Benthic foraminifera associated with cold methane seeps on the northern California margin: Ecology and stable isotopic composition

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Abstract

Release of methane from large marine reservoirs has been linked to climate change, as a causal mechanism and a consequence of temperature changes, during the Quaternary and the Paleocene. These inferred linkages are based primarily on variations in benthic foraminiferal stable isotope signatures. Few modern analog data exist, however, to assess the influence of methane flux on the geochemistry or faunal characteristics of benthic foraminiferal assemblages. Here we present analyses of the ecology and stable isotopic compositions of living (Rose Bengal stained) and dead (fossil) foraminifera (>150 µm) from cold methane seeps on the slope off of the Eel River, northern California (500–525 m), and discuss potential applications for reconstructions of methane release in the past and present. Calcareous foraminiferal assemblages associated with *Calyptogena* clam bed seeps were comprised of species that are also found in organic-rich environments. Cosmopolitan, paleoceanographically important taxa were abundant; these included *Uvigerina*, *Bolivina*, *Chilostomella*, *Globobulimina*, and *Nonionella*. We speculate that seep foraminifera are attracted to the availability of food at cold seeps, and require no adaptations beyond those needed for life in organic-rich, reducing environments. Oxygen isotopic values of the tests of living foraminiferal assemblages from seeps had a high range (up to 0.69‰) as did carbon isotopic values (up to 1.02‰). Many living foraminiferal isotope values were within the range exhibited by the same or similar species in non-seep environments. Carbon isotopic values of fossil foraminifera found deeper in the sediments (18–20 cm), however, were 4.10‰ (*U. peregrina*) and 3.60‰ (*B. subargentea*) more negative than living δ^{13}C values. These results suggest that δ^{13}C values of foraminiferal tests reflect methane seepage and species-specific differences in isotopic composition, and can indicate temporal variations in seep activity. A better understanding of foraminiferal ecology and stable isotopic composition will enhance paleo-seep recognition, and improve interpretations of climatic and paleoceanographic change. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: benthic foraminifera; methane; gas seeps; cold seeps; stable isotopes; C^{13}/C^{12}; O^{18}/O^{16}; benthic ecology; California continental margin

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1. Introduction

One of the most challenging aspects of climate research is the determination of the causes of global climate change. The role of greenhouse gases, such as methane, in global temperature change is of particular relevance to modern concerns. Late Quaternary records from polar ice cores indicate that significant changes in atmospheric methane occurred during the past few ice age cycles (Stauffer et al., 1988; Raynaud et al., 1988; Chappellaz et al., 1993). Marine reservoirs are a potential source of methane flux to the atmosphere. Advection of methane from sediments into overlying marine waters might be expected to result in excursions of bicarbonate stable isotope values. Large shifts in stable isotopic compositions of benthic foraminifera during climate changes in the Quaternary (Wefer et al., 1994; Kennett et al., 1996) and Late Paleocene (Dickens et al., 1995, 1997) have prompted researchers to suggest that the release of methane from marine environments is linked with paleoclimate and paleoceanographic changes during these intervals. Other workers have also suggested that the spatial distributions of foraminiferal species are influenced by pore-water methane (Wefer et al., 1994; Akimoto et al., 1994). However, few modern analog data exist to assess the influence of methane flux on the geochemistry or faunal characteristics of benthic foraminiferal assemblages. Modern environments, in which methane gas migrates up through porous sediments (seeps), are now known to be geographically widespread, and very common on the eastern Pacific continental margin (Hovland and Judd, 1988; Sibuet and Olu, 1998). Cold methane seep environments (those which have ambient sediment temperatures similar to adjacent non-seep settings) are ideal modern habitats in which to examine the influence of methane seepage on living benthic foraminifera.

Here we present results from an on-going study of the ecology and geochemistry of cold methane seeps on the Pacific margin. The objectives of this investigation were to (1) determine the relationships between cold, methane seeps (vents) and the stable isotopic compositions ($\delta^{13}C$ and $\delta^{18}O$) of living deep-sea benthic foraminifera, (2) assess the ecology and vertical distribution patterns of benthic foraminiferal species associated with methane seeps, and (3) use these modern analog data to assess whether foraminiferal characteristics can be used to reconstruct the history of methane release.

2. Previous work

2.1. Seep foraminifera

Previous studies that examined foraminifera from hydrothermal vent and cold seep environments have typically done so in an opportunistic manner, rarely distinguishing living from dead specimens (Arnold et al., 1985; Molina-Cruz and Ayala-López, 1988; Nienstedt and Arnold, 1988; Van Dover et al., 1988; Jones, 1993; Akimoto et al., 1994; Quinterno, 1994; Jonasson et al., 1995). In one of the few studies that examined living foraminifera associated with seeps, Sen Gupta et al. (1997) described the distribution of hydrocarbon seep species in the Gulf of Mexico. From the limited data available, it is apparent that benthic foraminifera can be abundant in seep/vent communities. Some taxa may have higher tolerances to the stressful environmental conditions associated with seeps. For example, Akimoto et al. (1994) suggest that the occurrence of *Rutherfordoides cornuta* is related to high methane gas content of the sediments and is associated with *Calyptogena* clam communities, while *Bulimina striata* distributions are influenced by the hydrogen sulfide gas content of ambient waters. Ancient seeps typically have been recognized in the geologic record from macrofaunal fossils (e.g., Kauffman et al., 1996). The presence of methane-influenced pore waters, however, have been inferred from ancient fossil foraminifera (Wefer et al., 1994; Kennett et al., 1996; Sarkar et al., 1996).

2.2. Stable isotopic composition of foraminifera as an environmental indicator

The ultimate source of hydrate methane is buried organic matter in large quantities, which is then altered by microbial or thermal processes (Kvenvolden, 1993). A compilation of $\delta^{13}C$ values and concentrations of methane from clathrate samples shows that most known gas hydrates contain over 99 percent methane and have $\delta^{13}C$ values between −40‰ and −94‰, with the majority having val-

ues more negative than −60‰ PDB (Kvenvolden, 1993). Significant amounts of methane reaching the oxic environments near the sediment–water interface could considerably decrease the $\delta^{13}C$ of bicarbonate and dissolved inorganic carbon (DIC) in near-surface pore waters. Some studies suggested that, as a result of methane influence, benthic foraminiferal carbonate tests secreted in seepage areas will have more negative $\delta^{13}C$ values compared to those from non-seep sites (Wefer et al., 1994; Kennett et al., 1996).

The geochemistry of benthic foraminiferal carbonate is a function of ambient pore-water chemistry and vital effects (inherent biological fractionation) (e.g., McCorkle et al., 1990, 1997). Differences in $\delta^{13}C$ values of up to 3‰ to 4‰ have been observed between species of benthic foraminifera living at the same time in the same core (McCorkle et al., 1990, 1997; Rathbun et al., 1996). Comparisons of the $\delta^{13}C$ values of benthic foraminifera species and their microhabitat preferences reveal that the $\delta^{13}C$ signatures of epifaunal taxa (those that live on or within the upper 1 cm of sediment) reflect the $\delta^{13}C$ values of bottom-water dissolved inorganic carbon. Carbon isotope values of infaunal species (species capable of living deeper than 1 cm in the sediments) are more closely aligned with the more negative $\delta^{13}C$ values of pore waters to which they are exposed (McCorkle et al., 1990, 1997). This correspondence between microhabitat preference and isotopic composition indicates that the $\delta^{13}C$ values of benthic foraminifera are directly or indirectly influenced by ambient conditions and ecological preferences (McCorkle et al., 1990, 1997; Rathbun et al., 1996). Contrary to expectations based on pore-water chemistry, however, any given species that has a broad depth range within the sediments typically has low variability of $\delta^{13}C$ values regardless of the sediment depth where it is found (Rathbun et al., 1996; McCorkle et al., 1997). Although this consistency within a species has been suggested to result from microenvironments, growth in a narrower depth range, or food preferences (Rathburn et al., 1996; McCorkle et al., 1997), questions still persist regarding the relationships between pore-water chemistry, vital effects, and the isotopic composition and ecology of benthic foraminifera.

