

# Living benthic foraminifera in sediments influenced by gas hydrates at the Cascadia convergent margin, NE Pacific

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**ABSTRACT:** Living (Rose Bengal stained) foraminifera in gas-hydrate-influenced sediments at the Cascadia convergent margin were investigated. Foraminiferal assemblages from the southern Hydrate Ridge and neighboring basins were compared in terms of abundances, vertical distribution, diversity, and species composition. At Hydrate Ridge, the presence of shallow gas hydrates and increased porewater sulfide concentrations was indicated by extensive bacterial mats of *Beggiatoa* sp. and clam beds of the bivalve mollusk *Calyptogena* sp., generating different biological zones. Living foraminifera were found in all biological zones, in sediment layers down to 5 cm. They showed highly variable densities within all zones. The average abundance of benthic foraminifera at Hydrate Ridge differs from neighboring basins. Average species diversities are comparable between biological zones, while the average number of species increases from bacterial mats to clam fields and surrounding sediments. Foraminifera can be characterized by 5 principal component communities which explain 97.3% of the variance of the live assemblages at the southern Hydrate Ridge and neighboring basins. At Hydrate Ridge, 2 foraminiferal zones can be distinguished: (1) an *Uvigerina peregrina* community which characterizes sediments covered with bacterial mats and clam fields; (2) a *Spiroplectammina biformis* community in the surrounding non-seep sediments. Foraminiferal assemblages in the neighboring Western and Eastern Basin differ from the Hydrate Ridge stations.

**KEY WORDS:** Benthic foraminifera · Methane hydrate · Gas seeps · Hydrate Ridge · Cascadia subduction zone

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## INTRODUCTION

Gas hydrates are solid ice-like structures in which low molecular weight compounds (mainly methane) are enclosed in a lattice of water molecules (Sloan 1990). Marine gas hydrates typically occur at continental margins buried several meters deep in the sediment. But at a few localities, e.g. the Hydrate Ridge in the Cascadia convergent margin off Oregon (Suess et al. 2001) or the northern Gulf of Mexico (MacDonald et al. 1994), they can be found in near-surface sediments. From these surface gas hydrates, and probably from deeper sediment layers, methane is transported towards the sediment surface by diffusion and advection (Luff & Wallmann 2003). The exposure of gas hydrates

near the sediment surface, and venting processes in these areas, provide an enormous nutrient and energy pool for benthic life, leading to the formation of a unique ecosystem where ecological niches and a biological zoning of characteristic communities are developed (Sahling et al. 2002). Dissolved methane in gas-hydrate-bearing sediments can be used in bacterial aerobic and anaerobic methane oxidation, which, coupled with sulfate reduction, results in the formation of sulfide (Treude et al. 2003). Differences in sulfide concentrations and fluxes cause the zonation of chemoautotrophic communities (Sahling et al. 2002, Treude et al. 2003). At Hydrate Ridge, high sulfide concentrations and sulfide fluxes of up to 63 mmol m<sup>-2</sup> d<sup>-1</sup> can be found in methane-enriched sediments (Sahling et al.

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2002). Bacterial mats of the filamentous sulfide-oxidizing bacteria *Beggiatoa* cover gas hydrate and sulfide-rich surface sediments (Sahling et al. 2002). These chemoautotrophic bacterial mats can be several meters in diameter. At lower sulfide fluxes of  $18 \text{ mmol m}^{-2} \text{ d}^{-1}$ , the outer rims of bacterial mats are populated by fields of vesicomid clams of the genus *Calyplogena*, which at further decreasing sulfide fluxes are, in turn, surrounded by deeper living solemyid bivalves (*Acharax* sp.) (Sahling et al. 2002). These clam fields are enclosed by sediments without any seep community (Sahling et al. 2002), which we call non-seep sediments. We called them non-seep sediments. No dissolved sulfide was recorded in these sediments (D. Rickert unpubl. data). *Calyplogena* and *Acharax* species contain chemoautotrophic sulfide oxidizing bacterial symbionts. Additionally, heterotrophic endemic seep macrofauna can be observed in the different zones (Sahling et al. 2002). Comparable characteristic benthic surface communities are described from cold seeps, hydrothermal vents, and other sulfide-rich reduced sediment environments (e.g. Olu et al. 1997, Levin et al. 2000).

Much work has been done during the last few years to investigate the biogeochemistry as well as microbial and macrofaunal community structures of gas-hydrate-influenced sediments. However, information about meiofaunal organisms is rare. Sommer et al. (2003) found new species and large numbers of rotifers in gas-hydrate-bearing sediments at the southern crest of Hydrate Ridge. One of the most abundant and diverse meiofaunal classes in marine sediments is the group of benthic foraminifera (Protista: Granuloreticulosa). These single-celled organisms can exist in all marine environments, including deep-sea areas and extreme ecosystems. Species composition, abundance, and distributional pattern of living benthic foraminifera mainly depend on environmental conditions, such as food supply and oxygen distribution (e.g. Jorissen et al. 1995). Although foraminifera are generally aerobes, certain species can inhabit sulfidic, oxygen-depleted sediments (Bernhard & Sen Gupta 1999). Living (Rose Bengal stained) foraminifera were observed at methane discharge and sulfide-enriched seep sites (Montagna et al. 1989, Akimoto et al. 1994, Sen Gupta & Aharon 1994, Sen Gupta et al. 1997, Rathburn et al. 2000, Bernhard et al. 2001, Rathburn et al. 2003), including, principally, the taxa *Uvigerina*, *Bolivina*, *Epistominella* and *Nonionella*, which seem to be adapted to high organic, low oxygen, and reducing environments (Hill et al. 2003). Torres et al. (2003) and Hill et al. (2004) report about living benthic foraminifera at the Hydrate Ridge. Both studies investigated the carbon isotopic composition of the shells of selected living and dead planktic and benthic species to document a possible influence of anaerobic methane

oxidation and  $^{13}\text{C}$ -depleted dissolved inorganic carbon on the  $\delta^{13}\text{C}$  of foraminiferal shells.

In this study, we present the record of living (Rose Bengal stained) foraminiferal assemblages found in different biological zones (bacterial mats, clam fields, surrounding non-seep sediments) at the Hydrate Ridge in the Cascadia convergent margin off Oregon. Additionally, sediment samples from deeper sites west and east of the Hydrate Ridge are included in our investigations. We compare foraminiferal densities, assemblages and distribution patterns between these different ecological habitats and zones to determine species-specific habitat demands and possible biological zonation of foraminifera.

## MATERIALS AND METHODS

**Study area and sample processing.** Sediment samples were collected at the southern Hydrate Ridge during the RV 'Sonne' cruise So 143 in August 1999. In this area, methane hydrate exposures, vent communities and authigenic carbonates were discovered (Sahling et al. 2002, Torres et al. 2002). Cores from different biological zones (bacterial mats, clam fields, surrounding non-seep sediments) were taken with a video-controlled multicorer (TV-MUC) that allowed specific sampling of a certain zone. Non-seep sediments were only 100 to 600 m away from clam fields and bacterial mats. They were characterized by the lack of any seep community as well as differences in the macrofauna and biomass (Sahling et al. 2002). No dissolved sulfide was recorded in the upper 20 cm of these sediments (D. Rickert unpubl. data), and no increased autotrophic production was observed (Sommer et al. 2002). Additional sediments were sampled in the Western and Eastern Basin that abut on Hydrate Ridge 10 to 15 km distance from the seepage sites.

