ORIGINAL ARTICLE

Community structure and nutrition of deep methane-seep macrobenthos from the North Pacific (Aleutian) Margin and the Gulf of Mexico (Florida Escarpment)

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Abstract

Methane seeps occur at depths extending to over 7000 m along the world's continental margins, but there is little information about the infaunal communities inhabiting sediments of seeps deeper than 3000 m. Biological sampling was carried out off Unimak Island (3200–3300 m) and Kodiak Island (4500 m) on the Aleutian margin, Pacific Ocean and along the Florida Escarpment (3300 m) in the Gulf of Mexico to investigate the community structure and nutrition of macrofauna at these sites. We addressed whether there are characteristic infaunal communities common to the deep-water seeps or to the specific habitats (clam beds, pogonophoran fields, and microbial mats) studied here, and ask how these differ from background communities or from shallow-seep settings sampled previously. We also investigated, using stable isotopic signatures, the utilization of chemosynthetically fixed and methane-derived organic matter by macrofauna from different regions and habitats. Within seep sites, macrofaunal densities were the greatest in the Florida microbial mats $(20,961 \pm 11,618 \ \text{ind}\cdot\text{m}^{-2})$, the lowest in the Florida pogonophoran fields $(926 \pm 132 \ \text{ind}\cdot\text{m}^{-2})$, and intermediate in the Unimak and Kodiak seep habitats. Seep macrofaunal densities differed from those in nearby non-seep sediments only in Florida mat habitats, where a single, abundant species of hesionid polychaete comprised 70% of the macrofauna. Annelids were the dominant taxon (>60%) at all sites and habitats except in Florida background sediments (33%) and Unimak pogonophoran fields (27%). Macrofaunal diversity (H′) was lower at the Florida than the Alaska seeps, with a trend toward reduced richness in clam bed relative to pogonophoran field or non-seep sediments. Community composition differences between seep and non-seep sediments were evident in each region except for the Unimak margin, but pogonophoran and clam bed macrofaunal communities did not differ from one another in Alaska. Seep δ^{13}C and δ^{15}N signatures were lighter for seep than non-seep macrofauna in all regions, indicating use of chemosynthetically derived carbon. The lightest δ^{13}C values (average of species' means) were observed at the Florida escarpment (−42.8‰). We estimated that on average animal tissues had up to 55% methane-derived carbon in Florida mats, 31–44% in Florida clam beds and Kodiak clam beds and pogonophoran fields, and 9–23% in Unimak seep habitats. However, some taxa such as hesionid and capitellid polychaetes exhibited tremendous intraspecific δ^{13}C variation (>30‰) between patch types. Overall we found few characteristic communities or features common to the three deep-water seeps (>3000 m), but common

properties across habitats (mat, clam bed, pogonophorans), independent of location or water depth. In general, macrofaunal densities were lower (except at Florida microbial mats), community structure was similar, and reliance on chemosynthesis was greater than observed in shallower seeps off California and Oregon.

Problem

Methane seepage is now recognized as a widespread but patchy feature of active and passive continental margins globally, with seeps distributed from shallow shelf to trench depths (Sibuet & Olu 1998; Levin 2005). Seepage typically is associated with a sediment matrix exhibiting distinct geochemical conditions, including high alkalinity, hydrogen sulfide, methane and ammonium concentrations in pore fluids and limited oxygen availability (e.g., Chanton et al. 1993; Gieskes et al. 2005). Such conditions are challenging to metazoan life forms, for which sulfide is toxic and oxygen is required.

Seep assemblages are typically characterized by their large, symbiont-bearing megafauna (mytilid mussels, vesicomyid clams, vestimentiferan and pogonophoran polychaetes, gastropods, or sponges) or by the presence of surficial microbial mats (Sibuet & Olu 1998; Sibuet & Olu-LeRoy 2002). Each of these epibenthic taxa typically occurs in fairly homogeneous patches and forms biogenic structures that shape local 'habitats' (sensu Levin et al. 2003) for associated fauna. Within the sediments in these habitats there is a wealth of diversity present among the smaller macrofauna, meiofauna, and protozoans (reviewed in Levin 2005). The study of these organisms offers insight into how biogenic structures, stressful geochemical conditions, and associated microbial processes shape ecological communities.

Research that describes the sediment-dwelling macroinfauna of seep sediments in detail focuses mainly on shelf or upper slope sediments of the NE Pacific Ocean (Levin et al. 2000, 2003; Sahling et al. 2002) or the North Sea (Dando et al. 1991, 1994). These sediment studies indicate that there are limited or sometimes variable amounts of specialization among the fauna of shelf seeps. For example, over 40% of the infaunal species inhabiting vesicomyid clam beds of the Eel River seep (500 m) are also present in nearby non-seep sediments (Levin et al. 2003). The macrofauna associated with large biogenic structures such as mussel beds (e.g., Turnipseed et al. 2003, 2004; Bergquist et al. 2005) and tube-worm bushes (Bergquist et al. 2003; Cordes et al. 2005) have also been described. These communities are believed to include numerous seep endemic species, whose distribution and diversity are closely tied to aggregation age, oxygen, methane, and sulfide availability. However, valid comparisons with background faunas are scarce because of the lack of comparable substrate and sampling techniques.

Studies of seep meiofauna in the Gulf of Mexico (Powell & Bright 1981; Powell et al. 1983; Buck & Barry 1998; Robinson et al. 2004), at the Hatsushima cold seep (Shirayama & Ohta 1990), and at the Hakon Mosby mud volcano (Van Gaever et al. 2006) reveal no consistent patterns. Densities of meiofauna are enhanced, depleted, or unchanged relative to nearby background sediments (reviewed in Levin 2005). Strongly specialized nutrition, reproduction, or symbioses may be present in some seep meiofauna (Buck et al. 2000; Van Gaever et al. in press).

Although some of the macrofauna inhabiting seeps at upper slope depths are seep-habitat endemics, only a few taxa show nutritional specializations such as symbioses or chemosynthesis-derived carbon in tissues (Levin 2005). The food sources of the many heterotrophic infaunal invertebrates inhabiting seep sediments are difficult to determine because the organisms are small in size and gut contents are amorphous. Stable isotope analyses have provided a primary means of assessing the role of chemosynthetic versus photosynthetic food sources, and of determining the contribution of methane to the tissue carbon pool (Conway et al. 1994; Levin & Michener 2002). It has been predicted that heterotrophic species inhabiting deeper seep sites are more likely to rely on chemosynthetically fixed carbon than their shallow counterparts because less surface-derived organic matter is available at depth (Levin & Michener 2002). However, there are few tests of this hypothesis, largely because nutritional studies have not been conducted at most deep seeps.

Here we examine macrofaunal community structure within seep sediments from 3200 to 4500 m water depth, at two locations along the Aleutian Margin, Pacific Ocean and at the Florida Escarpment, the Gulf of Mexico (Fig. 1). The Pacific and the Gulf of Mexico seeps are driven by fundamentally different geochemical and tectonic processes, thus comparisons between them cannot link communities to common processes. However, all three regions support seep sediments with elevated sulfide supply relative to background sediments (Chanton et al. 1993; Gieskes et al. 2005; Ziebis et al. 2005). For the Kodiak, Unimak, and Florida Escarpment seeps we ask the following questions: (1) Are there characteristic communities or features common to the deep-water seeps studied here? (2) Are sediment communities similar among habitats (clam
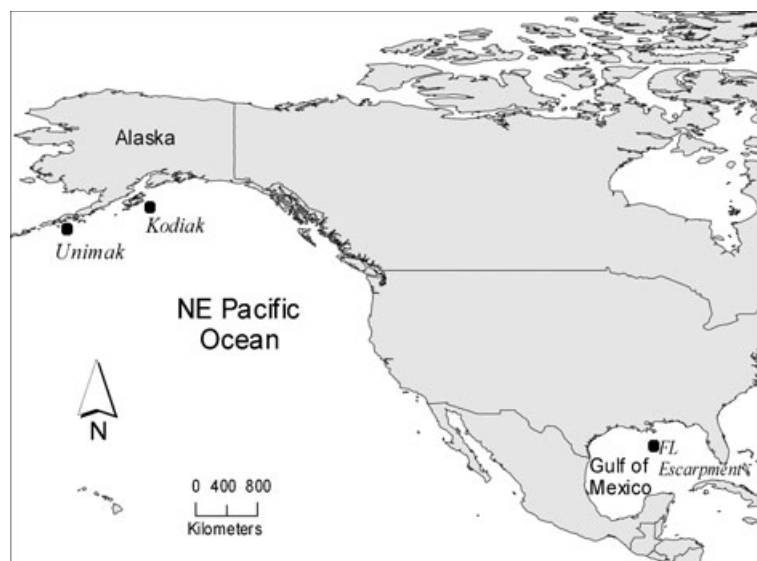
Fig. 1. Map showing location of the three methane seep sites sampled: Kodiak margin, Alaska, Unimak margin, Alaska and Florida Escarpment, the Gulf of Mexico.

beds, pogonophoran fields, microbial mats) within a region? (3) Do macrofaunal densities, diversity and composition at seeps differ from those of surrounding non-seep sediments? (4) To what extent do deep-seep macrofauna utilize organic matter of chemosynthetic origin or derived from methane? and (5) How do densities, community structure, and nutrition of macrofauna compare with those of shallower seep settings studied in the NE Pacific? The seeps at >3000 m water depth may be expected to exhibit differences from seeps examined at shallower, bathyal depths in terms of taxonomic composition, diversity, and their relationship to the surrounding deep-sea community. We hypothesized that deeper seeps, surrounded by relatively oligotrophic sediments, should support sediment-dwelling faunas that are more dependent on seep production than those at shallow seeps.