There are no published data for the stable isotopic compositions of living foraminiferal carbonate associated with methane seeps. A single data set of isotope compositions of unstained (dead or fossil?) specimens from seep samples in the Gulf of Mexico revealed a possible tendency for the $\delta^{13}C$ of foraminiferal carbonate to be depleted by 0.4 to 4.0‰ PDB relative to tests from non-seep environs (Sen Gupta and Aharon, 1994; also reported in Sen Gupta et al., 1997). This study reported variations at a seep of 3 to 4‰ within the species, *Uvigerina peregrina*. Since the wide range of $\delta^{13}C$ values reported by Sen Gupta and Aharon (1994) has not been observed in this or other taxa in modern environments (see McCorkle et al., 1990, 1997; Rathbun et al., 1996), these differences may result from differences in the influence of methane on ambient pore-waters. Foraminiferal $\delta^{18}O$ values appear unaffected by hydrocarbon venting (Sen Gupta and Aharon, 1994), which is to be expected if methane venting is not associated with temperature or salinity anomalies.

3. Study area

Samples were collected from clam beds (500–525 m) on the margin off the Eel River, northern California (40º47.08N, 124º35.68W) (Fig. 1). Sediments containing hydrate were documented in the region by Field and Kvenvolden (1985) and Kennicutt et al. (1989). Field and Kvenvolden (1987) reported considerable methane seepage near our study site. In one area, methane samples had $\delta^{13}C$ values of −43 to −44‰ (Field and Kvenvolden, 1987). Trawling and piston-coring on the slope (450–600 m) recovered shells and live organisms, including gastropods (*Neptunea* spp.) and clams (*Calyptogena pacifica*) that exhibited tissue isotopic compositions indicative of the presence of chemosynthetic endosymbionts (Kennicutt et al., 1989).

This area was revisited with submersibles by investigators from MBARI in August 1997 (Brewer et al., 1997) and from Scripps Institution of Oceanography (SIO) in October, 1997 (this study). Real-time observations captured on video revealed active, and in some cases, rapid, venting of methane gas from sediments at ∼520 m (Orange et al., 1997; Orange, 1999; this study). Over an area of at least 1 km^2 we observed many patches ∼100 cm^2 to >15 m^2 of living, densely aggregated clams (*Calyptogena pacifica*). Large outcrops of authigenic carbonate were
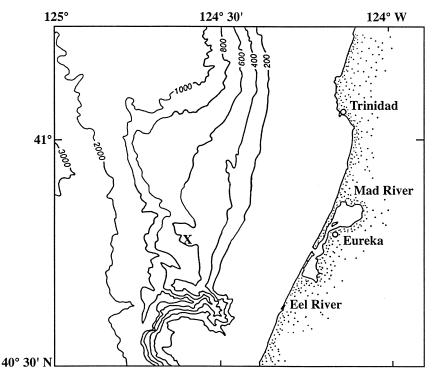
Fig. 1. Map of the northern California Margin showing the location of the clam bed seeps sampled for this study. Contour intervals are 200 m to 1000 m, and 1000 m in deeper water. Adapted from Kennicutt et al. (1989).

common, and carbonate nodules were abundant in the sediments. We measured bottom-water oxygen levels of 30 to 40 μM (0.6 to 1.0 ml/l) in October, 1997 at this site. Based on October, 1997 chlorinity values, bottom-water salinity was 34.31 (±0.003). During August, 1997, bottom temperatures were 5.6 to 5.94°C (Brewer et al., 1997).

Four tube cores from clam beds sampled during the October, 1997 cruise were analyzed for pore fluid composition. In all cores there was an indication of increased chlorides with depth (8–30 cm), indicating upward movement of more saline fluids, possibly originating from greater depth, where hydrate formation will lead to salt exclusion and hence enhanced chloride concentrations. Magnesium concentration depth profiles also indicate upward advection of deeper fluids (J. Gieskes and C. Mahn, unpubl.). Any upward advection of methane-enriched fluids will lead to enhanced sulfate reduction with consequent increases in alkalinity and dissolved sulfide. Bicarbonate production causes the precipitation of carbonates.

4. Methods

Sediments were obtained from *C. pacifica* clam beds (numbers 2, 4 and 5) using the U.S. Navy ROV *Scorpio* during our 1997 sampling program. Two tube cores (8.3 cm diameter), one each from clam bed 4 and 5 (only tens of meters apart), were designated for foraminiferal analyses. These sediments were vertically subsampled at 0.5 cm intervals down to 3 cm and at 1 cm intervals down to 5 (clam bed 4) or 10 cm (clam bed 5) within the sediments. Each of these 'slices' of sediment was preserved in 200 ml of 4% buffered formalin. In the laboratory, foraminiferal samples were stained with Rose Bengal for at least 1 week, and the original volume of sediment was measured using volumetric procedures outlined in Rathburn and Corliss (1994). Samples were then sieved with nested 63 and 150 μm mesh sieves, and typically split into manageable volumes for examination (see Tables 1 and 2). Stained benthic foraminifera from the >150 mm fraction were wet-picked from the sample, sorted, and identified

in the manner described in Rathburn and Corliss (1994). To facilitate comparisons of vertical distribution patterns, volume (number of specimens/50 cm^3) is used; when comparing total abundances, area (standing stock, number of specimens/50 cm^2) is used. Foraminifera from scoop samples recovered in clam bed 2 and a site with no evidence of seep activity (within 1 km of the clam beds) were analyzed for carbon and oxygen isotopes only.

Despite limitations, Rose Bengal remains the stain of choice by researchers to distinguish foraminifera collected alive (e.g., Corliss, 1985; Lutze and Altenbach, 1991; Gooday, 1993, 1996; Gooday and Rathburn, 1999). Although other techniques are available to distinguish living protists, these techniques are typically used for small samples (e.g., 2.5 cm diameter syringes), and not for community analyses of large samples of foraminifera. In studies which employ other techniques to distinguish living specimens, Rose Bengal is also typically used where larger samples or higher abundances are required for community-level analyses (e.g., Bernhard and Reimers, 1991; Alve and Bernhard, 1995; Bernhard et al., 1997). In addition, previous work has demonstrated the effectiveness of using Rose Bengal to identify carbonate from living foraminifera in isotopic studies (McCorkle et al., 1990, 1997; Rathburn et al., 1996). In this study, we relied primarily on Rose Bengal stain because: (1) it is the most practical stain available to distinguish living specimens in reasonably large quantities (8–10 cm diameter subcores), (2) the data generated are comparable with previous studies which used Rose Bengal to distinguish living specimens, (3) the effects of other staining techniques on the isotopic signatures of foraminiferal carbonate are unknown.

Fossil foraminifera (unstained) from clam bed 5 were obtained from the same samples as living (stained) specimens. Fossil foraminifera from clam bed 4 were taken from sieved and dried samples that were frozen on board the ship. These samples were collected from a different tube core, taken in the same clam bed within meters of the one examined for living (stained) foraminifera.