For each sampling site 1 core was investigated, except for the bacterial mat sediment of Stns 187-1 and 187-4, which were pooled together to enlarge the available sediment amount. Sampling sites are shown in Fig. 1a–c and listed in Table 1. TV-MUC cores were subsampled with cut off syringes of 2.1 cm diameter. Surface area of the subcores was about  $3.5 \text{ cm}^2$ . Subsamples were sectioned at 1 cm intervals down to 5 cm sediment depth. For faunal analysis at each station, 2 subsamples were combined and studied, except for Stns 105 and 179, where only 1 subsample was available. Each layer was preserved separately with 4 to 10% formalin (buffered with borax, pH 8.2) and stored. Rose Bengal (1 g Rose Bengal per 1 l formalin) was added 14 d before starting faunal analysis to distinguish living (containing red stained protoplasm) from dead foraminifera. The sediment was washed through a  $30 \mu\text{m}$  mesh screen. The

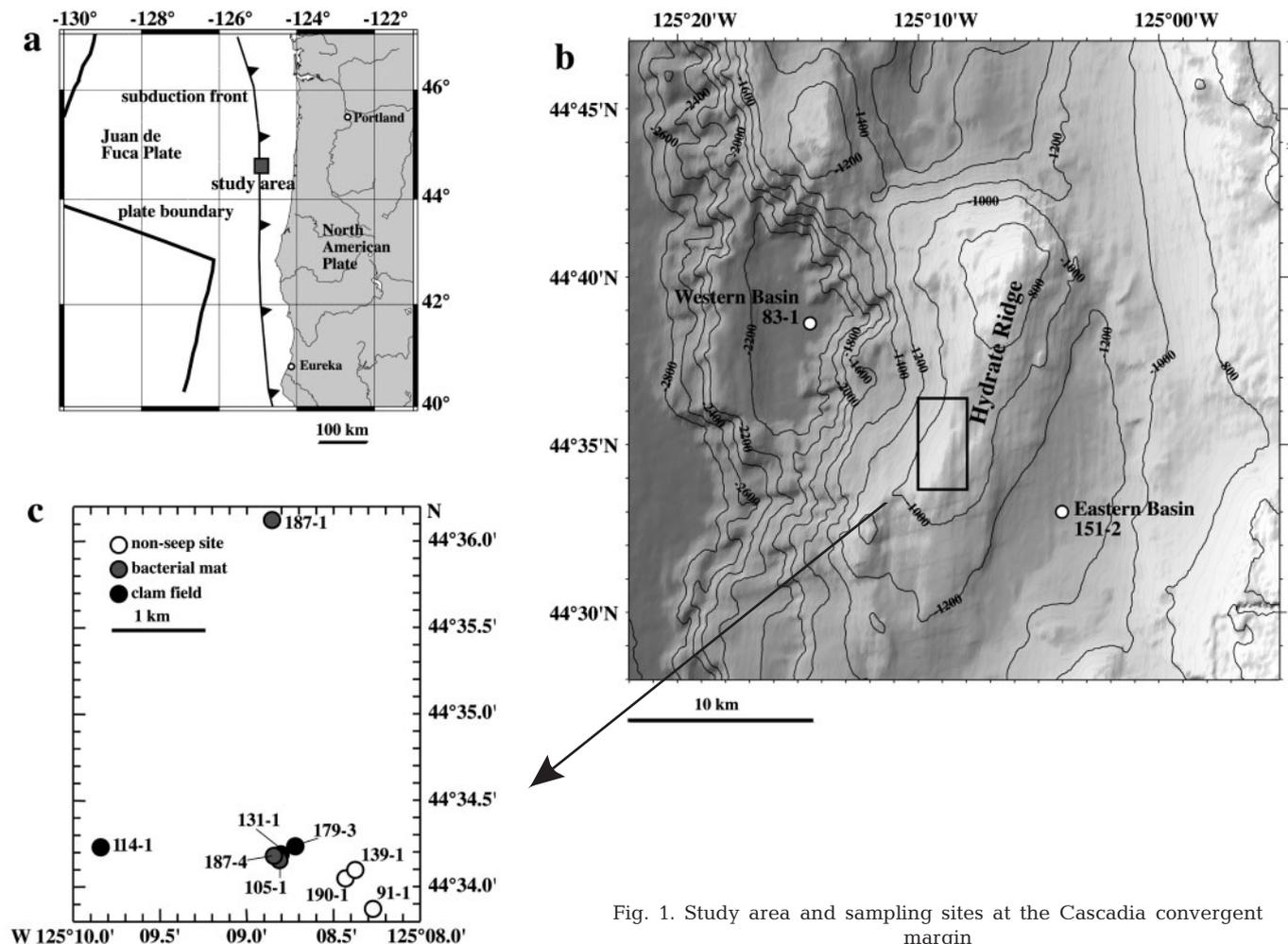


Fig. 1. Study area and sampling sites at the Cascadia convergent margin

residue was dried and fractionated into 3 different size classes: 30–63  $\mu\text{m}$ , 63–125  $\mu\text{m}$ , and >125  $\mu\text{m}$ . All fractions were weighed for particle size analysis. Sediment samples of the 2 larger fractions were investigated for living foraminifera. To minimize wrongly identified living foraminifera, fractions were wetted with water during picking and only foraminifera containing well-stained dark red protoplasm were counted. Sampled volumes differ between sampling sites because of the inconsistent number of subsamples (1 to 2) used for the analysis. For comparison, number of foraminifera of each station and each sediment depth were calculated to a volume of 10  $\text{cm}^3$ .

This standard method using Rose Bengal to investigate foraminiferal populations has its limitations, because cytoplasm degradation time and the persistence of staining in dead tissue is unknown, especially in low oxygenated sediments (Bernhard 1988). However, the detection of seasonal patterns of

foraminifera, even in oxygen-poor settings (e.g. Gooday & Rathburn 1999) and the high percentage of correct identifications when done accurately, suggest the fast decay of protoplasm in deep-sea environments. A first report about living (Rose Bengal stained) benthic foraminifera at the Hydrate Ridge was given in Torres et al. 2003. This staining was used for other oxygen-depleted methane seeps with high sulfide concentra-