Study Site Background

Unimak margin, Alaska

The seabed off Unimak Island (53° N, 163° W) is highly dynamic, with canyons, faulting, turbidity flows, and seismic activity (Dobson *et al.* 1996). A massive landslide was hypothesized to be the source of a powerful and devastating tsunami that followed a magnitude 7.4 earthquake in April 1946 near Unimak Island (Johnson & Satake 1997; Fryer *et al.* 2004). The earthquake originated under the inner slope of the Aleutian Trench from a shallow, low-angle thrust fault movement. However, extensive multibeam mapping of the seafloor yielded no evidence of a landslide (G. Fryer and M. Tryon, personal communication). Instead, an isolated, 800-m high mound-like feature (referred to later as a mudmount) was identified on the abyssal terrace through seabeam mapping. No biological

surveys have been conducted previously on the deep margin near Unimak Island and seeps had not been reported from this area. Several samples from the nearby Aleutian Trench have been analyzed (Belyaev 1966; Jumars & Hessler 1976).

The seep sites studied here consisted of small, mixed-species aggregations (1–5 m²) of *Vesicomya extenta* and *V. diagonalis* at 3267 m and a nearby sparse patch (5–10 m²) of pogonophorans (*Siphonobrachia*: Siboglinidae) at 3283 m. Large conglomerate boulders cemented by carbonates and lithified sediments were present at the site. The area was surrounded by relatively featureless non-seep, slope sediment (3300 m).

Kodiak margin, Alaska

The Kodiak seeps (∼4400 m; 56°55′ N, 149°32′ W) were found near Kodiak Seamount in 1999, during exploration with the submersible ALVIN. The only report of the Kodiak seeps to date focuses on nutrition of macrofauna (Levin & Michener 2002) from *Calyptogena phaseoliformis* beds and pogonophoran fields (*Spirobrachia* and *Polybrachia* spp.). Gieskes *et al.* (2005) describe the chemistry of pore fluids from Kodiak seeps, recording hydrogen sulfide concentrations of up to 3 mM in the upper 10 cm (habitats not specified). Descriptions of the geochemistry and epibiota at somewhat deeper seeps at the Edge and Shumagin sites nearby are found in Wallmann *et al.* (1997) and Suess *et al.* (1998).

Florida escarpment

The Florida escarpment is a large, Lower Cretaceous carbonate feature that has been continually eroded since its

formation (Twichell *et al.* 1991). Where the platform meets the sediment, brines rich in sulfide, methane and ammonia migrate to the sediment surface. In 1984, the first seep communities were discovered here at depths of 3266 m (26° N, 84° W); they consisted of extensive microbial mats, tubeworm bushes and mussel beds replete with trochid gastropods (Paull *et al.* 1984). Descriptions of the biological communities on the Florida Escarpment to date have focused primarily on large epifauna (Paull *et al.* 1984; Hecker 1985) and invertebrates associated with mussel beds (Turnipseed *et al.* 2004). Porewater studies at this site reveal that the fluid chemical composition was dominated by processes occurring within the carbonate platform rather than by *in situ* microbial processes (Chanton *et al.* 1993). Measured porewater hydrogen sulfide concentrations reach a maximum of 5.7 mM. Early studies characterized sediments as black, grey, or tan with black supporting microbial mats, mussels, or tube worms and grey being the transitional boundaries between the tan hemipelagic sediments and seep-influenced black sediments (Paull *et al.* 1984; Chanton *et al.* 1993). This study focused on sediments with characteristic black and white color (referred to as microbial mat), with aggregations of non-vestimentiferan pogonophorans, and with vesicomyid clams. We did not sample aggregations of vestimentiferan tube worms or mussel beds.

Defining habitats

The seep sites visited exhibited characteristic aggregations of vesicomyid clams, pogonophorans (non-vestimentiferan

siboglinids), and off Florida, microbial mats. As these aggregations introduce biogenic structures that define the substrate and environmental conditions for associated smaller organisms that are the focus of this study, we refer in the remainder of the paper to clam beds, pogonophoran fields and microbial mats as 'habitats.' Sediments that provided no visual evidence of seepage (no organisms, microbial mat, or discoloration) are referred to as non-seep sediments and are considered an additional type of habitat.

Material and Methods

Sampling

Sampling on the Aleutian margin was conducted at 4413–4445 m during August 1999 by the submersible ALVIN aboard the RV Atlantis at seeps near Kodiak Seamount in the Gulf of Alaska (56°55.6′ N, 149°32.9′ W) and further west at 3267–3310 m during July 2004 by the ROV Jason II aboard the RV Thompson at seeps off Unimak Island (53° N, 163° W) (Fig. 1; Table 1). In these two regions we sampled sediments with assemblages of living vesicomyid clams – *Vesicomya phaseoliformis* off Kodiak and *V. extenta* and *V. diagonalis* off Unimak (referred to here as clam beds) and sediments containing aggregations of pogonophorans – *Polybrachia* sp. and *Spirobrachia* sp. off Kodiak and *Siphonobrachia* sp. off Unimak (referred to as pogonophoran fields). We also sampled nearby non-seep sediments. In the Kodiak region this was done by night-time multicoring at sites on all sides of the seep (Table 1). On the Unimak margin we used Jason II to

Table 1. Sample locations, dates, depths, and gear used to sample macrofauna.

	date	water depth (m)	latitude (° N)	longitude (° W)	dive number	corer type (diam in cm)	no. of samples
Florida Escarpment							
microbial 'mat'	Oct. 12, 2003	3290	26°1.81′	84°54.66′	AD 3916	tube corer (6.94)	4
pogonophoran field	Oct. 13, 2003	3234	27°4.01′	85°36.54′	AD 3915	tube corer (6.94)	2
vesicomyid clam bed	Oct. 12, 2003	3290	26°1.80′	89°54.66′	AD 3916	scoop (non-quantitative)	1
non-seep	Oct. 11, 2003	3290	26°1.75′	84°54.77′	AD 3917	tube corer (6.94)	3
Kodiak margin, Alaska							
vesicomyid clam bed	Aug. 6, 10, 11, 1999	4413–35	56°55.66′	149°32.85′	AD 3444, 48, 49	tube (6.56)/box corer (7, 10)	6
pogonophoran field	Aug. 8–10, 1999	4414–44	56°55.67′	149°32.94′	AD 3446, 47, 48	tube (6.56)/box corer (7,10)	3
non-seep	Aug. 7, 1999	4327	56°55.14′	149°34.70′	N/A	Multicorer (9.6)	1
non-seep	Aug. 8, 1999	4342	56°55.10′	149°34.85′		Multicorer (9.6)	1
non-seep	Aug. 9, 1999	4353	56°57.61′	149°31.70′		Multicorer (9.6)	1
non-seep	Aug. 9, 1999	4428	56°59.10′	149°24.50′		Multicorer (9.6)	1
non-seep	Aug. 10, 1999	4480	56°50.39′	149°61.01′		Multicorer (9.6)	1
Unimak margin, Alaska							
vesicomyid clam bed	July 15, 18, 2004	3267	53°30.81′	163°26.69′	J2 90	tube corer (8.3)	3
pogonophoran field	July 18, 2004	3283	53°30.78′	163°26.70′	J2 91	tube corer (8.3)	3
non-seep – slope	July 15, 2004	3302–10	53°30.79′	163°26.09′	J2 90	tube corer (8.3)	3
non-seep – mudmount	July 12, 2004	3165–90	53°17.48′	164°02.77′	J2 87	tube corer (8.3)	5

AD, Alvin Dive; J2, Jason Dive; N/A, not available.

sample non-seep sites within a few hundred meters of the seep site, and at an isolated 1000-m high bump (mudmount) separated from the main slope but at similar water depths. The ALVIN/Atlantis was also used to sample seep sediments along the Florida Escarpment (26°01′ N, 84°55′ W) during October 2003. We cored sediments from black and white microbial mat patches (3290 m), within aggregations of an unidentified pogonophoran (3234 m at the FL Elbow), and background sediments (3290 m). Animals from these cores and from a non-quantitative scoop sample collected within aggregations of vesicomyids (3290 m; *Calyptogena* aff. *kaikoi*) were used in isotope studies.

Tube cores and Ekman-style box corers were used to sample sediments to depths of 10–15 cm. Details of sample locations, water depths, core dimensions, and core numbers are given in Table 1. Sample sizes for each habitat type are small (typically three to five cores) due to limited access. However, because there are no other published data for seep macrofauna at depths >3000 m, we feel the information is useful. Sediment cores were sectioned vertically (0–1, 1–2, 2–5, 5–10, 10–15 cm) soon after recovery; deeper fractions were not analyzed in this study. The upper 5 cm were preserved unsieved in 8% buffered formalin, but the fractions below 5 cm were sieved using a 0.3 mm mesh prior to preservation in 8% buffered formalin. In the laboratory, all sediments were passed through a 0.3 mm mesh sieve; retained invertebrates were sorted at 12× magnification with a dissecting microscope and identified to the lowest taxonomic level possible.

