dates and three nearby points to ODP Site 1255 (418 m water depth). Sediment was processed via disaggregation in DI water, washing (150-μm sieve), and oven drying (50 °C). Benthic invertebrates included molluscs, echinoderms, and ostracods (Table S1). Molluscs were identified to the lowest taxonomic resolution possible with the fossil evidence (Table S2). Ostracod diversity was not determined. Density (Mollusca, Ostracoda; individuals/cm3) and presence/absence (Echinodermata) were calculated. Molluscs were assessed using a running 5-cm value of Shannon’s Index of Diversity (H’). Trophic guild frequency (%) of the mollusc community was calculated, and the assemblage was partitioned into the following categories: chemosynthetically associated, deposit, suspension, deposit/suspension, carnivore/ detritivore, carnivore/deposit, and detritivore (Table S2). Trace fossils of molluscan predation were identified to trophic guild (gastropod, crustacean, or annelid), and the frequency of predation events was calculated at a 10-cm resolution (Fig. S3). Benthic foraminiferal density (individuals/cm2), Shannon’s Index of Diversity (H’), and relative frequency (%) of oxygen-sensitive taxa groups (19) were used to reconstruct seafloor oxygenation changes.

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Supporting Information

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Fig. S1. Oxygen isotopic ($\delta^{18}$O) records for MV0811-15JC, GISP2, and ODP Site 893A and sedimentation rates for MV0811-15JC. (A) GISP2 $\delta^{18}$O (1–4). (B) ODP Site 893A planktonic foraminifer (G. bulloides) $\delta^{18}$O stratigraphy (5, 6). (C) Site MV0811-15JC planktonic foraminifer (G. bulloides) $\delta^{18}$O stratigraphy (7). (D) Site MV0811-15JC benthic foraminifer (Uvigerina peregrina (blue circles, blue line) and Bolivina argentea (red circles, red line)) $\delta^{18}$O stratigraphy (8). (E) Sedimentation rates (cm ka$^{-1}$) for site MV0811-15JC (7). Timescale is shown in thousands of years before present (ka) in this and following figures. Major climatic events are identified for this and following figures, including the Last Glacial Maximum (LGM), Bølling-Allerød (B/A), Younger Dryas (YD), and Holocene. Data from ref. 7.

Fig. S2. Changes in diversity of foraminiferal (A) and molluscan (B–E) groups, mollusc density (F), and total molluscan numbers (G) during the late Pleistocene in core MV0811-15JC. See Table S2 for molluscan taxonomic group designations. (A) Shannon’s Index of foraminiferal diversity ($H'$). (B) Shannon’s Index of molluscan diversity ($H'$, 5-cm moving average). (C) Bivalve taxonomic group diversity. (D) Gastropod taxonomic group diversity. (E) Scaphopod taxonomic group diversity. (F) Mollusc density (fossils/cm$^3$, 5-cm moving average). (G) Total mollusc fossils recovered per 1-cm sediment sample.
Fig. S3. Frequency of molluscan predation trace fossils (at 10-cm resolution), scanning electron microscope images of trace fossils (A–C) that resulted from predation, and total molluscan density for core MV0811-1SJC. High frequencies reflect an increase in predation pressure; a total of 18 straight holes (A), 11 breakage points (B), and 22 beveled holes (C) were recorded. (D) Frequency of straight predation holes resulting from annelid worm predation. (E) Frequency of breakage point predation evidence resulting from crustacean predation. (F) Frequency of beveled predation holes resulting from gastropod predation. (G) Mollusc density (log individuals/cm$^3$).
Fig. S4. Details of metazoan community response to deglacial climatic episodes from 11 to 15.5 ka in MV0811-15JC; high-resolution climate intervals, including the Pre-Bølling Warming, Oldest Dryas, Bølling, Allerød, Younger Dryas, and PreBoreal, are detailed on the figure. Biological community transition intervals between climatic episodes are highlighted in gray and have been identified on the basis of the first and last disappearances or reappearances of metazoan community members, including molluscan classes, ostracods, and ophiuroids. Episodes include Termination 1A (14.7 ka), Termination 1B (11.7 ka), and the Allerød-Younger Dryas transition (12.9 ka) (1). (A) Changes in relative frequency (5-cm moving average) of molluscan trophic guilds (including chemosynthetically associated, deposit, suspension, deposit/suspension, carnivore/detritivore, carnivore/deposit, detritivore, and unknown). (B) Log bivalve density (valves/cm$^3$). (C) Scaphopod density (tusks/cm$^3$). (D) Gastropod density (shells/cm$^3$). (E) Mollusc density (fossils/cm$^3$, 5-cm moving average). (F) Shannon’s Index of mollusc diversity ($H'$, 5-cm moving average). (G) Ophiuroids (brittle stars) presence (presence = 1, absence = 0, 5-cm moving average). (H) Ostracod valve density (valves/cm$^3$, 5-cm moving average).