Table 1. Dates and sampling stations at the Cascadia convergent margin

Stn	Coordinates		Depth (m)	Date (Aug 1999)	Biological zone
	Latitude	Longitude			
83-1	44° 38.500' N	125° 14.500' W	2304	2	Western Basin
187-1	44° 36.160' N	125° 08.860' W	786	19	Bacterial mats
187-4	44° 34.190' N	125° 08.820' W	785	19	Bacterial mats
105-1	44° 34.140' N	125° 08.810' W	787	6	Bacterial mats
114-1	44° 34.210' N	125° 09.850' W	786	7	Clam fields
179-3	44° 34.210' N	125° 08.740' W	786	17	Clam fields
190-1	44° 34.050' N	125° 08.410' W	824	20	Non-seep sediment
139-1	44° 34.100' N	125° 08.380' W	826	12	Non-seep sediment
91-1	44° 33.880' N	125° 08.290' W	852	4	Non-seep sediment
151-2	44° 33.000' N	125° 04.000' W	1285	14	Eastern Basin

tions (Montagna et al. 1989, Akimoto et al. 1994, Sen Gupta & Aharon 1994, Sen Gupta et al. 1997, Rathburn et al. 2000). Foraminifera originating from a cold seep site were tested by Bernhard et al. (2001) with different independent vital methods (ATP concentration, cellular ultrastructure) and conventional Rose Bengal staining. We tested isolated foraminifera from bacterial mat sediments during a new cruise to Hydrate Ridge in July 2002 for their enzymatic hydrolyses of cytoplasmic esterases, comparable to Geslin et al. (2004) and references therein, and found metabolic activity (Pfannkuche et al. 2002). Both investigations indicate that certain species can inhabit seep areas, and also that the use of Rose Bengal staining is valid.

**Statistical analysis.** For all foraminiferal community analyses, the abundance data for each centimeter of sediment were calculated as ind. per 10 cm<sup>3</sup>. Different diversity indices were calculated: Fisher  $\alpha$  Index (Fisher et al. 1943) and Shannon-Wiener Index H(S) (Shannon & Weaver 1963). The Shannon-Wiener Index H(S) accounts for the distribution of species within the sample, the Fisher  $\alpha$  Index not. This can cause different trends between the indices, especially when one or a few species dominate the total fauna very strongly. Equitability ( $e$ ) was calculated as  $e^{H(S)}/S$ , where  $S$  was the number of observed species (species richness) (Buzas & Gibson 1969). When species are totally equally distributed, the ratio reaches its maximum value of 1. Rank 1 dominance (R1D) as percentage of most abundant species (Magurran 1988) was evaluated. Q-mode principal component analysis was carried out with SYSTAT 5.2.1. This analysis compares and identifies samples (objects), which contain mainly the same species (possibly correlated variables) in similar proportions, and pools these samples in groups. Therefore, high numbers of species (variables) get transformed and reduced into a small amount of uncorrelated variables or assemblages (principal components). Only species constituting more than 0.5% in any one of the samples were used. Factor loadings of 0.5 for the Q-mode principal component analysis were considered as significant (Backhaus et al. 1989).

## RESULTS

For particle size comparison between different stations, total sediment size distribution is given in Fig. 2. In most of the examined cores from Hydrate Ridge, particles >125  $\mu\text{m}$  made up the largest part of the investigated sediment (>30  $\mu\text{m}$ ), and dominated markedly in the non-seep sediments. Single chunks of carbonate were found at bacterial mats and clam field sediments, while very coarse olive green particles are the main constituent of the surrounding non-seep sediments.

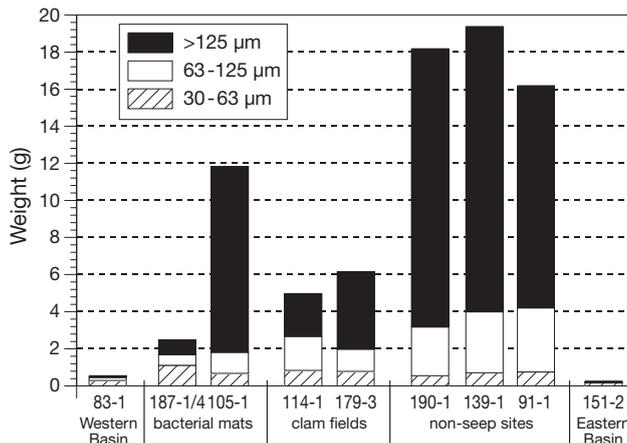


Fig. 2. Grain size distribution of the upper 5 cm of sediment at different stations

Basin stations recorded only small masses of coarse materials in the sediment. At the Western Basin, we found high densities of fecal pellets in the silty sediment. Surface sediment of the Eastern Basin contained sticky high amounts of organic material, which were red colored because of the addition of Rose Bengal to stain the living foraminifera.

Living foraminifera were found in all biological zones (bacterial mats, clam fields, non-seep sediments). Standing stocks for the first 5 cm of sediment are shown in Fig. 3. High variability was observed in all zones. Average density of benthic foraminifera was slightly lower at non-seep sites (226 ind. 50 cm<sup>-3</sup>), compared to bacterial mats and clam field sediments. Bacterial mats and clam field sediments showed similar mean abundances, between 290 and 296 ind. 50 cm<sup>-3</sup>. In the Western Basin, diminished numbers of foraminifera were recorded (131 ind. 50 cm<sup>-3</sup>). Maximum abundances were counted at the Eastern Basin

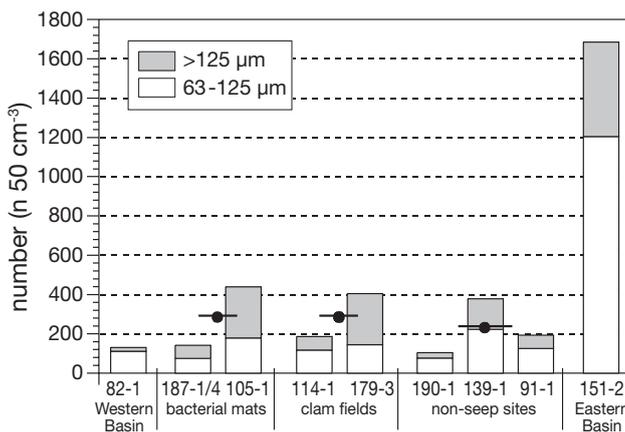


Fig. 3. Living (stained) foraminiferal densities in the upper 5 cm of sediment at different stations (horizontal bars indicate means for each biological zone)

(1685 ind.  $50\text{cm}^{-3}$ ), where large amounts of aggregated organic matter were observed. Many foraminifera were found embedded within this sticky material. For many stations, foraminifera were more abundant in the 63 to 125  $\mu\text{m}$  fraction than in the  $>125\ \mu\text{m}$  fraction.

A comparison of the vertical distribution of benthic foraminifera (Fig. 4) shows that living individuals were found in sediment layers down to 5 cm depth. At non-seep Stn 139-1, sediment was tested for living specimens in deeper layers, but no well-stained foraminifera were found between 5 and 7 cm. Except for the Western Basin, all stations recorded highest foraminiferal abundances in the upper first centimeter and decreasing numbers with increasing sediment depth. The concentration of stained individuals in the top 1 cm at the Eastern Basin site (Stn 151-2) is particularly notable.