Stable isotope studies

Parallel cores or scoop-bag samples (to sediment depths of 10 cm) were collected from the regions and habitats described above, kept cold (5 °C), sieved through a 0.3 mm mesh, and sorted live at sea to collect macrofauna for stable isotopic analyses. Living specimens were identified, allowed to clear guts overnight in filtered seawater, washed in milli Q water and placed in preweighed tin boats or combusted vials (500 °C overnight) and frozen at −70 °C. In the laboratory, specimens were oven dried (60 °C), weighed and acidified with 1% $PtCl_2$ to remove inorganic C. Stable isotope measurements ($\delta^{13}C$, $\delta^{15}N$) were made on single individuals, parts of individuals or several small specimens of a single species combined. Analyses were conducted on a Finnigan Conflow 2 continuous flow system and a Fisons NA 1500 elemental analyzer coupled to a Finnegan Delta S isotope ratio mass spectrometer at Boston University and on a continuous flow PDZ Europa 20/20 isotope ratio mass spectrometer at UC Davis. Isotope ratios are expressed as $\delta^{13}C$ or $\delta^{15}N$ in units of per mil (‰). Standards were Pee Dee Belem-

nite and nitrogen gas (atmospheric). Kodiak seep stable isotope data were presented previously in Levin & Michener (2002) as online appendices. Estimates of the percentage of methane-derived carbon in the macrofaunal carbon pool of each region and habitat were generated using a two-source, single isotope mixing model as in Fry & Sherr (1984). The formula is

$$F_m = \frac{\delta_i - \delta_{POC}}{\delta_m - \delta_{POC}}$$

where δ_i, δ_{POC}, and δ_m refer to the $\delta^{13}C$ signatures of infauna, particulate organic carbon (POC), and methane, respectively. The POC value was taken to be the average $\delta^{13}C$ signature of non-seep fauna sampled by this study in each region. No trophic shift was included as this is negligible (<1‰ per trophic level) for $\delta^{13}C$. The methane value was estimated to be −85‰ (average of values −80‰ to −90‰ cited in Cary *et al.* 1989) for the Florida Escarpment and −70‰ for the Alaska seeps (Levin & Michener 2002).

Statistics tests and indices

All data are expressed as mean ± 1 SE unless indicated otherwise. Abundance data (for animals within the upper 15 cm of each core) were normalized to number per m^2 for comparison across habitats and sites. Diversity was measured as number of species per core (richness), H′ (log base 10), and J′ (evenness). Macrofaunal abundances, diversity, and stable isotope data were tested for normality and log_{10}-transformed or arcsin transformed (percentages, J′) when necessary. Location and habitat differences were tested via one-way ANOVA; followed by Tukey's HSD. If transformation did not achieve normality, non-parametric tests (Kruskall–Wallis and Wilcoxon) were used. These analyses were performed using JMP 4.2 software. Community structure of macrofauna was compared across habitats within each site, and polychaete family structure was compared across sites using ANOSIM, SIMPER and non-metric Multi-Dimensional Scaling based on Bray–Curtis similarity indices (Primer software V.5). Limited opportunity for quantitative sampling and a non-uniform distribution of habitats yielded quantitative pogonophoran field and non-seep samples in all three regions, vesicomyid clam bed samples only at the Kodiak and Unimak sites, and microbial mat samples only in Florida, precluding most direct cross-basin community comparisons. To conduct statistical tests on stable isotope values, data for multiple individuals of a single species were averaged within each site and habitat. Tests of site or habitat effects then used species as replicates to avoid overrepresentation of the most abundant taxa.

Results

Density

Background (non-seep) macrofaunal densities were lower on the Florida Escarpment (264 ± 152 ind·m^{-2}) than off Alaska ($F_{2,15}$ = 5.57, P = 0.018), but did not differ between the Unimak (5344 ± 154 ind·m^{-2} on the slope and 2874 ± 1167 ind·m^{-2} on a more distant mudmount) and Kodiak (3426 ± 322 ind·m^{-2}) sites. In contrast, macrofaunal densities of seep samples (all habitats combined) did not differ between the three regions ($F_{2,20}$ = 0.268, P = 0.755) (Fig. 2). Seep densities were highly variable, however, among habitat types, with maximum values in Florida Escarpment microbial mats (20,961 ± 11,618 ind·m^{-2}), minimum values in Florida pogonophoran fields (926 ± 132 ind·m^{-2}), and intermediate densities at Unimak and Kodiak seeps (Fig. 2). When seep habitat types were considered separately, macrofaunal densities in Florida mat sediments were higher than in Florida pogonophoran field or Unimak clam beds ($F_{5,20}$ = 5.367; P = 0.005). Comparison of macrofaunal densities in seep sediments to those in background sediments within each location yielded differences only in Florida ($F_{2,7}$ = 16.57; P = 0.006), where mat densities were elevated by nearly two orders of magnitude over pogonophoran field and background densities. In Alaska, seep macrofaunal densities did not differ from those in nearby background sediments on the Kodiak margin ($F_{2,13}$ = 1.47; P = 0.271) or Unimak margin, although the Unimak pogonophoran field densities were higher than those at comparable depths on an isolated mudmount ($F_{3,13}$ = 4.018, P = 0.041) (Fig. 2).

Composition

Annelids were the dominant taxon at most seep and background sites. They comprised 86–92% of the total
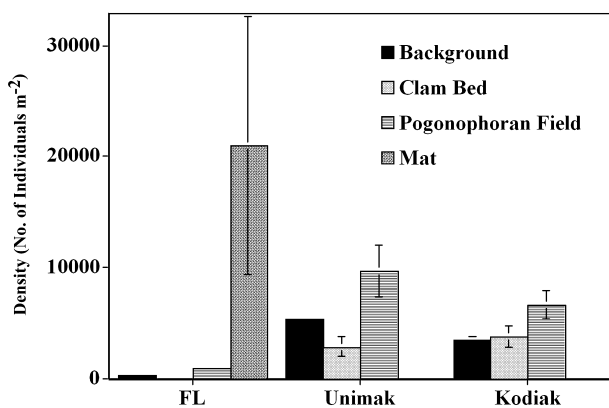
macrofauna at the Florida seep sites, 65–70% of the total in the Unimak vesicomyid clam bed and non-seep sediments, and 61–68% of the fauna in the Kodiak vesicomyid clam bed, pogonophoran field, and non-seep sediments (Fig. 3). Notably different were the macrofauna of the Florida Escarpment non-seep sediments with 33% Annelida and Unimak pogonophoran fields with 27% Annelida. Within the pogonophoran field cores, pogonophorans accounted for 49% of sampled individuals at Kodiak, 1% at Unimak, and 0% in Florida.
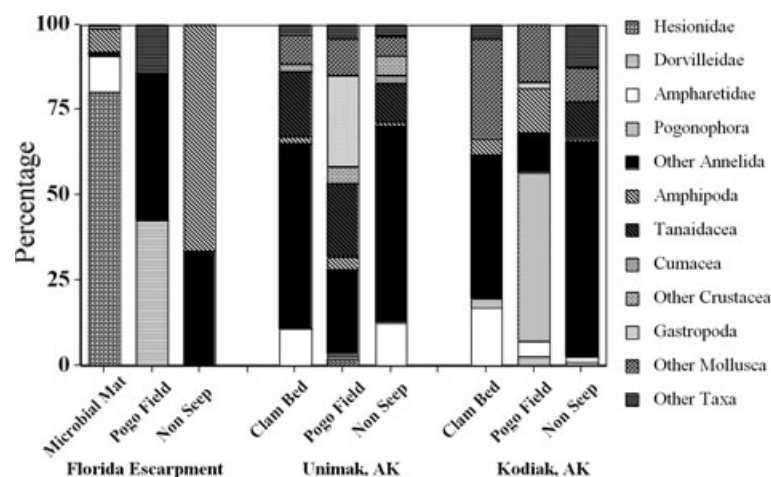
The Florida seep sediments were characterized by high proportions of single annelid taxa. The hesionid *Orseis* sp. comprised 70% of all individuals in mat sediments and Dorvilleidae (*Ophryotrocha* sp. and *Protodorvillea keiferstein*) were 30% in pogonophoran fields. *Amphisamytha* sp., *Sigambra tentaculata*, and gammarid amphipods were the other dominant taxa in Florida seep sediments. In background sediments only two gammarid amphipods and one spionid polychaete were collected (Appendix 1).

At Unimak, the most abundant species in the pogonophoran fields was an unidentified gastropod (18% of the total individuals). Gastropoda as a group formed 36% of the total, and Mollusca 46% of the macrofauna in this habitat. In the Unimak clam beds, mollusks were only 9% of the fauna and tanaids were dominant (20%). Crustaceans formed 17–24% of macrofauna in the Unimak seep and background habitats (Appendix 3).

Kodiak seep macrofauna differed from the Unimak and Florida macrofauna in (a) pogonophoran dominance (49%), followed by bivalves (16%), within the pogonophoran fields, and (b) bivalves (24%), ampharetid (14%), and cirratulid polychaetes (11%) as dominants in the clam beds. Tanaids were notably absent from the Kodiak seep sites, but comprised 11% of the non-seep fauna (Appendix 2).