To minimize the possibility of contamination by calcite overgrowths or carbonate grains, each foraminiferal specimen used for isotope analyses was cleaned ultrasonically, rinsed with Milli-Q water,

and microscopically examined. All carbonate isotope samples were roasted at 380ºC, then dissolved at 73ºC with anhydrous phosphoric acid in a Finnigan MAT carbonate extraction system (Kiel device) connected to a Finnigan MAT 251 isotope ratio mass spectrometer at the University of Michigan. Data are reported in standard notation (δ^{13}C, δ^{18}O) relative to the Pee Dee Belemnite (PDB) standard.

5. Results

5.1. Living foraminiferal assemblage composition

Densities of stained specimens in the top 1 cm were 275/50 cm^3 in the clam bed 5 core and 342/50 cm^3 in the top 1 cm of the clam bed 4 core (Fig. 2a; Tables 1 and 2). Standing stocks of the entire assemblage in the upper 5 cm, however, were much higher at clam bed 5 (1540 individuals/50 cm^2) than at clam bed 4 (1098/50 cm^2) (Table 3). Cosmopolitan, paleoceanographically important taxa were abundant, including *Uvigerina*, *Bolivina*, *Chilostomella*, *Globobulimina*, and *Nonionella* (Table 3). Several infaunal species had a density maximum at 2.5–3 cm within clam bed 4 sediments, as did total foraminiferal density (Fig. 2a,b). In clam bed 5 infaunal taxa typically exhibited maxima in the upper 2.5 cm, with reduced abundances in the uppermost interval (Fig. 2a,b; Tables 1 and 2).

5.2. Stable isotopic signatures of biogenic carbonate

Carbon isotopic analyses of living (stained) specimens of 9 species of benthic foraminifera, shell material from two *Calyptogena pacifica* valves, and authigenic carbonate from clam beds confirm the presence of methane-influenced pore-waters (Table 4). The authigenic carbonate sample from surface sediments yielded a δ^{13}C value of −33.57‰, which is indicative of light δ^{13}C bicarbonate-rich fluids that probably resulted from methane oxidation. Samples taken from two *C. pacifica* shells (dead, from clam bed 5) indicate that clam carbonate can be highly variable in stable isotopic composition at this site (δ^{13}C values of −1.35‰ and 0.01‰; δ^{18}O values of 1.86‰ and 2.63‰).
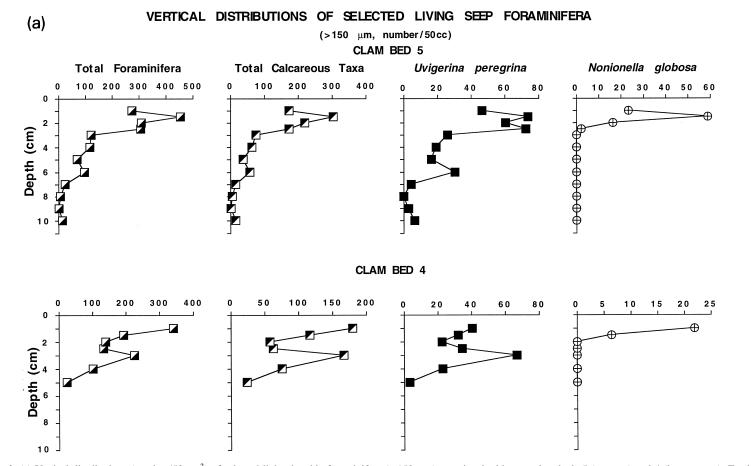
A broad range of δ^{13}C values also was evident

Fig. 2. (a) Vertical distributions (number/50 cm³) of selected living benthic foraminifera (>150 μm) associated with seep clam beds 5 (top row) and 4 (bottom row). Total foraminifera = agglutinated taxa plus calcareous taxa.
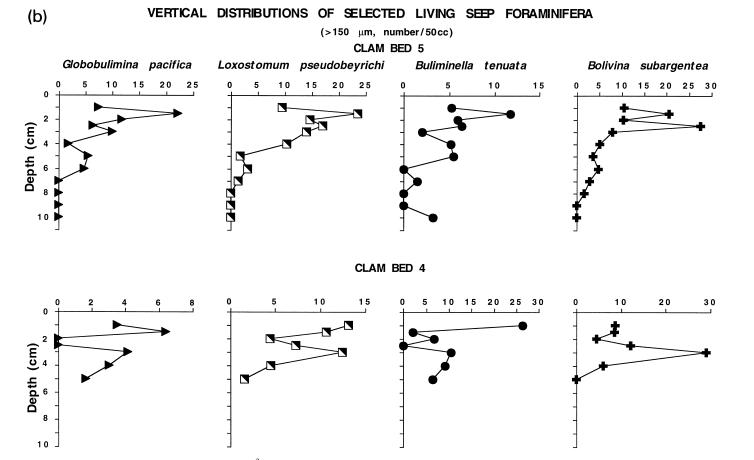
Fig. 2 (continued). (b) Vertical distributions (number/50 cm^3) of selected living benthic foraminifera (>150 associated μm) with seep clam beds 5 (top row) and 4 (bottom row).

Table 1
Number of living benthic foraminifera from clam bed 5 (number/50 cc) for each 1 cm and 0.5 cm interval from 0 to 10 cm in tube core 1 [a]