Species diversity (H(S), Fisher  $\alpha$ ), the number of species (S), R1D, and the equitability (e) of different stations are given in Table 2. Important benthic foraminifera of the Cascadia convergent margin are shown in Figs. 5 & 6. The highest diversity was recognized at the Western Basin. Sediment samples of the southern Hydrate Ridge possessed lower but variable species diversity. Average values for each biological zone were comparable (1.9) using H(S), but slightly increasing from bacterial mats (3.25) to clam fields (4.11) and non-seep sediments (5.05) for Fisher  $\alpha$ . The average number of species in Hydrate Ridge sediments increased from bacterial mats (13.5 species) to clam field (17.5 species) and surrounding non-seep sediments (19 species). The Eastern Basin recorded low to lowest diversity, but maximum species numbers. R1D was highest for this station, and *Stainforthia apertura* was strongly dominant forming 74 % of the fauna. Lower R1Ds were observed in Hydrate Ridge sediments (26 to 60 %) and in the Western Basin (27 %). Equitability followed a similar gradient to H(S), with the highest value at the Western Basin, slightly lower but variable values at the

Table 2. Diversity indices (H(S), Fisher  $\alpha$ ), number of observed species (S), Rank 1 dominance (R1D) in percentage, and equitability (e) calculated for the different stations

Biological zone	Stn	H(S)	Fisher $\alpha$	S	R1D (%)	e
Western Basin	83-1	2.58	8.61	24	27	0.55
Bacterial mats	187-1/4	1.89	4.23	15	43	0.44
Bacterial mats	105-1	1.85	2.27	12	46	0.53
Clam fields	114-1	2.15	4.91	18	31	0.48
Clam fields	179-3	1.65	3.32	16	60	0.33
Non-seep sediment	190-1	1.88	4.78	16	50	0.41
Non-seep sediment	139-1	1.71	4.79	21	44	0.26
Non-seep sediment	91-1	2.25	5.59	20	26	0.47
Eastern Basin	151-2	1.21	4.56	27	74	0.12

different Hydrate Ridge sediments, and the lowest value at the Eastern Basin.

A principal component analysis was performed to compare faunal assemblages at the different stations. Foraminifera were characterized by 5 principal component communities, which explained 97.30 % of the variance of the live assemblages. Species with a score higher than 6.0 were considered to be dominant species, and those with scores between 2.4 and 5.9 as associated species. A summary (percentage of the variance, species composition, and scores) of the 5 principal component communities (= PCCs) is given in Table 3. Dominant communities are demonstrated in Fig. 7. For PCC 4, factor loadings were always lower than 0.5 and therefore not significant and not presented in Fig. 7. The Hydrate Ridge stations were mainly characterized by a community that was dominated by *Uvigerina peregrina*, associated by *Epi-stominella exigua*. At the non-seep sediments, an additional *Spiroplectammia* community can be described. This *Spiroplectammia* community is also found at the Western Basin, additionally with a community composed of *Recurvoides contortus*, *Cassidelina* sp., and ?*Spiroplectammia biformis*. The Eastern Basin was influenced by a very different faunal community, dominated by *Stainforthia apertura*.