Diversity

Richness measured as the number of species per core was tested only for habitat differences within each region due to the use of different core sizes in each study. There was a trend toward lower macrofaunal richness per core in clam bed cores than in pogonophoran field or adjacent non-seep samples. In contrast, community evenness (J′) was significantly lower in the pogonophoran fields relative to clam bed and non-seep habitats, and H′ did not differ among habitats (Table 2). At the Florida Escarpment, the microbial mat and pogonophoran field cores had higher species richness per core than non-seep samples, but the mat community had lower evenness than the pogonophoran field community (Table 2).

Fig. 2. Mean (±1 SE) density of macrofauna (>0.3 mm) in different seep habitats and background sediments of the Florida Escarpment, the Gulf of Mexico and on the Unimak and Kodiak margins, Alaska.

Fig. 3. Percent composition of major macrofaunal taxa (>0.3 mm) in different seep habitats and background sediments of the Florida Escarpment, the Gulf of Mexico and on the Kodiak and Unimak margins, Alaska, NE Pacific Ocean.

Table 2. Diversity and dominance measures for seep and background macrofauna.

	Dominant Taxon	RID	No. Species/Core	H′ log 10	J′
Florida Escarpment			P = 0.0009 (N < P,M)	NS	P = 0.043 (M < P)
Microbial 'mat'	*Orseis* sp.	0.76	3.75 + 0.25	0.31 ± 0.05	0.60 ± 0.11
Pogonophoran Field	none	0.29	3.5 + 0.50	0.54 ± 0.06	1.00
Non Seep	Gammarid amphipod	0.67	0.67 + 0.33	NA	NA
Kodiak margin, Alaska			NS	NS	P = 0.006 (P < C = N)
Vesicomyid Clam Bed	Ampharetidae	0.14	7.8 ± 1.6	0.78 ± 0.08	0.94 ± 0.02
Pogonophoran Field	Siboglinidae	0.50	11.0 ± 0.6	0.73 ± 0.07	0.70 ± 0.05
Non Seep	Spionidae	0.20	12.6 ± 1.3	0.97 ± 0.04	0.90 ± 0.02
Unimak margin, Alaska			P = 0.042	NS	P = 0.017(P < C = N)
Vesicomyid Clam Bed	Tanaidacea	0.20	9.33 ± 2.03	0.91 ± 0.09	0.96 ± 0.03
Pogonophoran Field	Gastropoda sp. A	0.18	16.67 ± 3.18	0.90 ± 0.07	0.75 ± 0.02
Non Seep - slope	Tanaidacea	0.12	15.33 ± 2.19	1.10 ± 0.07	0.93 ± 0.01
Non-Seep - mudmount	Gammarid amphipod	0.18	7.60 ± 1.81	0.76 ± 0.10	0.91 ± 0.03

P values reflect results of one-way ANOVA testing for differences among habitats within a region.

Significant a *posteriori* testing results are given in parentheses, NS = not significant

N = non seep, M = microbial mat, P = pogonophoran field and C = clam bed Note: Because different core sizes were used in each region, species richness per core can only be compared among habitats within a region. NA = not available due to low sample size.

Comparisons of all seep data across sites yielded lower overall macrofaunal diversity (H′) at Florida seeps than in Unimak or Kodiak seeps (H′; $F_{2,33}$ = 21.52; P < 0.0001) but no significant difference in evenness (J′; $F_{2,32}$ = 3.01; P = 0.064). Analysis of habitat differences (all regions combined) indicated lower evenness in microbial mat and pogonophoran field macrofauna than in clam bed or background macrofauna. Rank 1 dominance was the highest in the Florida mat habitat (76%) and in the pogonophoran field at Kodiak (50%), but was similar (11–29%) in other locations and habitats (Table 2).

Community structure

The Florida microbial mat assemblage (Fig. 4A) was distinct from non-seep (P = 0.029) and to a lesser extent

pogonophoran field assemblages (P = 0.067) (ANOSIM), due largely to high densities of the hesionid polychaete *Orseis* sp. and an ampharetid polychaete (*Amphisamytha* sp.) in the mat assemblage (SIMPER). At Kodiak, the clam bed and pogonophoran assemblage were similar (P = 0.27, ANOSIM) and both differed from the non-seep assemblage (P = 0.013 for clam bed *versus* non-seep assemblage; P = 0.018 for pogonophoran *versus* non-seep assemblage) (Fig. 4B). Driving the seep/non-seep differences (Global R = 0.452, P = 0.006) were more pogonophorans, bivalves, and ampharetids at seeps and more spionids and cirratulids in non-seep sediments (SIMPER). On the Unimak margin (Fig. 4C), macrofaunal assemblages in the seep habitats did not differ from those in non-seep sediments or from each other (pogonophoran *versus* clam bed) (Global R = −0.003, P =
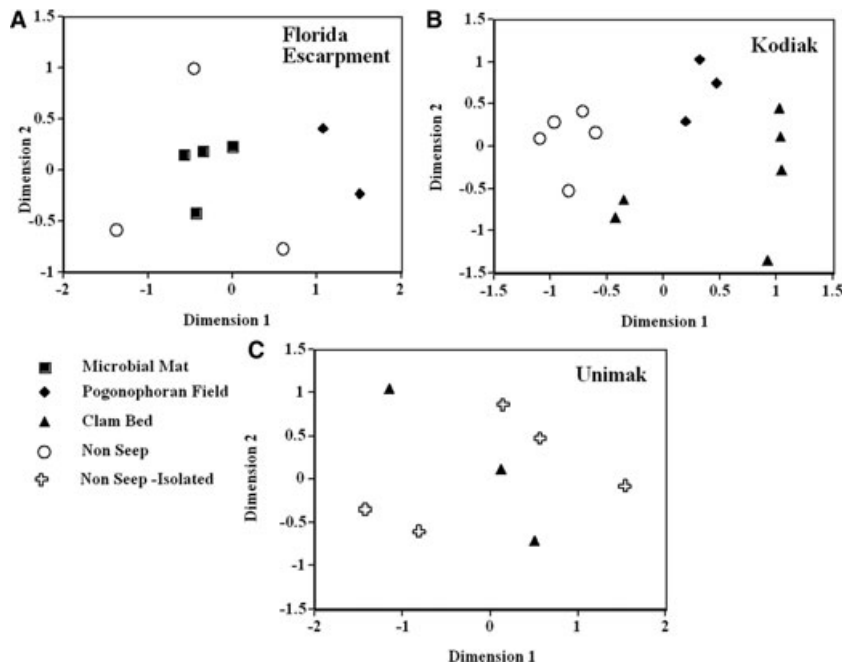
Fig. 4. Multi-dimensional Scaling (MDS) plots illustrating similarity of macrofaunal composition in different seep habitats and background sediments of (A) the Florida Escarpment, the Gulf of Mexico (stress = 0.00) and on the margins off (B) Kodiak (stress = 0.14), and (C) Unimak (stress = 0.19) islands, Alaska.
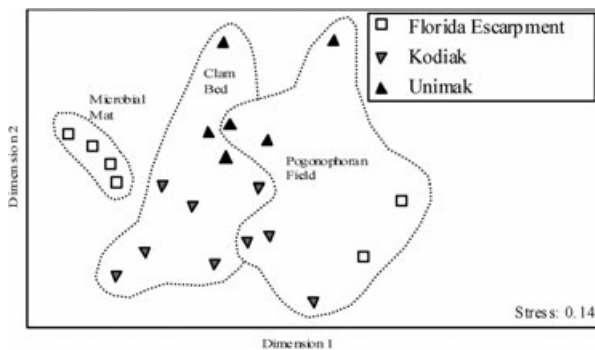
Fig. 5. MDS plot illustrating similarity of polychaete family composition in seep habitats from the Florida Escarpment, the Gulf of Mexico and the margins off Kodiak and Unimak islands, Alaska. Samples from similar habitat types are indicated.

0.496). To compare assemblages across regions we examined polychaete family structure, as few species occurred in common and polychaetes were the dominant taxon at most sites (Fig. 3). Kodiak, Unimak, and Florida seep sediments all exhibited significant differences in polychaete familial composition (ANOSIM: R = 0.433 P < 0.05; Fig. 5). Hesionids contributed more than 20% of the dissimilarity (SIMPER) between the Florida Escarpment and the Alaska sites (Kodiak and Unimak). Polychaete family composition also differed among habitat types independent of location (ANOSIM: R = 0.433 P < 0.05; Fig. 5).

Stable isotopic signatures

Stable isotope signatures of heterotrophic macroinfauna exhibited a tremendous range of values ($\delta^{13}C$ from −95.93 to −11.03‰, $\delta^{15}N$ from −5.95 to 15.94‰) (Table 3), with lightest values reflecting input from methane-derived carbon ($\delta^{13}C$) or utilization of locally fixed nitrogen ($\delta^{15}N$). When all seep data were combined, average $\delta^{13}C$ signatures were significantly lighter on the Florida Escarpment ($\delta^{13}C$ = −42.8 ± 3.6) and at Kodiak sites ($\delta^{13}C$ = −32.9 ± 2.5) than on the Unimak margin ($\delta^{13}C$ = −26.5 ± 2.1) (χ^2 = 17.517, df = 2, P < 0.0002). The $\delta^{15}N$ signatures of heterotrophic seep macrofauna were significantly lighter on the Florida Escarpment ($\delta^{15}N$ = 1.10 ± 0.89) than on the Kodiak ($\delta^{15}N$ = 8.72 ± 0.61) or Unimak ($\delta^{15}N$ = 9.58 ± 0.52) margins (χ^2 = 36.37, df = 2, P < 0.0001). In each region, the seep sediment fauna (all habitats combined) had lighter $\delta^{13}C$ and $\delta^{15}N$ signatures than the macrofauna in non-seep sediments (all P << 0.05 except FL $\delta^{13}C$, where P = 0.06) (Fig. 6).