| Depth (cm) | 0–1 | 1–1.5 | 1.5–2 | 2–2.5 | 2.5–3 | 3–4 | 4–5 | 5–6 | 6–7 | 7–8 | 8–9 | 9–10 |
Volume examined (cm^3)	47.5	34	34	23.5	25	29	27.5	31.5	34.5	30.5	17.25	15.5
Angulogerina angulosa	1.05	7.35	2.94	2.13	0.00	3.45	1.82	1.59	0.00	0.00	0.00	0.00
Bolivina pacifica	3.16	5.88	1.47	0.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Bolivina sp.	2.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Bolivina spissa	8.42	10.29	13.24	10.64	0.00	5.17	0.00	7.94	0.00	1.64	0.00	0.00
Bolivina subargentea	10.53	20.59	10.29	27.66	8.00	5.17	3.64	4.76	2.90	1.64	0.00	0.00
Bolivina sp.	0.00	0.00	1.47	0.00	0.00	1.72	3.64	0.00	0.00	0.00	0.00	0.00
Buliminella tenuata	5.26	11.76	5.88	6.38	2.00	5.17	5.45	0.00	1.45	0.00	0.00	3.23
Bulimina mexicana	2.11	0.00	1.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chilostomella ovoidea	11.58	16.18	16.18	6.38	6.00	3.45	0.00	3.17	0.00	0.00	0.00	0.00
Cibicides wuellerstorfi	0.00	4.41	4.41	4.26	0.00	1.72	0.00	3.17	0.00	0.00	0.00	0.00
Cushmanina fieldeniana	0.00	2.94	2.94	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dentalina sp.	1.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Epistominella smithi	0.00	2.94	1.47	2.13	0.00	1.72	0.00	0.00	4.35	3.28	0.00	6.45
Epistominella sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.59	0.00	0.00	0.00	0.00
Eponides leviculus	0.00	1.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Fissurina spp.	3.16	5.88	1.47	4.26	2.00	1.72	0.00	1.59	0.00	0.00	0.00	0.00
Fursenkoina bramlettei	0.00	1.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Globocassidulina braziliensis	0.00	0.00	1.47	0.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Globocassidulina subglobosa	0.00	0.00	0.00	2.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Globobulimina pacifica	7.37	22.06	11.76	6.38	10.00	1.72	5.45	4.76	0.00	0.00	0.00	0.00
Globobulimina spinifera	2.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lagena sulcata var. *interupta*	1.05	1.47	1.47	0.00	0.00	3.45	0.00	0.00	0.00	0.00	0.00	0.00
Lagena striata	0.00	4.41	2.94	4.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lagena cf *L. distoma*	0.00	0.00	1.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lenticulina sp.	0.00	0.00	1.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Loxostomum pseudobeyrichi	9.47	23.53	14.71	17.02	14.00	10.34	1.82	3.17	1.45	0.00	0.00	0.00
Nonionella globosa	23.16	58.82	16.18	2.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nonionella basispinata	3.16	2.94	4.41	2.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nonionella labradorica	3.16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nonionella sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nonion sp. *A*	1.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oolina cf. *hexagona*	2.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.45	0.00	0.00	0.00
Pyrgo sp.	1.05	0.00	1.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pyrgo sp. B	5.26	2.94	10.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pyrgo sp. D	0.00	4.41	4.41	2.13	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Quinqueloculina sp. D	0.00	2.94	11.76	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Quinqueloculina sp. C	7.37	10.29	1.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Quinqueloculina sp. A	3.16	0.00	2.94	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Quinqueloculina sp.	0.00	0.00	7.35	0.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sigmoilopsis schlumbergeri	4.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Triloculina sp.	0.00	1.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Uvigerina peregrina	46.32	73.53	60.29	72.34	26.00	18.97	16.36	30.16	4.35	0.00	2.90	6.45
Valvulineria auricana	3.16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Unknown calcareous	2.11	4.41	0.00	2.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Total calcareous taxa	173.68	304.41	219.12	174.47	76.00	63.79	38.18	58.73	15.94	6.56	2.90	16.13
Total agglutinates	101.05	151.47	89.71	134.04	46.00	53.45	30.91	38.10	8.70	0.00	0.00	0.00
Total benthic foraminifera	274.74	455.88	308.82	308.51	122.00	117.24	69.09	96.83	24.64	6.56	2.90	16.13

[a] The volume of sediments examined is also included to facilitate conversion of data to number/area.

Table 2
Number of living benthic foraminifera from clam bed 4 (number/50 cc) for each 1 cm and 0.5 cm interval from 0 to 5 cm in tube core 6 [a]

| Depth (cm) | 0–1 | 1–1.5 | 1.5–2 | 2–2.5 | 2.5–3 | 3–4 | 4–5 |
Volume examined (cm^3)	57	23.5	22.5	20.5	24	33	31
Angulogerina angulosa	1.75	4.26	0.00	0.00	6.25	4.55	0.00
Bolivina pacifica	13.16	4.26	0.00	0.00	0.00	0.00	0.00
Bolivina sp.	0.00	0.00	0.00	2.44	0.00	0.00	6.45
Bolivina spissa	0.88	0.00	0.00	0.00	8.33	4.55	0.00
Bolivina subadvena	0.88	0.00	0.00	0.00	0.00	0.00	0.00
Bolivina subargentea	8.77	8.51	4.44	12.20	29.17	6.06	0.00
Buliminella tenuata	26.32	2.13	6.67	0.00	10.42	9.09	6.45
Chilostomella ovoidea	0.88	10.64	0.00	0.00	6.25	1.52	0.00
Cibicides wuellerstorfi	1.75	0.00	4.44	0.00	2.08	3.03	0.00
Cushmanina fieldeniana	0.88	0.00	0.00	0.00	0.00	0.00	0.00
Dentalina sp.	0.88	0.00	0.00	0.00	0.00	0.00	0.00
Epistominella sp.	2.63	0.00	0.00	2.44	6.25	3.03	0.00
Fissurina spp.	0.88	0.00	4.44	2.44	4.17	6.06	3.23
Globobulimina pacifica	3.51	6.38	0.00	0.00	4.17	3.03	1.61
Globobulimina spinifera	0.88	0.00	0.00	0.00	0.00	0.00	0.00
Lagena sulcata var. *interupta*	0.88	2.13	0.00	0.00	0.00	0.00	0.00
Loxostomum pseudobeyrichi	13.16	10.64	4.44	7.32	12.50	4.55	1.61
Nodosaria sp.	0.00	0.00	0.00	2.44	2.08	0.00	0.00
Nonionella stella	16.67	17.02	2.22	0.00	0.00	0.00	0.00
Nonionella globosa	21.93	6.38	0.00	0.00	0.00	0.00	0.00
Nonionella basispinata	7.89	0.00	0.00	0.00	0.00	0.00	1.61
Nonionella labradorica	0.88	0.00	0.00	0.00	2.08	0.00	0.00
Oolina cf. *hexagona*	0.88	0.00	0.00	0.00	2.08	0.00	0.00
Oolina sp. C	1.75	0.00	0.00	0.00	0.00	0.00	0.00
Pyrgo sp. B	4.39	0.00	0.00	0.00	0.00	0.00	0.00
Sigmoilopsis schlumbergeri	2.63	8.51	0.00	0.00	0.00	1.52	0.00
Other miliolidae	3.51	0.00	0.00	0.00	0.00	0.00	0.00
Uvigerina peregrina	40.35	31.91	22.22	34.15	66.67	22.73	3.23
Unknown calcareous	0.88	4.26	8.89	0.00	2.08	3.03	0.00
Total calcareous taxa	179.82	117.02	57.78	63.41	166.67	75.76	24.19
Total agglutinates	162.28	76.60	82.22	70.73	58.33	25.76	0.00
Total benthic foraminifera	342.11	193.62	140.00	134.15	225.00	101.52	24.19

[a] The volume of sediments examined is also included to facilitate conversion of data to number/area.

in isotope values within some benthic foraminiferal species (Table 2; Figs. 3 and 4). Living *U. peregrina* δ^{13}C values had a wide range within a clam bed (differences of up to 1.02‰ in clam bed 5 and 0.63‰ in clam bed 4), and between clam beds (differences of up to 0.46‰ between clam beds which were only tens of meters apart; Figs. 3 and 4). A wide range of carbon isotope values within and between clam beds was also evident in *Buliminella tenuata* (differences up to 0.5‰ within a single clam bed and 1.40‰ between clam beds) and *Chilostomella ovoidea* (0.34‰ within a clam bed and 0.5‰ between clam beds). These latter two species both had more negative values deeper in the sediment (Fig. 4),

and may more closely reflect downcore pore-water δ^{13}C changes. With such a small number of analyses for each foraminiferal species, however, isotopic variability within a species is difficult to assess.