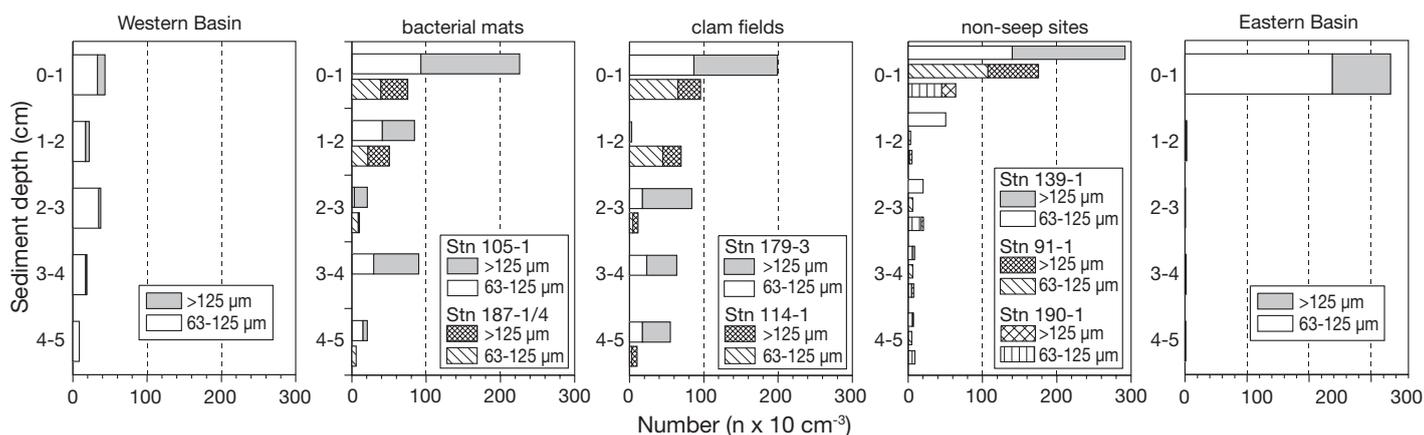


Fig. 4. Vertical distribution pattern of living (stained) benthic foraminifera

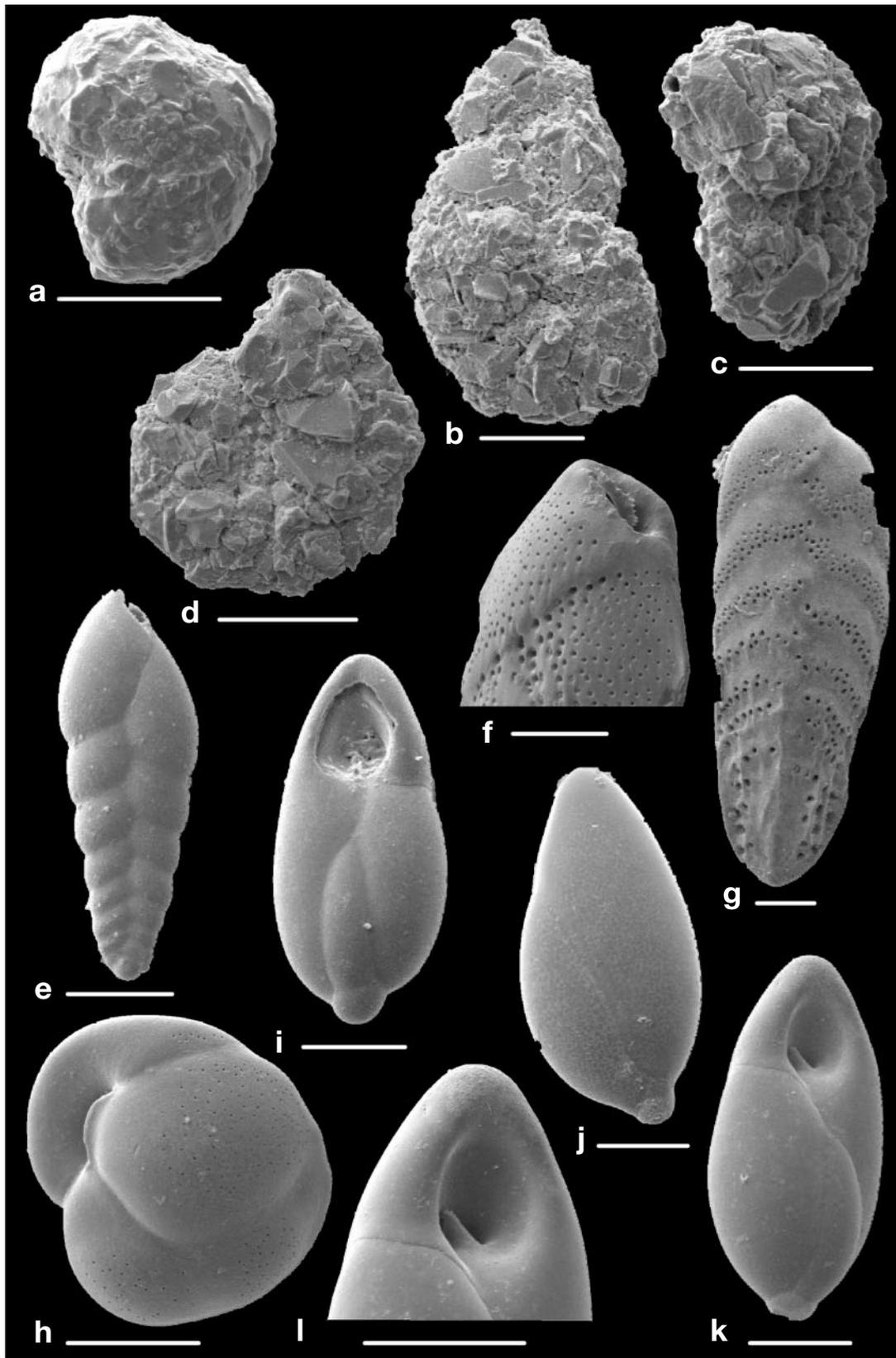


Fig. 5. Scanning electronic micrographs of important benthic foraminifera of the Cascadia convergent margin (scale bars = 50 µm). (a) *Recurvoides contortus*, (b–d) *?Spiroplectammina biformis*, (e) *Bolivina pacifica*, (f,g) *Bolivina spissa*, (h) *Cassidulina delicata*, (i–l) *Stainforthia apertura*

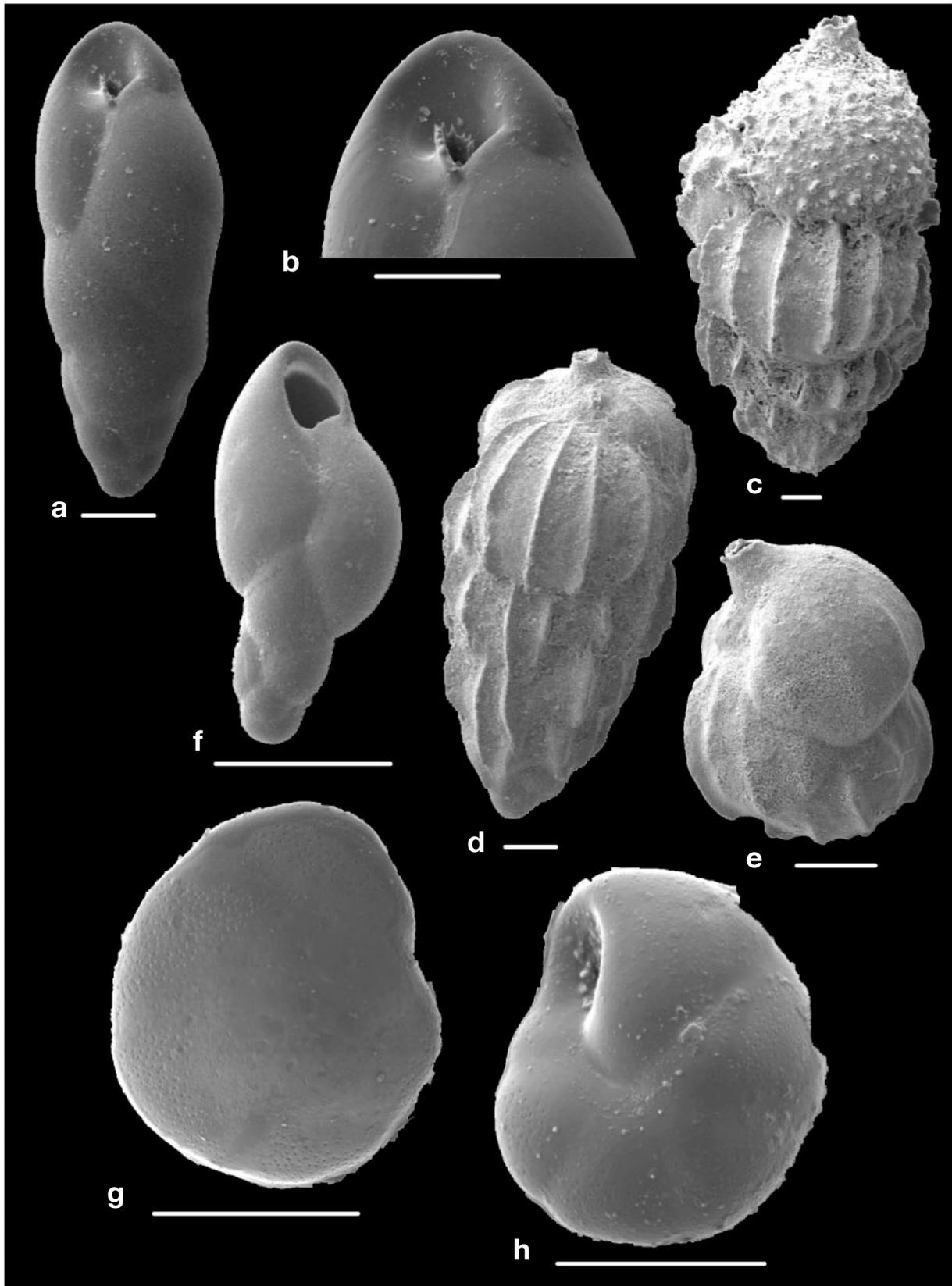


Fig. 6. Scanning electronic micrographs of important benthic foraminifera of the Cascadia convergent margin (scale bars = 50  $\mu$ m). (a,b) *Buliminella tenuata*, (c–e) *Uvigerina peregrina*, (f) *Cassidelina* sp., (g,h) *Epistominella exigua*

Table 3. Principal component communities of living (stained) benthic foraminifera

PCC	Variance (%)	Dominant species	Score	Associated species	Score
1	51.09	<i>Uvigerina peregrina</i>	6.56	<i>Epistominella exigua</i>	2.46
2	23.80	? <i>Spiroplectammina biformis</i>	6.62	–	–
3	11.83	<i>Stainforthia apertura</i>	–7.21	–	–
4	3.52	<i>Epistominella exigua</i>	–6.23	–	–
5	7.06	–	–	<i>Recurvoides contortus</i>	3.83
				<i>Cassidelina</i> sp.	2.57
				? <i>Spiroplectammina biformis</i>	2.44