Analyses of isotope signatures within each sampling region yielded some interesting habitat differences (Fig. 6). In Florida the macrofaunal $\delta^{13}C$ and $\delta^{15}N$ signatures were lighter in microbial mat than non-seep sediments ($F_{3,19}$ = 3.41, P = 0.043; $F_{3,19}$ = 3.27, P = 0.049 for $\delta^{13}C$ and $\delta^{15}N$, respectively) (Table 3). The black mat infauna, consisting of hesionids, amphipods and an unidentified polychaete, exhibited lighter average $\delta^{13}C$ (−61.50 ± 3.18‰) and $\delta^{15}N$ (−2.92 ± 1.38‰) values than

Table 3. Isotopic signatures of heterotrophic seep macrofauna. Where n>1, average values are given.

| Taxon	Microbial Mat			Clam Bed			Pogonophoran Field			Non Seep		
	n	δ^{13}C	δ^{15}N	n	δ^{13}C	δ^{15}N	n	δ^{13}C	δ^{15}N	n	δ^{13}C	δ^{15}N
Florida Escarpment												
Polychaeta												
Amphisamytha sp.	2	−34.82	4.86	1	−58.37	−3.23						
Capitellidae				1	−34.32	2.45	1	−34.76	0.75			
Synelmis sp.				3	−42.74	1.42						
Orseis sp. (Black mat)	2	−69.22	1.28									
Orseis sp. (White mat)	5	−36.88	−0.70									
Unid. Polychaeta	2	−52.37	−4.08									
Polynoidae	1	−42.11	−0.17				1	−39.87	4.92			
Maldanidae										1	−16.45	12.00
Crustacea												
Gammaridae A (Black mat)	2	−62.92	−5.95	2	−56.21	−2.28	1	−21.23	2.29			
Gammaridae A (White mat)	2	−53.64	−0.13									
Gammaridae B				1	−17.85	3.81						
Unid Amphipoda				1	−22.57	0.68						
Tanaidacea							1	−46.10	3.97			
Isopoda										1	−19.45	1.50
Other												
Turbellarian	1	−95.93	−1.40									
Unimak												
Annelida												
Ampharetidae				1	−28.48	4.96	2	−24.46	8.80	3	−20.11	9.68
Cirratulidae				1	−22.46	7.49				2	−18.06	12.08
Capitella sp. (Clam shell)				5	−32.32	2.35						
Capitella sp. (sediment)				5	−60.81	12.29						
Unid. Dorvilleidae				1	−33.80	−0.45						
Exallopus sp. (Dorvilleidae)				1	−25.07	11.57						
Glyceridae				1	−20.90	12.85						
Goniadidae				1	−34.45	11.96	1	−20.05	9.18			
Lumbrineridae				1	−23.51	12.21	2	−21.48	12.40	1	−25.36	8.91
Maldanidae A				1	−16.88	12.96						
Maldanidae B				1	−36.29	6.93						
Nerididae				1	−57.46	13.76						
Opheliidae				1	−20.08	11.59				1	−17.07	12.65
Paraonidae				2	−26.39	8.92						
Phyllodocidae A				1	−51.58	13.40						
Phyllodocidae B				1	−20.57	14.01	1	−17.90	11.07			
Prionospio sp.				1	−32.79	7.83						
Polynoidae				2	−29.22	6.60	1	−19.23	11.96	1	−19.23	11.96
Serpulidae										1	−26.90	10.18
Sphaerodoridae										1	−11.03	15.09
Sternaspidae				1	−22.18	12.13	1	−19.58	10.11	1	−18.79	11.45
Spiophanes sp.										1	−17.36	10.96
Spionidae				1	−25.44	5.36				1	−18.97	10.20
Terebellidae				1	−18.85	13.30						
Trichobranchidae				1	−19.04	11.06						
Oligochaeta				1	−32.13	10.96						
Crustacea												
Amphipoda A				3	−38.38	9.75						
Unid. Amphipoda				1	−25.62	11.81						
Unid. Gammaridae B				2	−40.15	9.64						
Isopoda A				1	−31.22	5.18	1	−38.46	2.08			
Isopoda B							1	−20.00	10.44	1	−20.14	12.09
Cumacea										1	−18.65	10.48
Mysidacea				1	−28.35	5.25						

Table 3. Continued.

Taxon	Microbial Mat n	δ^{13}C	δ^{15}N	Clam Bed n	δ^{13}C	δ^{15}N	Pogonophoran Field n	δ^{13}C	δ^{15}N	Non Seep n	δ^{13}C	δ^{15}N
Tanaidacea				1	−31.28	9.68	1	−20.27	14.34			
Mollusca												
Bivalvia				1	−19.15	9.75				1	−20.27	14.34
Gastropoda				1	−31.47	−1.38						
Other												
Sipunculida				1	−22.89	8.38						
Anemone				2	−32.73	4.31						
Nematoda				4	−43.23	9.29						
Ophiuroidea				1	−12.41	9.94						
Nemertean							1	−39.95	−3.15			
Turbellarian										1	−22.25	12.42
Kodiak												
Polychaeta												
Ampharetidae				2	−36.10	1.86						
Capitellidae										1	−21.16	12.82
Cirratulidae				1	−29.17	11.21				1	−20.39	9.24
Dorvilleidae				1	−90.62	7.47						
Glyceridae							1	−21.19	15.94			
Goniadidae										1	−19.38	14.43
Lumbrineridae				1	−35.77	6.56	1	−58.54	5.72			
Maldanidae				1	−53.09	8.16	1	−50.49	13.34	2	−20.52	11.54
Nephtyidae				1	−34.00	7.60	1	−43.61	7.87	1	−17.70	14.80
Nereididae				2	54.41	7.91						
Ophelina sp.										1	−20.53	14.35
Onuphidae				1	−39.79	8.28						
Polynoidae				1	−36.05	−0.87						
Syllidae				1	−20.51	15.39						
Terebellidae				1	−36.09	4.89						
Trichobranchidae				1	−24.07	7.99	1	−26.60	9.32			
Crustacea												
Gammarid amphipod							1	−64.78	4.47			
Caprellid amphipod				1	−49.45	7.06						
Isopoda				1	−42.10	6.85						
Tanaidacea										1	−33.37	5.72
Galatheid crab				1	−53.30	7.81	2	−47.23	8.06			
Mollusca												
Bivalvia (*Yoldiella* sp.?)				1	−35.89	5.74	1	−43.31	6.85	1	−19.79	7.98
Montacuta sp.				1	−28.55	4.54						
Scaphopoda										1	−25.21	10.97
Gastropoda A				2	−43.71	3.54						
Other												
Cnidaria				1	−38.14	4.64	1	−49.12	2.26			
Sipunculida							1	−24.92	16.69	1	−19.34	10.35
Holothuroidea										1	−19.75	12.08
Ophiuroidea										1	−21.79	11.88
Amphiura sp.										1	−21.31	13.18

the white mat infauna (δ^{13}C = −46.08 ± 5.14‰; δ^{15}N = 0.50 ± 1.57‰), which were comprised mainly of hesionids, ampharetids, and amphipods. However, only the δ^{13}C values were significantly different between microbial mat types (δ^{13}C: χ^2 = 6.40, df = 1, P = 0.011; δ^{15}N, t_{15} = 1.220, P = 0.241). The Florida clam bed and pogonophoran field macrofaunal values did not differ from those in either mat type, or in non-seep sediments. On the Alaska margin, both the Unimak and Kodiak site macrofaunal δ^{13}C signatures did not differ between clam bed and pogonophoran field sediments. However, the pogonophoran faunas were significantly lighter than those in non-seep sediments at Kodiak (χ^2 = 19.085, df = 2, P < 0.0001), whereas the clam bed sediment fauna was
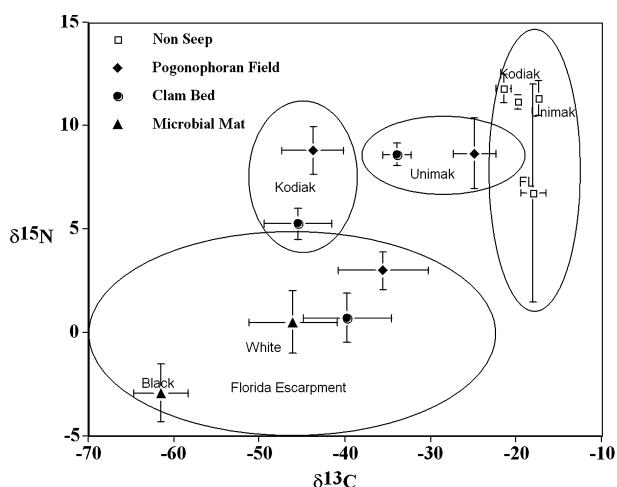
Fig. 6. Mean (±1 SE) stable isotopic signatures of heterotrophic macrofauna from different seep habitats and background sediments of the Florida Escarpment, the Gulf of Mexico and on the Unimak and Kodiak margins, Alaska. Black and white refer to different types of microbial mats sampled on the Florida Escarpment.

lighter than that of non-seep sediments at the Unimak margin ($F_{2,58} = 9.15$; P = 0.0004). Macrofaunal $\delta^{15}N$ signatures did not differ among habitats on the Unimak margin (P = 0.098), but $\delta^{15}N$ was lighter in the clam bed than in non-seep sediments on the Kodiak margin ($F_{2,41} = 6.99$; P = 0.003).