Carbon isotopic compositions of fossil foraminifera were quite different from living specimens of the same species from more recent sediments in the same core and between adjacent clam beds. On average, clam bed 5 fossils from deeper in the core had different (more positive) isotope values than living representatives of the same species, but did not show definitive methane seep influence (Table 4; Fig. 4). Only *U. peregrina* had sufficient numbers of specimens to make this comparison statistically

Table 3
Standing stock (number/50 cm^2) of total living (stained) foraminifera for clam bed 5 (0–5 cm and 0–10 cm) and clam bed 4 (0–5 cm)

Clam bed 5	Total (0–5 cm)	Total (0–10 cm)	Clam bed 4	Total (0–5 cm)
Angulogerina angulosa	15.72	17.57	*Angulogerina angulosa*	16.64
Bolivina pacifica	12.02	12.02	*Bolivina pacifica*	17.57
Bolivina sp.	3.70	3.70	*Bolivina* sp.	9.25
Bolivina spissa	44.38	55.47	*Bolivina spissa*	13.87
Bolivina subargentea	78.59	89.68	*Bolivina subadvena*	0.92
Bolivina sp.	6.47	6.47	*Bolivina subargentea*	62.87
Buliminella tenuata	38.83	44.38	*Buliminella tenuata*	62.87
Bulimina mexicana	4.62	4.62	*Chilostomella ovoidea*	17.57
Chilostomella ovoidea	55.47	55.47	*Cibicides wuellerstorfi*	11.09
Cibicides wuellerstorfi	11.09	14.79	*Cushmanina fieldeniana*	0.92
Cushmanina fieldeniana	3.70	3.70	*Dentalina* sp.	0.92
Dentalina sp.	1.85	1.85	*Epistominella* sp.	13.87
Epistominella smithi	6.47	23.11	*Fissurina* spp.	21.26
Epistominella sp.	0.00	1.85	*Globobulimina pacifica*	18.49
Eponides leviculus	0.92	0.92	*Globobulimina spinifera,*	0.92
Fissurina spp.	17.57	19.42	*Lagena sulcata* var. *interupta*	2.77
Fursenkoina bramlettei	0.92	0.92	*Lagena striata*	3.70
Globocassidulina braziliensis	2.77	2.77	*Loxostomum pseudobeyrichi*	50.85
Globocassidulina subglobosa	1.85	1.85	*Nodosaria* sp.	3.70
Globobulimina pacifica	56.40	61.95	*Nonionella stella*	34.21
Globobulimina spinifera	3.70	3.70	*Nonionella* sp. aff. *N. globosa*	28.66
Lagena sulcata var. *interupta*	7.40	7.40	*Nonionella basispinata*	10.17
Lagena striata	8.32	8.32	*Nonionella labradorica*	2.77
Lagena cf *L. distoma*	0.92	0.92	*Oolina* cf. *hexagona*	2.77
Lenticulina sp.	0.92	0.92	*Oolina* sp. C	1.85
Loxostomum pseudobeyrichi	81.36	86.91	*Pyrgo* sp. B	4.62
Nonionella globosa	89.68	89.68	*Sigmoilopsis schlumbergeri*	12.02
Nonionella basispinata	12.02	12.02	Other miliolidae	3.70
Nonionella labradorica	5.55	5.55	*Uvigerina peregrina*	205.25
Nonion sp. A	1.85	1.85	*Valvulineria* sp.	1.85
Oolina cf. *hexagona*	3.70	5.55	Unknown calcareous	17.57
Pyrgo sp.	2.77	2.77		
Pyrgo sp. B	17.57	17.57	Total calcareous taxa	655.51
Pyrgo sp. D	9.25	9.25	Total agglutinates	442.86
Quinqueloculina sp. D	9.25	9.25	Total benthic foraminifera	1098.37
Quinqueloculina sp. C	20.34	20.34		
Quinqueloculina sp. A	7.40	7.40		
Quinqueloculina sp.	6.47	6.47		
Sigmoilopsis schlumbergeri	7.40	7.40		
Triloculina sp.	0.92	0.92		
Uvigerina peregrina	289.39	341.16		
Valvulineria auricana	5.55	5.55		
Unknown calcareous	8.32	8.32		
Total calcareous taxa	963.39	1081.73		
Total agglutinates	576.92	632.40		
Total benthic foraminifera	1540.31	1714.13		

(Student's $t = 2.82$, $p = 0.020$). Clam bed 4 fossil foraminifera, however, had very negative carbon isotope values compared to living specimen values (*U. peregrina* Student's $t = 6.05$, $p < 0.001$), indicating methane seep influence on isotopic values. Discounting the more excessive carbon isotope values of -16.31 to $-21.60‰$, differences of up to 4.1‰ (*U. peregrina*) and 3.6‰ (*Bolivina subargentea*) were
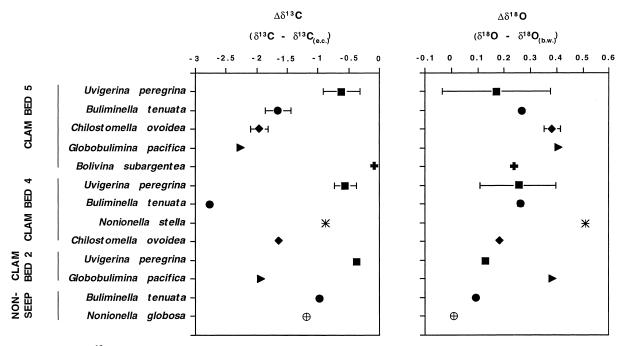
Fig. 3. Average $\Delta\delta^{13}C$ values (see discussion in text) and standard deviations for each species analyzed. We estimate the bottom water $\delta^{13}C$ value ($\delta^{13}C_{(ec)}$) to be about $-0.58‰$ (PDB), and the $\delta^{18}O$ value to be about $-0.10°$ (SMOW). Using equations from McCorkle et al. (1997), we calculate $\delta^{18}O$ (PDB) of calcite in equilibrium with water ($\delta^{18}O_{(bw)}$) to be 2.35‰.

observed between living and fossil isotope values for the same species (Table 4, Fig. 4). Fossil specimens from older material at 18–21 cm had more negative values than fossils at 6–9 cm (a difference of 4.75‰ in *U. peregrina*), which had more negative values than living specimens (Fig. 4). Combined data from the two clam beds indicate significant shifts in isotope values through the history of seepage in the small area (Table 4, Fig. 4).

Oxygen isotope values of living benthic foraminifera of the same species also had a wide range in clam bed 5 (maximum difference of 0.69‰ in clam bed 5 and 0.38‰ in clam bed 4) (Table 4). Relatively small standard deviations in $\delta^{18}O$ (Figs. 3 and 5), however, suggest that the temperature and salinity of ambient bottom-waters and pore-waters near the sediment–water interface had not recently changed appreciably. Fossil $\delta^{18}O$ values were more positive compared to those of living representatives of the same species (clam bed 5 *U. peregrina* Student's $t = 6.56$, $p < 0.001$; and clam bed 4 Student's $t = 4.06$, $p = 0.004$). This can result from cooler ancient bottom-water temperatures or changes in seep

pore-water characteristics. Without accurate ages for the fossil specimens, it is not possible to evaluate temperature or salinity changes in seep fluids.