Table S1. Total sampling number, mean density (fossil/cm³ ± 1σ) or presence/absence, number of taxa, and percentage of samples containing faunal group, for molluscan and foraminiferan communities at MV0811-15JC

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<th>Classification (number of sediment samples intervals), mean density (fossil/cm³ ± 1σ) or presence/absence</th>
<th>Primary fossil evidence</th>
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</thead>
<tbody>
<tr>
<td>Mollusca (n = 922) 0.14 ± 0.65 (all sediment intervals) 0.52 ± 1.16 (excluding depauperate intervals absent of molluscs)</td>
<td>Tusks, valves, shells</td>
<td>28</td>
<td>28.3</td>
</tr>
<tr>
<td>Ophiuroidea (n = 922) Presence/absence</td>
<td>Vertebral ossicles</td>
<td>Not documented</td>
<td>20</td>
</tr>
<tr>
<td>Spatangoida (n = 922) Presence/absence</td>
<td>Fragmented spines and tests</td>
<td>Not documented</td>
<td>100</td>
</tr>
<tr>
<td>Ostracoda (n = 922) 0.79 ± 1.85 (all sediment intervals); 2.47 ± 2.55 (excluding depauperate intervals absent of ostracods)</td>
<td>Valves</td>
<td>Not documented</td>
<td>32.1</td>
</tr>
<tr>
<td>Foraminifera (n = 92) 582.6 ± 497.3</td>
<td>Shells</td>
<td>22</td>
<td>100</td>
</tr>
</tbody>
</table>

Mollusc and ostracod mean density is partitioned into total mean density (all sediment intervals) and density for only samples with the faunal group (excluding depauperate intervals).
Table S2. Molluscan taxa identified and total counts of fossils recovered for MV0811-15JC, as well as trophic guild association for each taxonomic group