Methane contribution

Estimates of the fraction of the seep macrofaunal carbon pool derived from methane varied across regions and habitats. This fraction was the greatest in the Florida Escarpment microbial mat macrofauna (55 ± 9%) and the least in the Unimak pogonophoran field macrofauna (9 ± 5%). The clam bed and pogonophoran field estimates were intermediate in Florida (clam bed 31 ± 10%, pogonophoran field 26 ± 8%), in the Unimak clam bed (22 ± 4%) and at Kodiak (clam bed 38 ± 5%, pogonophoran field 44 ± 9%). The mat macrofauna utilized more methane-derived carbon than macrofauna in the clam bed habitats but not than in the pogonophoran field (all data combined: $\chi^2 = 5.69$, df = 2, P = 0.058). Unimak macrofauna clearly experience less methane input to the carbon pool (or had a very different initial methane signature) than the Kodiak and Florida Escarpment macrofauna ($\chi^2 = 15.8$, df = 2, P = 0.0004).

Several taxa exhibited notably light $\delta^{13}C$ signatures, indicating that a high fraction of their carbon was derived from methane. Taxa with over 60% of carbon estimated to be methane-derived included ampharetid (FL), capitellid (Unimak), hesionid (FL), dorvilleid (Kodiak), lum-

brinerid (Kodiak) and nereidid (Unimak, Kodiak) polychaetes as well as gammarid amphipods (FL, Kodiak) and a turbellarian (FL). Most of these taxa are traditionally assumed to be deposit feeders or omnivores (with jaws). Among these, several individual species exhibited extreme intraspecific $\delta^{13}C$ variation, apparently associated with microhabitat-specific diet differences. For example, at the Florida Escarpment, *Orseis* sp. $\delta^{13}C$ signatures were −69.22 ± 0.99‰ and −36.88 ± 2.13‰ in black and white microbial mat patches, respectively. At the Unimak site, *Capitella* sp. $\delta^{13}C$ signatures were −60.81‰ ± 1.60 (n = 5) for animals scooped from sediment and −32.32‰ ± 0.65 (n = 5) for individuals building tubes on the shells of *Calyptogena extenta* ($t_8 = -16.5$; P < 0.0001).

Discussion

Abundance patterns

Densities of deep-water macrofauna (>2000 m) outside of seep settings are typically only a few thousand individuals per m^2 and are believed to be controlled primarily by food supply (Levin & Gooday 2003; Smith & Demopoulos 2003). Factors that can counteract depth-related food limitation include proximity to land (*i.e.*, to a source of terrestrial or coastal productivity), upwelling-induced elevated surface production, and *in situ* chemosynthetic production. With the exception of the FL non-seep and pogonophoran field samples, most of the regions and habitat types yielded sample densities at the upper end of what might be expected for water depths >3000 m (*e.g.*, see Fig. 5.7 in Levin & Gooday 2003 for Atlantic comparisons). All the regions studied are adjacent to, but varying distances from a continent or islands. The Gulf of Alaska and Aleutian margins experience upwelling and high productivity as well as frequent turbidite flows triggered by seismic activity (Dobson *et al.* 1996). Few deep-water macrobenthic data are available for this region. The densities recorded here for the Kodiak and Unimak margins (both seep and non-seep) are higher than for two cores from 6460 and 7298 in the Aleutian Trench where densities were approximately 1300 ind·m^{-2} (Jumars & Hessler 1976). The Gulf of Mexico is a low-productivity water body compared with the Northeast Pacific, with relatively low densities and biomass recorded for deep-water benthic communities dependent on allocthonous inputs (Tyler 2003).

Florida microbial mat sediments supported mean macrofaunal densities (∼20,000 ind·m^{-2}) much higher than at the other sites and habitats studied here (Fig. 2), but comparable to densities observed within microbial-mat covered sediments at shallower seeps off Eel River, CA (Levin *et al.* 2003), Hydrate Ridge, OR (L. Levin,

unpublished data) and in the Gulf of Mexico (Robinson *et al.* 2004). While microbial mat patches on the Florida Escarpment clearly provide enhanced food supply for infauna (relative to background sediments), the lack of density differences between seep and non-seep settings on the Aleutian margin suggests limited seep enhancement of local infaunal productivity. The Alaska result mirrors seep/non-seep comparisons of macroinfauna off California (Levin *et al.* 2003; Levin 2005). There are no other seep macroinfaunal density data from depths >3000 m for comparison with those presented here. At Escanaba Trough (3200–3270 m), a sedimented hydrothermal vent, the macrofauna also did not differ in density from those of ambient sediments (Grassle & Petrecca 1994).

Community structure: composition and diversity

The overwhelming dominance of the hesionid *Orseis* and an ampharetid (*Amphisamytha* sp.) in the Florida seeps resembles the situation in Guaymas Basin hydrothermal sediments (the Gulf of California), where *Orseis grasslei* reached densities of 2844 ind·m^{-2}, and was co-dominant with the ampharetid polychaete *Amphisamytha galapagensis* and the dorvilleid polychaete *Ophryotrocha akessoni* (Petrecca & Grassle 1990). We have also observed hesionids to be abundant in microbial-mat covered sediments at Hydrate Ridge, Oregon (770 m HR South; L. Levin, unpublished observation). Dominance of microbial-mat covered seep sediments by one or two annelid taxa has been observed at upper slope depths off California (Eel River margin 500 m; Levin *et al.* 2003) and off the coast of Louisiana (Green Canyon, ~700 m; Robinson *et al.* 2004).

A comparison of FL seep infauna with the macroinvertebrates present in the FL Escarpment mussel beds (Turnipseed *et al.* 2004) reveals high dominance in both systems, but hesionids were only 2% of the community in the mussel beds. Ampharetid polychaetes and amphipods, abundant as infauna, were 21% and 5% of the mussel bed fauna, respectively. Similarities in community structure between FL infauna and mussel-bed fauna may reflect proximity (to similar source faunas) and the influence of sulfide and food supply.

High densities of gastropods and pogonophorans were observed in seep sediments at the Kodiak and Unimak sites (Appendices 2 and 3). Gastropod aggregations are common in microbial mats at Hydrate Ridge (Sahling *et al.* 2002) and on mussel beds in many locations at a wide range of depths (Sibuet & Olu 1998). While pogonophoran aggregations can appear on the upper slope (Dando *et al.* 1994; Gebruk *et al.* 2003), they occur at high densities forming 'fields' in deep water in the North Pacific and the Gulf of Mexico (Suess *et al.* 1998; this study).

Factors affecting infaunal composition and diversity at seeps are likely to include porewater hydrogen sulfide concentrations and fluxes, oxygen availability and sediment structural characteristics (Sahling *et al.* 2002; Levin *et al.* 2003). Both vesicomyid clams (Wallmann *et al.* 1997) and seep vestimentiferans (Cordes *et al.* 2003, 2005) are capable of modifying sediment porewater characteristics by bringing oxygen and sulfate down into the sediments, enhancing sulfate reduction, and removing hydrogen sulfide for use by sulfur oxidizing symbionts. Comparable information about pogonophoran effects is not available. However, the observation of slightly lower diversity in clam beds than pogonophoran fields suggests that the two taxa may be having different geochemical and structural effects. Enhancement of sulfate reduction by the megafauna should increase porewater sulfide concentrations, creating lower infaunal diversity in some zones due to negative sulfide effects but diversifying microbial activities and possible infaunal food sources (Levin *et al.* 2003).

High sulfide concentrations are usually toxic to metazoans (Bagaranao 1992). The very high dominance of *Orseis* sp. in Florida seeps may be the result of a limited pool of infaunal species tolerant to such conditions. Sulfide measurements at the Florida Escarpment (Chanton *et al.* 1993; W. Ziebis, unpublished data) and on the Aleutian margin (Suess *et al.* 1998; Gieskes *et al.* 2005; Ziebis *et al.* 2005) suggest that the Florida mat sediments, which supported the highest macrofaunal densities, were characterized by less oxygen penetration (<2 mm) and greater hydrogen sulfide concentrations than the other sites. Elevated H$_2$S concentrations generate high microbial biomass, which provides the nutrition fueling high animal biomass.

Nutrition of macrofauna

Heterotrophic macrofauna residing in seep sediments may feed on a variety of organic matter sources with different isotope signatures. These include photosynthetically derived terrestrial material and phytoplankton (or plankton consumers), or organic matter generated from chemosynthetic processes. Microbial processes such as bacterial sulfide oxidation and sulfate reduction as well as anaerobic methane oxidation are particularly important in seep sediments (Valentine 2002; Ziebis & Haese 2005) and may produce isotopically light δ^{13}C signatures. Methane itself is very light ($-45\permil$ to $-100\permil$ or less; Schoell 1988) and archaeal lipids in Florida and Aleutian sediments reflect even greater fractionation of carbon to yield δ^{13}C of $\leq-100\permil$ (Elvert *et al.* 2000; Zhang *et al.* 2003). Use of local nitrogen by chemosynthetic microbes also produces light δ^{15}N values, although the processes are not well understood.