## DISCUSSION

### Environmental factors

Environmental factors like temperature, water depth, and salinity were constant between stations (except Western and Eastern Basin), but showed considerable variability with respect to biogeochemistry, e.g. fluxes and turnover of methane, oxygen and sulfide (cf. Boetius & Suess 2004, Luff & Wallmann 2003, S. Sommer et al. unpubl.), as well as benthic biota (Knittel et al. 2003, Sahling et al. 2002, Sommer et al. 2002, Treude et al. 2003). A comparison of the sediment particle size distribution (Fig. 2) shows the lack of similarity between the stations, with more coarse sediments at the southern Hydrate Ridge, compared to the Western and Eastern Basin. We were able to distinguish between bacterial mats and clam fields, containing single chunks of authigenic carbonates, and surrounding non-seep sites with mainly coarse particles. The variability of the sediments was also described by Sahling et al. (2002). However, the different sediment characteristics did not correlate with biological zones. This is

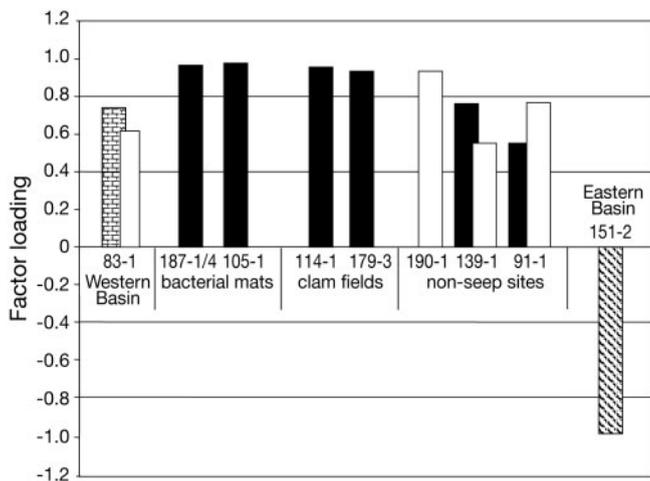


Fig. 7. Principal component communities of living (stained) foraminifera dominating the different stations (■ PCC 1, □ PCC 2, ▒ PCC 3, ▨ PCC 5). For PCC 4, factor loadings were not significant and so are not presented

related to differences in the sulfide flux. Substrate types can influence foraminiferal assemblages and the spread of single species can be correlated with specific sediment grain size. This can be observed for example for attached epifaunal surface-dwelling species and coarsely agglutinated foraminifera. But in our investigations, most species forming characteristic communities in the different biological zones do not belong to these taxa and appear not to be influenced by grain size differences.

### Foraminiferal densities

We found living foraminifera in all investigated core samples and studied the distribution of these species. Foraminiferal densities at Hydrate Ridge showed high variability within and between biological zones such as bacterial mats, clam fields and non-seep sites (between 105 and 439 ind. 50 cm<sup>-3</sup>, Fig. 3). The non-seep Stn MC 190-1 was especially striking because of low foraminiferal abundances. No calcareous specimen was found there (observed allogromid spiral forms were maybe rotaliids that lost their calcareous tests due to decalcification processes in the sediment; see Appendix 6, available at [www.int-res.com/articles/suppl/m304p077\\_app.pdf](http://www.int-res.com/articles/suppl/m304p077_app.pdf)). This patchy distribution is likely related to small-scale differences in environmental conditions such as interfacial fluxes of oxygen, methane, sulfate and sulfide or turnover rate of anaerobic methane oxidation (Treude et al. 2003). Seepage can be very diffuse and some influence of methane in non-seep sediments, and therefore an influence on living benthic foraminifera, cannot be excluded. The small amount of replicates for different zones and no replicates for single stations in such a variable region makes it very difficult to interpret data and shows the limitation of our results. Mean standing stocks between mats, clam fields, and surrounding non-seep sediments indicate slightly lower abundances at non-seep sites, compared with gas-hydrate-influenced sediments. But these differences are not significant and show only small-scale variability. A comparison of

average densities of benthic foraminifera at Hydrate Ridge with sediments from the neighboring basins shows more distinctive differences (with higher abundances at the Ridge compared to the Western Basin, and lower densities at the Ridge compared to the Eastern Basin) and seems to be more reliable.

Despite this variability, foraminiferal numbers at Hydrate Ridge are within the range of other deep-sea areas after strong phytodetritus deposits, such as in the North East Atlantic or Sagami Bay off Japan (Gooday 1986, Ohga & Kitazato 1997) during spring time. The investigations of Torres et al. (2003) concentrated on the isotopic compositions of selected foraminiferal species at Hydrate Ridge, but they additionally showed their recorded downcore distribution of living *Uvigerina peregrina* and total foraminiferal cell counts (>125  $\mu\text{m}$ ). They found elevated standing stocks of living foraminifera at sites with increased methane concentrations (Torres et al. 2003). When we compare their records with our foraminiferal fractions of the same size, we found slightly higher abundances in all biological zones in our study. But Hydrate Ridge foraminiferal standing stocks were lower than at cold-seep sites in Monterey Bay off Central California (Bernhard et al. 2001, Rathburn et al. 2003).

### Influence of organic material

In Monterey Bay cold seep sites, average abundances of living benthic foraminifera were reduced in comparison to non-seep sediments. At other seeps, foraminiferal populations increased near active fluid discharge sites (Rathburn et al. 2000). At Hydrate Ridge, we observed slightly but not significant higher average standing stocks at sites with increased sulfide concentrations compared to surrounding non-seep sediments. Similar results were recorded by Torres et al. (2003).

Elevated foraminiferal densities indicate adequate food supply. Biomass and abundance of benthic foraminifera are strongly influenced by surface ocean productivity and organic carbon flux to the sea bed (Altenbach et al. 1999). In laboratory experiments, the addition of organic material resulted in a rise of biomass, a higher number of food vacuoles (Altenbach 1992, Linke et al. 1995) and increased foraminiferal densities (Heinz et al. 2001, 2002). Although the effect of gas hydrates on benthic carbon flow is unknown at Hydrate Ridge, organic carbon might enter the benthic food web by different mechanisms. Primary production at the ocean surface leads to vertical organic carbon fluxes from the photic zone to the seafloor and currents cause lateral transport of organic material. In gas-hydrate-containing and cold-seep sediments, the

energy bound in methane is transferred to the higher biota such as meiofauna and macrofauna predominantly through bacterial aerobic and anaerobic oxidation of methane, which is coupled with the reduction of sulfate. Sulfide, being a major metabolite of the anaerobic methane oxidation, then becomes available to chemosynthetic endosymbiotic and free-living bacteria, building up biomass that potentially will be consumed by other heterotrophic organisms. Estimates of the autotrophic production of particulate organic carbon (POC) at Hydrate Ridge are about 5 to 17% of the bulk POC (defined as the sum of allochthonous and autochthonous POC influx) for non-seep sites, 35 to 68% for bacterial mats and 63 to 87% for clam field (Sommer et al. 2002).