6. Discussion

6.1. Comparisons of seep assemblages to those of other Pacific regions

As a result of the paucity of comparable Pacific Ocean settings examined for living foraminiferal assemblages, only a few studies are available for contrast. Foraminiferal densities (>150 μm fraction) in the 0–1 cm interval in clam beds 4 and 5 (275/50 cm^3 and 342/50 cm^3) were comparable to those of the San Pedro Basin, California borderlands (311 to 634/50 cc) at about 720 m (Silva et al., 1995), but were much lower than those from similar depths in the Sulu Sea (Rathburn and Corliss, 1994). Standing stocks for seep samples (1540/cm^2 and 1098/50 cm^2) also were comparable to those of the >150 μm fraction in the San Pedro Basin and the Sulu Sea.
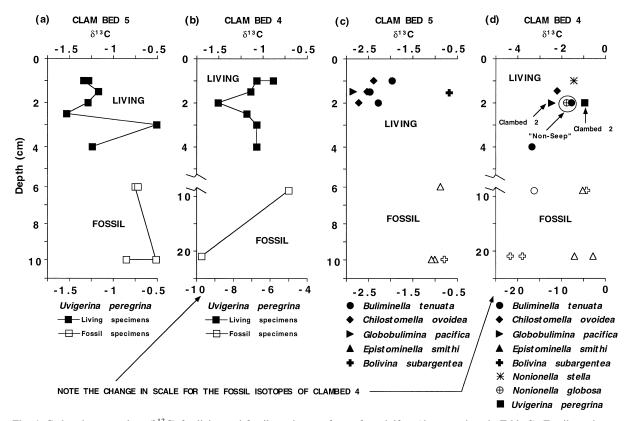
Table 4
Stable isotope values (δ^{13}C and δ^{18}O) of living (Rose Bengal stained) and fossil foraminifera from clam beds 4 and 5 [a]

Sample site	Sediment depth	δ^{13}C (PDB)	δ^{18}O (PDB)	Identification (No. of specimens)
Clam bed 5				
Living (stained)	0–1 cm	−1.34	2.17	*Uvigerina peregrina* (4)
Clam bed 5	0–1 cm	−1.28	2.60	*Uvigerina peregrina* (2)
Tube core 1	1–1.5 cm	−1.17	2.86	*Uvigerina peregrina* (5)
Dive 274	1.5–2 cm	−1.29	2.57	*Uvigerina peregrina* (5)
	2–2.5 cm	−1.53	2.32	*Uvigerina peregrina* (4)
	2.5–3 cm	−0.51	2.61	*Uvigerina peregrina* (1)
	3–4 cm	−1.24	2.52	*Uvigerina peregrina* (2)
	0–1 cm	−1.96	2.61	*Buliminella tenuata* (3)
	1–1.5 cm	−2.46	2.63	*Buliminella tenuata* (4)
	1.5–2 cm	−2.27	2.62	*Buliminella tenuata* (3)
	0–1 cm	−2.37	2.76	*Chilostomella ovoidea* (6)
	1–1.5 cm	−2.53	2.69	*Chilostomella ovoidea* (6)
	1.5–2 cm	−2.71	2.75	*Chilostomella ovoidea* (6)
	1–1.5 cm	−2.84	2.75	*Globobulimina pacifica* (6)
	1–1.5 cm	−0.65	2.59	*Bolivina subargentea* (3)
Fossil	5–6 cm	−0.75	3.32	*Uvigerina peregrina* (4)
Clam bed 5	5–6 cm	−0.72	3.16	*Uvigerina peregrina* (3)
Tube core 1	5–6 cm	−0.87	3.09	*Epistominella smithi* (3)
Dive 274	9–10 cm	−0.77	3.21	*Bolivina subargentea* (3)
	9–10 cm	−0.85	3.35	*Uvigerina peregrina* (4)
	9–10 cm	−0.51	3.46	*Uvigerina peregrina* (4)
	9–10 cm	−1.00	3.18	*Epistominella smithi* (5)
	9–10 cm	−1.07	3.27	*Epistominella smithi* (6)
Clam bed 5	surface	−1.35	1.86	*Calyptogena pacifica* [clam]
Scoop Bag 1	surface	0.01	2.63	*Calyptogena pacifica* [clam]
Dive 274	surface	−33.57	3.79	Authigenic carbonate
Clam bed 4				
Living (stained)	0–1 cm	−1.07	2.76	*Uvigerina peregrina* (3)
Clam bed 4	0–1 cm	−0.88	2.74	*Uvigerina peregrina* (4)
Tube core 6	1–1.5 cm	−1.14	2.53	*Uvigerina peregrina* (6)
Dive 274	1.5–2 cm	−1.51	2.45	*Uvigerina peregrina* (3)
	2–2.5 cm	−1.18	2.40	*Uvigerina peregrina* (3)
	2.5–3 cm	−1.07	2.57	*Uvigerina peregrina* (3)
	3–4 cm	−1.07	2.78	*Uvigerina peregrina* (3)
	3–4 cm	−3.36	2.61	*Buliminella tenuata* (4)
	0–1 cm	−1.45	2.86	*Nonionella stella* (4)
	1–1.5 cm	−2.21	2.53	*Chilostomella ovoidea* (4)
Fossil	6–9 cm	−5.11	2.94	*Epistominella smithi* (6)
Clam bed 4	6–9 cm	−4.98	2.99	*Uvigerina peregrina* (6)
Tube core 3	6–9 cm	−4.25	2.83	*Bolivina subargentea* (5)
Dive 274	6–9 cm	−16.31	3.35	*Buliminella tenuata* (5)
	18–21 cm	−7.06	2.97	*Epistominella smithi* (5)
	18–21 cm	−2.76	2.99	*Epistominella smithi* (5)
	18–21 cm	−9.73	3.42	*Uvigerina peregrina* (5)
	18–21 cm	−21.60	3.63	*Bolivina subargentea* (3)
	18–21 cm	−18.91	3.52	*Bolivina subargentea* (3)

Table 4 (continued)

Sample site	Sediment depth	$\delta^{13}C$ (PDB)	$\delta^{18}O$ (PDB)	Identification (No. of specimens)
Clam bed 2				
Living (stained)	surface	−0.96	2.48	*Uvigerina peregrina* (3)
Clam bed 2	surface	−2.53	2.73	*Globobulimina pacifica* (5)
Surface sediments; Dive 271				
Non-seep				
Living (stained)	0–2 cm	−1.55	2.44	*Buliminella tenuata* (4)
Non-seep	0–2 cm	−1.77	2.36	*Nonionella globosa* (12)
Tube core 2; Dive 278				

[a] Additional foraminiferal values are given for nearby clam bed 2 and another nearby site that had no evidence of seep activity. The number of specimens analyzed is given in parentheses. Also included are stable isotope values from the shell material of two dead *Calyptogena* clams and authigenic carbonate collected from surficial sediments in clam bed 5.

Fig. 4. Carbon isotope values ($\delta^{13}C$) for living and fossil specimens of seep foraminifera (data are given in Table 3). Fossil specimens are from separate cores than living specimens in clam bed 4. Note the vertical and horizontal scale differences for fossil specimens from clam bed 4. (a) $\delta^{13}C$ values of living (solid squares) and fossil (open squares) *Uvigerina peregrina* from clam bed 5; (b) from clam bed 4; (c) from clam bed 5; (d) $\delta^{13}C$ values of living (solid squares) and fossil (open squares) specimens of other dominant species from clam bed 4. Additional $\delta^{13}C$ values of living specimens are included from surficial sediments collected from nearby clam bed 2 and probable non-seep habitats.

SEEP FORAMINIFERA OXYGEN ISOTOPES

Fig. 5. Oxygen isotope values (δ^{18}O) for living and fossil specimens of seep foraminifera. Fossil specimens are from different cores than living specimens in clam bed 4. Note the vertical and horizontal scale differences for fossil specimens from clam bed 4. (a) δ^{18}O values of living (solid squares) and fossil (open squares) *Uvigerina peregrina* from clam bed 5; (b) from clam bed 4; (c) from clam bed 5; (d) δ^{18}O values of living (solid squares) and fossil (open squares) specimens of other dominant species from clam bed 4. Additional δ^{18}O values of living specimens are included from surficial sediments collected from nearby clam bed 2 and probable non-seep habitats.