Seep macrofauna in this study exhibited a large range of isotope signatures (Table 3) that must reflect habitat- and species-specific differences in importance of chemosynthesis to the food chain. However, the relationships among different microbial processes, the diets of heterotrophic seep infauna, and their isotopic signatures remain unclear. The Unimak, Kodiak, and Florida Escarpment macrofaunal communities each exhibit distinct isotope signatures, although in some cases habitat differences may exceed regional differences (Fig. 6). A comparison of macrofaunal $\delta^{13}C$ and $\delta^{15}N$ signatures in microbial-mat covered sediments to clam bed sediments yielded lighter values in mats on the Florida Escarpment (Fig. 6) and at Hydrate Ridge in Oregon (600 m), but not on the Eel River margin (California, 500 m) (Levin & Michener 2002). Fluid flow data suggest that microbial mats experience more consistent positive outflow of methane-rich fluids whereas clam beds may experience oscillatory flows at Hydrate Ridge (Tryon & Brown 2001; Tryon et al. 2002) and in the Gulf of Mexico (Tryon & Brown 2004). Higher methane flux could contribute to more sulfate reduction and anaerobic methane oxydation, which would yield lighter average microbial isotope signatures at these sites. The Florida mat sediments are likely to have had higher H_2S concentrations than observed in the other sites and habitats studied. Notably these 'mat' sediments did not support filamentous sulfide oxidizing bacteria (e.g., Beggiatoa or Thioploca), rather they appear to be amorphous, possibly Arcobacter or from a group of iron oxidizers. The difference in $\delta^{13}C$ signatures of infauna from 'black' and 'white' mat sediments at the Florida Escarpment (15‰ difference in average $\delta^{13}C$ values; Fig. 6) may reflect very different microbial processes supporting the food chain. These patches occur in close proximity (meters) and could mirror geochemically driven, small-scale spatial heterogeneity in the microbiology of seep sediments. Alternatively, they may reflect different local methane sources as the light and heavy mat signatures are characteristic of biogenic and thermogenic methane, respectively.

The source of the much lighter $\delta^{15}N$ signatures (about 5‰ lighter) in the Florida than Alaska habitats is unclear but it is notable that this trend extends to the non-seep fauna as well (Table 3, Fig. 6). The similarity of average $\delta^{13}C$ signatures for heterotrophic macrofauna in clam beds and pogonophoran fields across all sites suggests that macrofauna may have similar food sources in different habitats and even across ocean basins. Yet some species clearly utilize photosynthesis-based food resources while others specialize on isotopically light food sources such as anaerobic methane oxidizing archaea (Table 3); $\delta^{13}C$ values <−50‰ were frequent at all sites and values <−90‰ occurred in two taxa (a dorvilleid and a turbellarian).

Nematodes had some of the lightest $\delta^{13}C$ values in the Unimak clam beds (−43‰). While few isotopic data are available for meiofauna, similar light values have been reported for nematode dominating Beggiatoa mats at the Hakon Mosby mud volcano (Van Gaever et al. in press) and in the oxygen minimum zone off Mexico at 800 m (Levin et al., unpublished data). With an average $\delta^{13}C$ signature of −55‰, the Florida escarpment mat sediments support the 'lightest' macroinvertebrate assemblage $\delta^{13}C$ known from any seep (Fig. 6; Levin 2005), with over 50% of the macrofaunal tissue C derived from methane. The average % methane contribution was remarkably similar for the Florida clam bed and Kodiak seep habitats (∼30–40%). These estimates for methane contribution to animal tissues are higher than comparable estimates for infauna of shallower Pacific seeps (Levin & Michener 2002): 0–27% for macrofauna in Calyptogena pacifica beds off northern California (Eel River seeps, 500 m) and Oregon (Hydrate Ridge, 590 m) and 0–5% for macrofauna in microbial mats off Eel River. However, the Hydrate Ridge microbial mat fauna (590 m) had methane contributions of 20–44%, comparable with estimates for assemblages of the deeper seep regions and habitats studied in the present paper. Estimated methane contributions to the C pool for each species (Table 4) are upper estimates, as other food sources with $\delta^{13}C$ signatures lighter than phytoplankton may be used (these would lower the percentage estimate in the mixing model as in Levin & Michener 2002). Application of additional approaches such as fatty acid and lipid analysis could help resolve which diet items are generating the observed isotopic signatures.

Conclusions

While a comprehensive comparison of seeps across ocean basins is not possible given our limited data set, we found few characteristic communities or features common to Alaska and Florida deep-water seeps. Instead, our results suggest that common properties are more likely across habitats (microbial mats, clam beds, pogonophoran fields), independent of location or water depth. Within a region, the macrofaunal composition of clam bed and pogonophoran field habitats was fairly similar, but with different diversity patterns. Microbial mats on the Florida Escarpment exhibited high macrofaunal density and high dominance characteristic of shallower mat-covered seeps. There was little distinction between seep and non-seep sediments with respect to macrofaunal density (except on the Florida Escarpment), but there were large disparities in composition and sometimes diversity. The majority of heterotrophic seep macrofauna at the deep seeps exhibited stable isotopic evidence for chemosynthesis-based nutrition, with considerable utilization of methane-

Table 4. Estimated proportion of carbon in heterotrophic macrofaunal tissues derived from methane.

	Florida Escarpment			Unimak, AK		Kodiak, AK	
	Clam Bed	Microbial Mat	Pogonophoran Field	Clam Bed	Pogonophoran Field	Clam Bed	Pogonophoran Field
Polychaeta							
Amphisamytha sp.	0.60	0.25		0.17	0.09		
Capitellidae	0.24		0.05				
Capitella (Clam shell)				0.25			
Capitella (sediment)				0.82			
Cirratulidae				0.05		0.16	
Montacuta sp.						0.15	
Dorvilleidae						1.00	
Exallopus sp.				0.11			
Dorvilleidae				0.28			
Glyceridae				0.02			0
Goniadidae				0.29	0.01		
Orseis sp. (Black mat)		0.76					
Orseis sp. (White mat)		0.28					
Lumbrineridae				0.07	0.03	0.29	0.76
Maldanidae	0.35					0.65	0.60
Maldanidae A				0.00			
Maldanidae B				0.33			
Nephtyidae						0.26	0.46
Nereididae				0.75		0.68	
Opheliidae				0.01			
Onuphidae						0.38	
Paraonidae				0.13			
Phyllodocidae A				0.63			
Phyllodocidae B				0.02			
Polynoidae		0.36				0.30	
Spionidae				0.11			
Sternaspidae				0.05	0.00		
Syllidae						0.00	
Synelmis sp.	0.37						
Terebellidae				0.00		0.30	
Trichobranchidae						0.05	0.11
Unid. Polychaetea		0.51					
Oligochaeta				0.25			
Sipunculida				0.06			0.07
Turbellaria	0.26	1.00	0.31		0.40		
Nematoda				0.47			
Mollusca							
Bivalvia				0.00		0.30	0.45
Gastropoda				0.23		0.46	
Crustacea			0.25				
Gammarid amphipods	0.07			0.12			0.89
Gammaridae A	0.57	0.67		0.37			
Gammaridae B	0.00	0.53		0.37			
Caprellid amphipod						0.58	
Isopoda						0.43	
Isopoda A				0.23	0.37		
Isopoda B					0.00		
Tanaidacea			0.46	0.23	0.01		
Galatheidae crab						0.66	0.53
Mysidacea				0.17			
Ophiuroidea				0.00			
Cnidaria				0.26		0.34	0.57

Table 4. Continued.

	Florida Escarpment			Unimak, AK		Kodiak, AK	
	Clam Bed	Microbial Mat	Pogonophoran Field	Clam Bed	Pogonophoran Field	Clam Bed	Pogonophoran Field
Unidentified			0.10				
Average	0.31	0.55	0.23	0.21	0.11	0.39	0.44
Standard Error	0.06	0.08	0.07	0.04	0.06	0.06	0.09

derived C (40% of tissue C) observed for macrofauna at two of the three deep regions studied. Overall, macrofaunal densities were lower (except Florida mats), community structure was similar and reliance on chemosynthesis was equal or greater than in shallower seeps in the northeast Pacific Ocean.

Acknowledgements

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Appendix 1.

Table 1. Florida Escarpment macrofauna. Number per 37.8 cm^2 core. (SE)

Florida Escarpment	microbial mat	pogonophoran field	background
Annelida			
Polychaeta			
Hesionidae			
Orseis sp.	63.00 (25.58)	0.00 (0)	0.00 (0)
Ampharetidae			
Amphisamytha sp.	9.00 (3.19)	0.00 (0)	0.00 (0)
Pilargidae			
Sigambra tentaculata	0.75 (0.75)	0.00 (0)	0.00 (0)
Spionidae			
Prionospio(?) juv.	0.00 (0)	0.00 (0)	0.33 (0.33)
Dorvilleidae			
Ophryotrocha sp.	0.00 (0)	0.50 (0.5)	0.00 (0)
Protodorvillea cf. *kefersteini*	0.00 (0)	1.00 (0)	0.00 (0)
Fauveliopsidae			
Fauveliopsis sp.	0.00 (0)	0.50 (0.5)	0.00 (0)
Glyceridae			
Glycerid juvenile	0.00 (0)	0.50 (0.5)	0.00 (0)
Paraonidae			
Paraonid? (juv)	0.00 (0)	0.50 (0.5)	0.00 (0)
Arthropoda			
Crustacea			
Amphipoda			
Gammaridea			
Unid. gammarid	5.50 (3.01)	0.00 (0)	0.67 (0.67)
Echinodermata			
Ophiuroidea			
Unid. ophiuroidae	0.25 (0.25)	0.00 (0)	0.00 (0)

Table 1. Continued.