It is difficult to assess the lateral input of organic material in this area because the topography of the Ridge will influence lateral current systems. But the vertical POC fluxes scarcely differ between sites at southern Hydrate Ridge (Sommer et al. 2002). We assume that the influence of transported organic material will be more or less comparable between our sampling sites at the Ridge. Non-seep sites were only 100 to 600 m away from clam fields and bacterial mats. Transported and autochthonous POC will lead to elevated amounts of available food at these stations, especially at the bacterial mats and clam fields. This would explain slightly higher foraminiferal densities at gas-hydrate-influenced sites at Hydrate Ridge (mats and clam fields) compared to non-seep sites and especially compared to the Western Basin, where low numbers of living benthic foraminifera were recorded.

Sommer et al. (2002) also described concentrations of chlorophyll *a* and phaeopigments (to quantify POC input associated with lower phytodetritus), which were lower at bacterial mats and clam fields. They explained this by an enhanced microbial degradation of phytodetritus at these sites. Other meiofaunal groups showed high densities in gas hydrate influenced sediments. Significantly higher biomass of small-sized benthic biota has been described in clam fields, as compared to non-seep sites (Sommer et al. 2002). Rotifers, which have been scarcely reported in marine sediments, were present in large numbers at Hydrate Ridge (Sommer et al. 2003). The highest densities were found in clam fields, followed by bacterial mats, the Western Basin and the non-seep sediments at Hydrate Ridge. The lowest densities were found in the Eastern Basin.

In contrast to these data, we found highest foraminiferal abundances at the Eastern Basin station and high amounts of sticky, red-stained organic particles, which is in accordance to highest chlorophyll *a* and phaeopigment concentrations at this site (Sommer et al. 2002). We assume that this material originated from aggregates of rapidly sinking phytodetritus. The

Eastern Basin may accumulate high amounts of fresh organic material, which is transported from the continental slope. Additionally, gas hydrates and bacterial mats were detected in this basin, and the influence of autochthonous organic carbon can not be excluded (Pfannkuche et al. 2002). Concerning our sampling site (Stn 151-2) in the Eastern Basin, no seep community and no sulfide was recorded there (Sahling et al. 2002). High food availability will provide good living conditions for foraminifera and strongly enhance reproduction of opportunistic foraminifera species. It is well known that in deep-sea areas, some species can react very quickly to phytodetritus arriving on the sediment surface (e.g. Gooday & Hughes 2002, Witte et al. 2003, Nomaki et al. 2005). Many foraminifera were found fixed to the sticky material at this station, which may adulterate distribution within size fractions, because smaller individuals adhering to big organic particles were recorded in the coarser fraction (>125  $\mu\text{m}$ ). Similar effects were observed by Gooday & Hughes (2002) with small species embedded in phytodetritus aggregates. But even with this adulteration, the smaller size fraction 63 to 125  $\mu\text{m}$  dominated the sediment of our station in the Eastern Basin, indicating reproduction processes and/or the dominance of small species.

#### Vertical distribution in the sediment

Vertical distribution patterns of benthic foraminifera at the different stations were similar (Fig. 4). Living individuals were found down to 5 cm sediment depth, with a maximum in surface layers. Gas-hydrate-bearing sediments were difficult to sample and to slice in exact sediment layers because of shells and shell debris. Additionally, outgassing methane may have changed the vertical distribution to some extent. However, we are convinced that most stained foraminifera found in deeper layers were approximately in their original positions within the sediment. At Hydrate Ridge, especially at the gas-hydrate-bearing sites, deeper sediment horizons are anoxic and show high concentrations of sulfide (Sahling et al. 2002, Luff & Wallman 2003). Bacterial mats had a thickness of several millimeters down to 2 cm. Directly below these mats, sulfidic, black-colored anoxic sediment was observed. At clam fields, increased sulfide concentrations and anoxic conditions were found deeper in the sediment. Both faunal zones were inhabited by foraminifera that were able to survive in these anoxic and sulfidic environments. Generally, foraminifera are aerobically living organisms for which sulfide is highly toxic by blocking the cytochrome c oxidase of their respiratory chain (Baggarino 1992). However, certain

foraminiferal species are able to tolerate oxygen-poor and anoxic conditions and can inhabit these environments, at least for a few weeks to months (Bernhard & Sen Gupta 1999). The physiological mechanisms that enable these species to survive anoxia or even sulfidic conditions are not yet identified (cf. Fenchel & Finlay 1995). Recently, potential bacterial endosymbionts were described in the benthic foraminifer *Virgulinitella fragilis*, living under microaerophilic, sulfidic conditions (Bernhard 2003). But in contrast to these observations, Bernhard et al. (2001) did not find prokaryotic symbionts in investigated foraminifera from cold-seep sites (clam fields with bacterial mats and clam flats) in Monterey Bay.

Several species, mainly *Uvigerina peregrina*, normally living near the sediment surface were observed in large numbers down to 5 cm in the sediment at some gas-hydrate influenced stations, (especially Stns 179-3 and 105-1; Appendices 1 to 9, available at [www.int-res.com/articles/suppl/m304p077\\_app.pdf](http://www.int-res.com/articles/suppl/m304p077_app.pdf)). Higher densities of *U. peregrina* caused the dominance of the larger size fraction at Stns 105-1 and 179-3 (*U. peregrina* is a relatively big species and most individuals will be found in the size class >125  $\mu\text{m}$ ) (Fig. 3). Greater depths and depth ranges of some seep species, such as *U. peregrina*, were reported for foraminifera at cold seeps in Monterey Bay (Rathburn et al. 2003). The depth preference of the *Uvigerina* species is probably more dependent on the availability of fresh organic food material than on available oxygen (Geslin et al. 2004). We assume that adequate food is present for *U. peregrina* in deeper sediments of these gas-hydrate influenced stations, maybe in form of bacteria or other autotrophically produced organic carbon. Another possibility would be the downward transport of settled phytodetritus due to sediment turbulence, caused by gas fluxes and macrofaunal activities. Sommer et al. (2002) found a distinct surface peak of chlorophyll a and pheopigments, followed by an exponential decrease, at Stn 187-1/4 (bacterial mats). They concluded that bioturbation was strongly reduced there and that degradation of chlorophyll a is faster than its influx. We found nearly all *U. peregrina* at this station in the upper 2 cm (Appendix 2). In contrast to that, chlorophyll a was distributed deeper into the sediment at Stn 179-3 (clam field), with declining levels below sediment depths of 5 cm, while pheopigment concentration declined gradually with depth (Sommer et al. 2002). *U. peregrina* was recorded here in large numbers down to 5 cm sediment (Appendix 5) (additional vertical profiles of chlorophyll a and pheopigments of the non-seep Stn MC 190-1 were published in Sommer et al. 2002, but no calcareous specimen and therefore no *U. peregrina* was found at this station; Appendix 6).