<table>
<thead>
<tr>
<th>Class</th>
<th>Family, subfamily</th>
<th>Genus, species (taxonomic origin)</th>
<th>Fossils recovered: number of individual valves, shells, tusks</th>
<th>Trophic guilds</th>
<th>Citations on trophic guilds and additional notes on natural history</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bivalvia</td>
<td>Lucinidae, Codakiinae</td>
<td>Lucinoma aequizonatum (Stearns, 1890)</td>
<td>199</td>
<td>Chemosynthetically associated</td>
<td>L. aequizonatum colonizes the hypoxic–anoxic transition zone at a very narrow depth profile (500 ± 10 m below sea level) in the modern SBB (1, 2). This small bivalve lives in anaerobic sediments at 3–5 cm depths and has been collected live from cold seep Vesicomya spp. clam beds (3). L. aequizonatum is associated with low or patchy sulfide environments (1) and hosts sulfur-oxidizing chemosynthetic endosymbiotic bacteria in gill tissue (4, 5) that metabolize nitrate and respire at the same rate regardless of oxygen concentrations (1).</td>
</tr>
<tr>
<td>Gastropoda</td>
<td>Columbellidae, Pyreninae</td>
<td>Alia permodesta (Dall, 1890)</td>
<td>83</td>
<td>Chemosynthetically associated</td>
<td>Epifaunal gastropod A. permodesta colonizes seafloor environments associated with the Eastern Pacific OMZ (6) and is a part of chemosynthetic trophic pathways (7). A. permodesta occurs in tight affiliation with filamentous sulfur-oxidizing chemosynthetic bacterial mats (e.g., Beggiatoa or Thioploca) (8). No evidence exists that this species harbors sulfur-oxidizing endosymbionts (9). Rather, isotopic signatures reported for the species indicate A. permodesta graze on chemosynthetic bacteria (7).</td>
</tr>
<tr>
<td>Bivalvia</td>
<td>Lucinidae</td>
<td>Fleming, 1882</td>
<td>7</td>
<td>Chemosynthetically associated</td>
<td>Chemosymbiosis with sulfide-oxidizing and methane-oxidizing bacteria has been identified in the bivalve family Lucinidae (10). Lucinidae is the most diverse group of chemosymbiotic molluscs (10).</td>
</tr>
<tr>
<td>Bivalvia</td>
<td>Manzanellidae</td>
<td>Huxleyia munita (Dall, 1898)</td>
<td>1</td>
<td>Chemosynthetically associated</td>
<td>The presence of chemosynthetic bacteria in the gills of Manzanellidae has been demonstrated (11, 12).</td>
</tr>
<tr>
<td>Bivalvia</td>
<td>Psammobiidae</td>
<td>Fleming, 1882</td>
<td>7</td>
<td>Deposit</td>
<td>Ref. 13</td>
</tr>
<tr>
<td>Bivalvia</td>
<td>Tellinidae, Macomininae</td>
<td>Leach, 1819</td>
<td>4</td>
<td>Deposit</td>
<td>Ref. 13</td>
</tr>
<tr>
<td>Bivalvia</td>
<td>Tindariidae</td>
<td>Verrill and Bush, 1897</td>
<td>3</td>
<td>Deposit</td>
<td>Ref. 14</td>
</tr>
<tr>
<td>Bivalvia</td>
<td>Yoldiidae</td>
<td>Portlandia (Mörch, 1857)</td>
<td>2</td>
<td>Deposit</td>
<td>Ref. 15</td>
</tr>
<tr>
<td>Bivalvia</td>
<td>Nuculanidae</td>
<td>Adams and Adams, 1856</td>
<td>4</td>
<td>Deposit</td>
<td>Ref. 16</td>
</tr>
<tr>
<td>Bivalvia</td>
<td>Cardiidae</td>
<td>Lamarck, 1809</td>
<td>14</td>
<td>Suspension</td>
<td>Common observation</td>
</tr>
<tr>
<td>Bivalvia</td>
<td>Cardiidae, Clinocardinae</td>
<td>Clinocardium nuttalli (Conrad, 1837)</td>
<td>5</td>
<td>Suspension</td>
<td>Common observation</td>
</tr>
<tr>
<td>Bivalvia</td>
<td>Cardiidae, Trachycardiinae</td>
<td>Trachycardium (Mörch, 1857)</td>
<td>5</td>
<td>Suspension</td>
<td>Common observation</td>
</tr>
<tr>
<td>Bivalvia</td>
<td>Limidae</td>
<td></td>
<td>2</td>
<td>Suspension</td>
<td>Common observation</td>
</tr>
<tr>
<td>Bivalvia</td>
<td>Tellinidae, Macomininae</td>
<td>Macoma (Leach, 1819)</td>
<td>36</td>
<td>Deposit/Suspension</td>