It is difficult to compare our data with results from studies that do not separate the 63–150 μm fraction data from the >150 μm fraction data. Common seep species are also typically abundant in organic-rich, oxygen-poor settings, including the Santa Barbara Basin (see Tables 1 and 2, and Bernhard et al., 1997).

Vertical distribution patterns of seep foraminifera were similar to those of the same species from other regions. Most seep taxa can live below the sediment–water interface, and are considered 'infaunal' sensu Rathburn and Corliss (1994). This is expected in regions of relatively low oxygen concentration and high organic input (e.g., Silva et al., 1995). The most noteworthy aspects of the vertical distribution patterns are the lack of surface sediment abundance maxima for most taxa in clam bed 5 and the presence of a significant subsurface maxima for many, but not all, taxa in clam bed 4. Most vertical distribution profiles of total foraminiferal assemblages produce 0–1 cm maxima (e.g., Rathburn and Corliss, 1994; Gooday and Rathburn, 1999). It is not likely that clam bed 5 foraminifera are avoiding surface predation as this pervasive pattern was not observed in similar environments, including those of the adjacent clam bed. Clam bed 5 foraminifera may be attracted to some aspect of the 1–1.5 cm-interval environment, perhaps induced by seep chemistry or biota.

Density maxima at the 0–1 cm interval are evident for most taxa in clam bed 4 (Fig. 2a,b). The second,

subsurface peak at 2.5 to 3 cm, observed for many species is unusual. Since all taxa do not exhibit this pattern (e.g., *N. globosa*), distributions in this core are not an artifact of coring. This suggests that some aspect of the environment at 2.5–3 cm was favorable for many species. This subsurface distribution pattern may result from a burrow at this level, or a chemical zone or boundary that enhances food supplies (such as reducing bacteria). The single isotope value from *U. peregrina* living in this interval does not indicate a zone of high methane flux or unique pore water composition that might attract seep-loving taxa. Subsurface chemical and biological profiles are required to determine if foraminifera at either site respond to subsurface geochemical or biological characteristics of the clam bed sediments.

6.2. Diagenesis

The foraminiferal carbonate analyzed in this study does not appear to have been influenced by diagenesis, although three samples may have been contaminated by authigenic carbonate grains within the test chambers of small species. No carbonate overgrowths were visible, and all analyzed tests were pristine. Carbonate overgrowths can escape microscopic inspection, but the similarity of values from the other few fossil studies, and the $\delta^{18}O$ values indicate that the isotopic data do not reflect a diagenetic effect. Diagenesis is not applicable to tests of specimens that were living at the time of collection. The fossil data sets of Sen Gupta and Aharon (1994), Wefer et al. (1994), and Kennett et al. (1996) show a range of isotope values up to 5‰ in inferred methane-influenced environments. Except for three carbon isotopic signatures of deep (6–9 cm and 18–21 cm) fossil specimens from clam bed 4 (16.31‰, −18.91‰, and −21.60‰), our $\delta^{13}C$ values are within this range. These three very negative values are likely to have been influenced by authigenic carbonate grain contamination, as evidenced by their $\delta^{18}O$ values, which are similar to those of the authigenic carbonate samples. This is not the case with any of the other specimens. Additional work on living specimens from active seeps will determine whether or not the fossil isotope values in this investigation and previous seep stud-

ies result from contamination. Although we cannot entirely discount the possibility that some contamination of grains of authigenic carbonate remained in other fossil test chambers, foraminiferal isotopic values appear to reflect the isotopic signatures of the tests.

6.3. Comparisons of seep foraminiferal isotopic compositions with those from other regions

Previous studies have concluded that the carbon isotope values of *Calyptogena* clam carbonate result from bottom-water characteristics, and are not influenced by methane seepage (e.g., Berner et al., 1999). If this is correct, the variability of the clam carbonate in the present study $\delta^{13}C$ values of −1.35‰ and 0.01‰; $\delta^{18}O$ values of 1.86‰ and 2.63‰) suggests that the clam shells were secreted in different environments with much different bottom-water characteristics, or were influenced by contamination from authigenic carbonate. Since a portion of a living *Calyptogena* clam typically extends above the sediment–water interface, it is no great surprise that *Calyptogena* carbonate is primarily influenced by bottom-water. We would expect foraminiferal carbonate to be much more susceptible to porewater characteristics and methane seep influences than clam carbonate since most of the foraminifera found in the study area are able to live below the sediment–water interface.

By subtracting estimated bottom-water $\delta^{13}C$ values from foraminiferal $\delta^{13}C$ values ($\Delta\delta^{13}C$), it is possible to compare living foraminiferal $\delta^{13}C$ values collected from different areas (e.g., McCorkle et al., 1990, 1997; Rathburn et al., 1996) (Fig. 3). Based on Geosecs data from the region, we estimate the bottom water $\delta^{13}C$ value to be about −0.58‰ (PDB), and the $\delta^{18}O$ value to be about −0.10‰ (SMOW). Using equations from Rathburn et al. (1996) and McCorkle et al. (1997), we calculate $\delta^{18}O$ (PDB) of calcite in equilibrium with water to be 2.35‰. Values of $\Delta\delta^{13}C$ of foraminifera from the Eel River margin (Fig. 3) fall within the range of reported values for the same or similar species in other areas (see McCorkle et al., 1997). The wide range of $\delta^{13}C$ values for living representatives of a given species from the same site (range up to 1.02‰, Table 4), however, is unusual (see Rathburn et al., 1996).

The range of values observed for living *U. peregrina* in this study is atypical for this well-known deep-sea species. For example, the extensive data set of McCorkle et al. (1997) shows the range of $\delta^{13}C$ values for living *U. peregrina* at non-seep sites off North Carolina and California to be typically about 0.35‰, with a maximum range of 0.52‰ at one site. The range of carbon isotopic values observed within a species in our study (e.g., for living *U. peregrina*, differences of up to 1.02‰ within a clam bed, and up to 0.46‰ between adjacent clam beds) probably results from different pore-water isotopic chemistries, but these were not measured (Table 4). A wide range of carbon isotope values of foraminiferal carbonate might be expected in methane seep subenvironments because of the probable spatial heterogeneity in seepage. The variability of subenvironments and the range of $\delta^{13}C$ values would be expected to increase with the activity of the seep.

Assuming that the isotope values obtained from fossil foraminifera reflect pore-water conditions, we interpret changes in values to indicate that methane seepage at these clam beds was different than it is today. It appears that at the time represented by the 18–22 cm horizon, at least one clam bed seep was much more active than today. At the time of the 10 cm horizon, the two clam beds were different, with one much more active than the other. Although we do not know how old the fossil specimens are, sedimentation rates of about 2.5 mm/yr for the area (Alexander and Simoneau, 1999) would imply that the specimens from 18 cm were deposited at least 70 years ago (and probably much earlier). Based on foraminiferal isotope values, neither clam bed appears very active today. This is consistent with available geochemical profiles of the area (Martin et al., 1999; J. Gieskes and C. Mahn, unpubl.).