In comparison to foraminifera, rotifers showed an extremely variable vertical distribution in clam field and bacterial mat sediments (Sommer et al. 2003). In surrounding non-seep sediments, they decreased gradually with increasing sediment depth.

### Faunal assemblages at Hydrate Ridge

At the bacterial mats, clam fields and surrounding sites, species diversity was variable but in the same range (Table 2). It was lower than at the Western Basin. A reduced diversity at the southern Hydrate Ridge was expected because low oxygen availability and high sulfide fluxes cause extreme conditions and only a few highly adapted species are able to inhabit such environments. Both, bacterial mats and clam fields at the southern Hydrate Ridge were strongly influenced by a community that was dominated by *Uvigerina peregrina* associated with *Epistominella exigua*. This community explained 51% of the variance of the investigated live assemblages in our study. *U. peregrina* was the most dominant species forming up to 60% of the total living fauna at Hydrate Ridge. This is in agreement with investigations of Torres et al. (2003), who stated that *U. peregrina* represented 50 to 90% of the living and dead shells in 1998 to 1999. Other *Uvigerina* and *Epistominella* species additionally occur in smaller numbers, while only low numbers of agglutinated species were observed. The same *U. peregrina* community was found in the surrounding non-seep sediments. Both *U. peregrina* and *E. exigua* are species that indicate eutrophic conditions and high amounts of organic material at these sites and *Uvigerina* is known as a high-productivity genus (Loubere & Fariduddin 1999). *U. peregrina* occurs globally in high densities in many diverse eutrophic and suboxic environments, including different methane-enriched active seep sites (Sen Gupta & Aharon 1994, Sen Gupta et al. 1997, Rathburn et al. 2000, Bernhard et al. 2001). *E. exigua* can react very quickly to freshly arriving food material. It was described as an epifaunal opportunistic taxon that reproduces rapidly when it colonizes deposited phytodetrital aggregates (Goody & Turley 1990).

In the non-seep sediments of the southern Hydrate Ridge, we noticed an additional important community, dominated by an agglutinated species shown in Fig. 5b–d, which seems to be identical to *Spiroplectammina biformis* at Monterey Bay cold seep sites described by Bernhard et al. (2001). *Spiroplectammina* species start with a planispiral coiling, followed by biserially arranged chambers. However, the aperture of *Spiroplectammina* is normally a low arch at the inner margin of the final chamber (Loeblich & Tappan 1988). In our case, we observed a terminal aperture on

a neck of the final chamber and named it ?*Spiroplectammina biformis*. No statement can be made about a terminal aperture on a neck of Monterey Bay specimens at the moment (J. M. Bernhard pers. comm.). Thus, the correct generic assignment must be determined in future studies. In Monterey Bay, *S. biformis* was the only species that was restricted to the seep environment, but because it has been found at non-seep sites in other studies, it cannot be used as an indicator for seep environments (Bernhard et al. 2001). At Hydrate Ridge, we found small numbers of ?*Spiroplectammina biformis* individuals at gas-hydrate influenced sites, and large numbers in surrounding non-seep sediments. Additionally, the ?*Spiroplectammina biformis* community also dominated the station at the Western Basin. We explain the increase of the ?*Spiroplectammina biformis* community in non-seep sediments by the decrease of sulfide, and by changing food supply and food composition. In Monterey Bay, the description of the cold-seep biota *Uvigerina peregrina*, *Epistominella (exigua)* and others) and *S. biformis* was consistent with Hydrate Ridge samples. Some other important taxa were observed in both regions and are important in other methane-rich reduced sediments in the North East Pacific: *Bolivina spissa*, *Bolivina pacifica*, *Buliminella tenuata*, *Bulimina mexicata*, and *Cassidulina delicata* (Bernhard et al. 2001, Hill et al. 2003).

Hill et al. (2004) observed that the most abundant species in Hydrate Ridge samples from July 2002 were *Uvigerina peregrina*, *Cibicidoides mckannai* and *Globobulimina auriculata*. This indicates a change in faunal dominances between 1999 and the summer of 2002, where *Cibicidoides* and *Globobulimina* species were rare. Preliminary results from our own sediment cores taken in July 2002 confirmed high numbers of *Cibicidoides* and *Globobulimina* species.

### Faunal assemblages at the basins

At the Western Basin diversity was higher than the Hydrate Ridge. The ?*Spiroplectammina biformis* community also dominated this station. Additionally, other taxa not found in the southern Hydrate Ridge sediments (*Recurvoides contortus* and *Cassidelina* sp.) were found in significant numbers there. Diversity was low at the Eastern Basin station, characterized by a separate community, dominated by high densities of *Stainforthia apertura*, which forms 74% of the fauna. *S. apertura* is found only in the first centimeter of sediment in the Eastern Basin and Hydrate Ridge sediments, while it was found deeper in the sediment in the Western Basin. Many individuals of this species were found in or attached to the sticky organic material

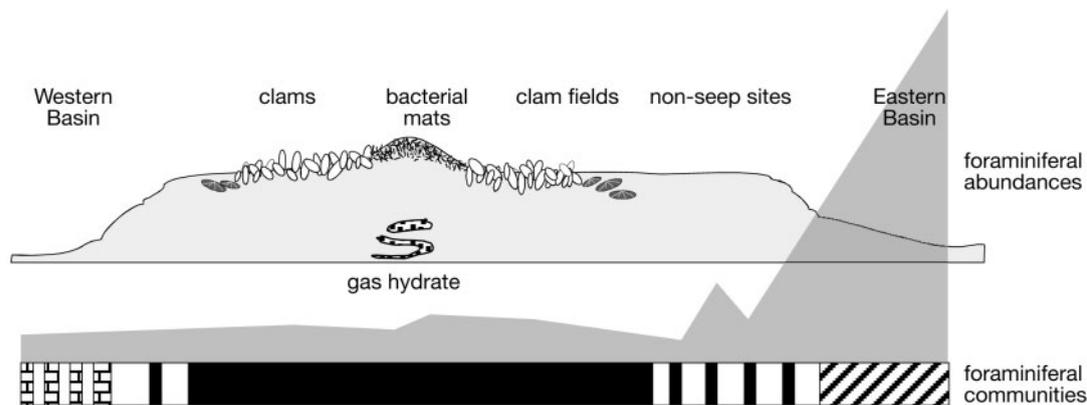


Fig. 8. Schematic summarization of foraminiferal assemblages at the southern Hydrate Ridge (■ PCC 1, □ PCC 2, ▨ PCC 3, ▩ PCC 5)

observed at this station. This species is fragile, and frequently, individuals lost their final chamber during the sampling procedure and picking. Most specimens recorded a body size between 70 and 90  $\mu\text{m}$ , even in the coarser (>125  $\mu\text{m}$ ) size fraction (caused by the embedding of these individuals in bigger organic aggregates). We interpret the dominance of *S. apertura*, often associated with existing organic particles, as an opportunistic reproductive reaction to freshly arrived phytodetritus. A schematic illustration (Fig. 8) summarizes foraminiferal assemblages at the southern Hydrate Ridge and neighboring basins.

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