<td>Macoma is an infaunal deposit and filter-feeding bivalve genus. There is no indication in the literature that Macoma are tolerant of hypoxia or associated with OMZ environments. Macoma are commonly associated with Arctic and circumboreal waters (13). In addition, low-oxygen conditions induce behavioral changes in one Macoma species, thought to increase vulnerability to predation, wherein the species does not bury as deeply in hypoxic condition (17).</td>
</tr>
<tr>
<td>Scaphopoda</td>
<td>Gadilidae</td>
<td>Stoliczka, 1886</td>
<td>61</td>
<td>Carnivore/Deposit</td>
<td>Scaphopods are associated with intermediate and mild levels of seafloor hypoxia ((O_2)(&gt;)0.5 mL(^{-1})) (18) and are motile predators and deposit feeders encased in elongate, fang-shaped shells. Scaphopods prey on foraminifera (19).</td>
</tr>
<tr>
<td>Scaphopoda</td>
<td>Rhabdidae</td>
<td>Chistikov, 1975</td>
<td>22</td>
<td>Carnivore/Deposit</td>
<td>Scaphopods are associated with intermediate and mild levels of seafloor hypoxia ((O_2)(&gt;)0.5 mL(^{-1})) (18) and are motile predators and deposit feeders encased in elongate, fang-shaped shells. Scaphopods prey on foraminifera (19).</td>
</tr>
<tr>
<td>Class</td>
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<td>Fossils recovered: number of individual valves, shells, tusks</td>
<td>Trophic guilds</td>
<td>Citations on trophic guilds and additional notes on natural history</td>
</tr>
<tr>
<td>-------------</td>
<td>-------------------</td>
<td>-----------------------------------</td>
<td>-------------------------------------------------------------</td>
<td>----------------</td>
<td>------------------------------------------------------------------</td>
</tr>
<tr>
<td>Scaphopoda</td>
<td>Gadilidae</td>
<td>Siphodontalium quadrifissatum</td>
<td>10 Carnivore/Deposit</td>
<td>Ref. 20</td>
<td></td>
</tr>
<tr>
<td>Scaphopoda</td>
<td>Gadilidae</td>
<td>Cadulus talmiei (Dall, 1897)</td>
<td>7 Carnivore/Deposit</td>
<td>Ref. 20</td>
<td>Scaphopods are associated with intermediate and mild levels of seafloor hypoxia ([O₂] &lt; 0.5 mL·L⁻¹) (18) and are motile predators and deposit feeders encased in elongate, fang-shaped shells. Scaphopods prey on foraminifera (19).</td>
</tr>
<tr>
<td>Scaphopoda</td>
<td>Gadilidae</td>
<td>Rhabdus recticus (Carpenter, 1864)</td>
<td>2 Carnivore/Deposit</td>
<td>Ref. 20</td>
<td></td>
</tr>
<tr>
<td>Scaphopoda</td>
<td>Gadilidae</td>
<td>Gadila aberrans (Whiteaves, 1887)</td>
<td>2 Carnivore/Deposit</td>
<td>Ref. 22</td>
<td></td>
</tr>
<tr>
<td>Gastropoda</td>
<td>Epitoniidae</td>
<td>Epitonium (Röding, 1798)</td>
<td>1 Carnivore/Deposit</td>
<td>Ref. 21</td>
<td></td>
</tr>
<tr>
<td>Gastropoda</td>
<td>Columbellidae, Pyreininae</td>
<td>Suter, 1919</td>
<td>2 Carnivore/Detritivore</td>
<td>Ref. 20</td>
<td></td>
</tr>
<tr>
<td>Gastropoda</td>
<td>Cerithiidae, Bittinae</td>
<td>Linobittum paganicum (Dall, 1919)</td>
<td>72 Detritivore</td>
<td>L. paganicum has been collected within methane seeps of Northern California (23) in association with vesicomyid bivalves (24).</td>
<td></td>
</tr>
<tr>
<td>Gastropoda</td>
<td>Cerithiidae, Bittinae</td>
<td>Lirobittum rugatum (Carpenter, 1896)</td>
<td>30 Detritivore</td>
<td>Ref. 20</td>
<td></td>
</tr>
<tr>
<td>Gastropoda</td>
<td>Columbellidae, Pyreininae</td>
<td>Amphissa bicolor (Dall, 1892)</td>
<td>1 Unknown</td>
<td>Ref. 10</td>
<td></td>
</tr>
<tr>
<td>Scaphopoda</td>
<td></td>
<td></td>
<td>5 Unknown</td>
<td>Ref. 12</td>
<td></td>
</tr>
<tr>
<td>Gastropoda</td>
<td></td>
<td></td>
<td>4 Unknown</td>
<td>Ref. 13</td>
<td></td>
</tr>
<tr>
<td>Bivalvia</td>
<td>Ungulinidae</td>
<td>Adams and Adams, 1856</td>
<td>2 Unknown</td>
<td>Ref. 14</td>
<td></td>
</tr>
</tbody>
</table>

Taxa with well-established trophic strategies are cited under “common observation,” as these affiliations are broadly acknowledged. Trophic guild association organizes table.