6.4. Foraminifera as indicators of methane release

Presently, active cold seep environments are most easily identified based on the presence of living, symbiont-bearing clams or vestimentiferan (tube) worms (e.g., Sibuet and Olu, 1998). These aggregations appear to be located in areas of relatively vigorous fluid flux, and have been used to map the patterns of subsurface faults (Ogawa et al., 1999). Although more diffuse flow clearly occurs in surrounding sediments, epifauna do not typically aggregate in these sediments (Olu et al., 1996; Sibuet and Olu, 1998), suggesting that they require at least periods of relatively high seep activity. Living foraminifera (because of a probable shorter life span) would isotopically record only the most recent characteristics of the seep. The clam, *Calyptogena pacifica*, on the other hand, may have been initially exposed to high seep activity, but is known to persist at very low levels of seepage (Barry et al., 1997; Olu et al., 1997; Sibuet and Olu, 1998). This scenario accounts for the range of isotope values of living and fossil foraminifera, clam shells, and authigenic carbonate. Foraminiferal tests may be a better, and perhaps, more quantitative, short-term indicator of methane seepage than aggregates of clams. This is consistent with recent data from diffuse seepage areas where benthic foraminifera (unstained) from Monterey Bay had significantly more negative $\delta^{13}C$ signals nearer the surface than deeper in the core (Martin et al., 1999). Foraminifera from visibly venting seeps with quantified pore water chemistry should be examined to establish modern relationships between test isotopic signatures and methane environments. With additional, and more continuous stratigraphy, it might be possible to assess the activity and duration of the Eel River margin seep system more accurately. This type of information is crucial for inventories of global carbon, methane, and clathrate, and is useful for reconstructions of regional tectonic activity and pore-water fluid flow dynamics.

Some foraminifera species may be attracted to methane gas emission or hydrogen sulfide gas (Akimoto et al., 1994; Kitazato, 1996). However, dominant calcareous species associated with seeps, including those of the Eel River margin, are also found in other areas where no methane seepage occurs. Based on the limited data available from this study and previously published work, we suggest that seep taxa are attracted to the organic enrichment typical of seeps. Species that are adapted to the conditions of organic-rich environments (including reducing conditions) appear to be pre-adapted for life at seeps, or taxa originating at seeps may have been pre-adapted for life elsewhere. Available data suggest that cold seeps do not support endemic calcareous foraminifera (see also Akimoto et al., 1994; Kitazato, 1996; Sen Gupta et al., 1997).

Similar results were observed for nematodes (metazoan meiofauna) at hydrothermal vents (Vanreusel et al., 1997). Calcareous foraminifera apparently do not require elaborate morphological specializations (as do some of the epifaunal macrofauna) to exploit seep environments, or other localized organic-rich settings, such as whale carcasses, turbidites, and organic deposits from sewage (see Gooday and Rathburn, 1999). Trophic specialists might be present, but if so, food sources exploited at seeps must also occur elsewhere. It is possible, however, that seep foraminifera have symbionts (e.g., Bernhard, 1996), similar in function to those found in *Calyptogena*. Symbionts could enable some foraminifera to survive in reducing environments, and potentially affect foraminiferal stable isotopic signatures. Since the presence of symbionts has not been determined for many foraminiferal species, it is unknown whether seep taxa contain symbionts in either seep or non-seep environments.

6.5. Geologic applications of foraminiferal seep results

A partial release of methane from marine reservoirs could have a significant impact on the radiative properties of the atmosphere, and thereby influence climate and the carbon budget (MacDonald, 1990; Kvenvolden, 1988, 1993). Some workers have proposed a strong positive feedback mechanism in the climate system whereby warmer temperatures promote the release of more methane (Kvenvolden, 1988; Nisbet, 1990a,b). Pressure changes due to sea level changes may be more important for seafloor methane release than temperature changes, however, and negative feedback mechanisms within the climate system have also been suggested (e.g., Paull et al., 1991). Wefer et al. (1994) remarked that an inventory of seafloor methane flux in response to climate change would be helpful to decide the feedback sign. They proposed that benthic foraminiferal isotopes and methane-indicator species may provide the tools to make these assessments.

Significant, negative excursions in $\delta^{13}C$ values of fossil benthic foraminifera have recently been noted in Quaternary records, suggesting to some researchers that seafloor methane has influenced biogenic carbonate in these intervals. Benthic forami-

niferal isotopic records showed significant negative shifts in Quaternary sediments at ODP site 680, B, Leg 112 on the Peruvian margin ($-1.5‰$ to $-4‰$; Wefer et al., 1994), and ODP site 893 in the Santa Barbara Basin (up to $-5‰$; Kennett et al., 1996; Cannariato and Kennett, 1996). Kennett et al. (1996) suggested that rapid shifts in foraminiferal carbon isotopes from Quaternary sediments in the Santa Barbara Basin result from the influence of methane released by dissociated clathrates and are linked with climate change. The abrupt warming of bottom-waters and climate change near the Paleocene/Eocene Boundary may also have released methane from seafloor clathrates (Dickens et al., 1995, 1997). The large shift in ($-2.5‰$) in $\delta^{13}C$ values of Late Paleocene benthic foraminifera (e.g., Zachos et al., 1994) is global in extent, however, and results from large changes in the global carbon reservoir (Dickens et al., 1995, 1997). This global, bottom-water isotope effect is different from the effect observed by Wefer et al. (1994) and Kennett et al. (1996), who interpreted $\delta^{13}C$ excursions in foraminifera as the result of Quaternary methane seepage in continental margin sediment pore-waters.

Quaternary records from the Santa Barbara Basin and the Peruvian margin show isotopic differences between co-existing benthic foraminiferal species during inferred methane release events. Based on differences in isotopic signatures of Quaternary foraminifera off Peru, Wefer et al. (1994) speculated that *Nonionella auris* is an indicator species for the presence of methane, and may specialize in feeding on methane-oxidizing bacteria. Although trophic specialists and symbiont-bearing foraminifera may exist in seep habitats, in the few seeps examined for living foraminifera, we find no clear evidence for seep-indicating species. The possibility that temporal changes toward more negative foraminiferal $\delta^{13}C$ values could result from changes in organic matter oxidation from sulfate reduction was discounted by Wefer et al. (1994) because *N. auris* would have to live within anoxic, H_2S-containing sediments, and they found no relationship between organic content and $\delta^{13}C$. Although these assumptions made by Wefer et al. (1994) are probably correct, recent work (see Bernhard, 1996; Sen Gupta et al., 1997) suggests that some taxa are able to live, at least temporarily, in anoxic, sulfidic environments

within the sediments. Since no isotope data are available from living representatives of these taxa within anoxic seep sediments, it is unknown whether these taxa are able to grow and generate test carbonate in these environments. These data raise interesting questions about the microhabitat preferences of seep foraminifera and the reasons why different species have different carbon isotope values during an inferred methane event. Our data suggest that different seep species maintain isotopic differences (vital effects). It is as yet unknown how isotopic differences between species ('vital effects') are maintained in methane seep environments, and if they correspond to differences in food preferences or other ecological parameters. Continued work on living seep assemblages should yield additional information about possible indicator species, the role of vital effects, and the ecological tolerances and preferences of paleoceanographically important species.

Our results indicate that the isotopic signatures of benthic foraminifera show promise as indicators of methane release in the geologic record. Changes in the $\delta^{13}C$ value of ambient bottom waters and increases in organic matter flux can cause the carbon isotopic signatures of benthic foraminifera to become more negative (e.g., McCorkle et al., 1990). However, fossil isotopic values observed in this study and the study by Wefer et al. (1994) cannot be easily explained by changes in water mass or productivity. Large excursions (3 to 4+‰) in carbon isotopic signatures within the same species living in the same area over a relatively short amount of time are indicative of methane influence. Our ongoing investigations of the living and fossil foraminifera associated with active seeps will enable us to more quantitatively assess the relationship between foraminiferal isotopic signatures and methane seepage. Without additional modern analog data, fossil isotope-based interpretations of methane seepage must remain speculative.

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