Florida Escarpment	microbial mat	pogonophoran field	background
Mollusca			
Bivalvia			
Unid. bivalve	0.25 (0.25)	0.00 (0)	0.00 (0)
Gastropoda			
Unid. gastropod	0.50 (0.5)	0.00 (0)	0.00 (0)
Cnidaria			
Anthozoa(?)			
undetermined phylum			
unknown	0.00 (0)	0.50 (0.5)	0.00 (0)
total macrofauna	79.25 (31.06)	3.50 (0.5)	1.00 (0.58)

Values are expressed as mean (1 SE).

Appendix 2.

Table 2. Kodiak seep macrofauna. Number per 100 cm^2. (SE)

	clam bed	non-seep	pogonophoran field
Annelida			
Oligochaeta			
Tubificidae			
Unid. tubificid	0.68 (0.68)	3.04 (1.29)	0.00 (0)
Polychaeta			
Siboglinidae			
Unid. pogonophoran	0.98 (0.98)	0.00 (0)	32.77 (6.28)
Ampharetidae			
Unid. ampharetid	5.33 (1.57)	0.55 (0.31)	3.05 (1.71)
Capitellidae			
Unid. capitellid	0.34 (0.34)	0.55 (0.31)	0.00 (0)
Chrysopetalidae			
Unid. chrysopetalid	0.00 (0)	0.00 (0)	0.36 (0.36)
Dysponetus spp.	0.34 (0.34)	0.00 (0)	0.00 (0)
Cirratulidae			
Unid. cirratulid	4.08 (2.58)	4.70 (1.02)	0.98 (0.98)
Cirratulidae sp. a	0.00 (0)	0.83 (0.76)	0.00 (0)
Cossuridae			
Unid. cossurid	0.34 (0.34)	0.28 (0.25)	0.98 (0.98)
Dorvilleidae			
Unid. dorvilleid	0.34 (0.34)	0.28 (0.25)	1.66 (0.87)
Lumbrineridae			
Unid. lumbrinerid	0.49 (0.49)	0.28 (0.25)	1.66 (0.87)
Maldanidae			
Unid. maldanid	0.49 (0.49)	0.00 (0)	0.00 (0)
Nereididae			
Unid. nereidid	0.34 (0.34)	0.00 (0)	0.00 (0)
Nephtydae			
Unid. nephtyid	1.32 (0.98)	0.00 (0)	0.00 (0)
Aglaophamus nr. *paucilamellata*	0.34 (0.34)	0.00 (0)	0.00 (0)
Nephtyidae sp. a	0.49 (0.49)	0.00 (0)	0.00 (0)
Opheliidae			
Unid. opheliid	0.00 (0)	1.11 (0.62)	0.00 (0)
Opheliidae sp. a	0.00 (0)	0.28 (0.25)	0.00 (0)
Paraonidae			
Unid. paraonid	0.00 (0)	1.11 (0.47)	0.36 (0.36)
Phyllodocidae			
Unid. phyllodocid	0.00 (0)	0.28 (0.25)	0.00 (0)

Table 2. Continued.

	clam bed	non-seep	pogonophoran field
Polynoidae			
Unid. polynoid	0.00 (0)	0.55 (0.31)	0.68 (0.68)
Sabellidae			
Unid. sabellid	0.00 (0)	0.28 (0.25)	0.00 (0)
Sphaerodoridae			
Unid. sphaerodorid	0.00 (0)	0.28 (0.25)	0.00 (0)
Spionidae			
Unid. spionid	0.34 (0.34)	6.91 (2.18)	0.00 (0)
Spionidae sp. b	0.00 (0)	0.55 (0.5)	0.00 (0)
Syllidae			
Unid. syllid	0.00 (0)	0.28 (0.25)	0.00 (0)
Parergodrilidae (?)			
Nr. Parergodrilidae	0.00 (0)	0.00 (0)	2.71 (0.87)
undetermined family			
Unid. polychaete	3.94 (2.6)	0.28 (0.25)	0.00 (0)
Sipunculida			
Unid. sipunculid	0.00 (0)	0.28 (0.25)	0.00 (0)
Nemertinea			
Unid. nemertean	1.36 (1.36)	0.28 (0.25)	0.98 (0.98)
Arthropoda			
Crustacea			
Isopoda			
Unid. isopod	1.02 (0.7)	1.66 (0.47)	2.03 (0.54)
Unid. caprellid	0.34 (0.34)	0.00 (0)	0.36 (0.36)
Amphipoda			
Unid. gammarid	0.34 (0.34)	0.00 (0)	3.17 (1.63)
Gammaridea sp. a	2.72 (1.8)	0.00 (0)	0.00 (0)
Unid. amphipod	0.00 (0)	0.28 (0.25)	1.04 (0.59)
Tanaidacea			
Unid. tanaid	0.00 (0)	3.87 (1.22)	0.00 (0)
undetermined order			
Unid. crustacean	0.00 (0)	0.83 (0.5)	0.00 (0)
Mollusca			
Bivalvia			
Solemya sp.	0.49 (0.49)	0.00 (0)	0.00 (0)
Bivalve sp. a	3.21 (2.67)	0.00 (0)	0.00 (0)
Bivalve sp. b	0.34 (0.34)	0.00 (0)	0.00 (0)
Bivalve sp. c	1.36 (0.86)	0.00 (0)	0.00 (0)
Unid bivalve	3.79 (2.39)	1.93 (0.64)	10.42 (5.04)
Gastropoda			
Unid. gastropod	0.00 (0)	0.00 (0)	1.35 (0.86)
Aplacophora			
Unid. aplacophoran	0.49 (0.49)	0.28 (0.25)	0.00 (0)
Scaphopoda			
Unid. scaphopod	0.34 (0.34)	1.11 (0.25)	0.00 (0)
Echinodermata			
Holothuroidea			
Unid. holothurid	0.00 (0)	0.00 (0)	0.68 (0.68)
Ophiuroidea			
Unid. ophiuroid	0.00 (0)	0.28 (0.25)	0.00 (0)
Porifera			
Unid. poriferan	0.00 (0)	0.28 (0.25)	0.00 (0)
Cnidaria			
cnidaria (?)	0.00 (0)	0.28 (0.25)	0.00 (0)
Unid. cnidarian	0.34 (0.34)	0.28 (0.25)	0.00 (0)
Anthozoa			
Unid. anthozoan	1.17 (0.54)	0.00 (0)	0.98 (0.98)

Table 2. Continued.

	clam bed	non-seep	pogonophoran field
Undetermined phylum			
unknown 6	0.34 (0.34)	0.00 (0)	0.00 (0)
unknown 7	0.00 (0)	0.28 (0.25)	0.00 (0)

Values are expressed as mean (1 SE).

Appendix 3.

Table 3. Macrofauna of Unimak margin seep. Number per 54.08 cm^2 core. (SE)

	vesicomyid clam bed	pogonophoran field	non-seep – slope	non-seep – mudmount
Depth (m)	3267	3283	3302–10	3165–90
Annelida				
Oligochaeta				
Tubificidae				
Unid. tubificid	0.67 (0.33)	0.33 (0.33)	0.00 (0)	0.40 (0.4)
Tubificidae (?)	0.00 (0.00)	0.00 (0)	0.67 (0.67)	0.00 (0)
Polychaeta				
Siboglinidae				
Unid. pogonophoran	0.00 (0.00)	0.33 (0.33)	0.00 (0)	0.00 (0)
Polynoidae				
Unid. polynoid	0.67 (0.67)	0.33 (0.33)	0.33 (0.33)	0.20 (0.2)
Ampharetidae				
Unid. ampharetid	1.67 (0.88)	1.33 (0.88)	3.00 (0.58)	0.60 (0.4)
ampharetid (?)	0.00 (0.00)	0.00 (0)	0.67 (0.67)	0.40 (0.4)
Sphaerodoridae				
Unid. sphaerodorid	0.33 (0.33)	0.33 (0.33)	0.00 (0)	0.00 (0)
Acrocirridae				
Unid. acrocirrid	0.67 (0.67)	0.67 (0.67)	0.33 (0.33)	0.60 (0.4)
Dorvilleidae				
Ophryotrocha platykephale	0.00 (0.00)	0.33 (0.33)	0.00 (0)	0.00 (0)
Unid. dorvilleid	0.00 (0.00)	0.00 (0)	0.33 (0.33)	0.00 (0)
Paraonidae				
paraonid sp. N	1.00 (0.58)	0.00 (0)	0.33 (0.33)	2.00 (1.76)
paronidae spp.	0.67 (0.33)	0.67 (0.33)	1.00 (0.58)	2.60 (1.33)
Lumbrineridae				
lumbrinerid (?)	0.67 (0.67)	0.00 (0)	1.00 (1)	0.20 (0.2)
Cossuridae				
Unid. cossurid	0.67 (0.67)	0.67 (0.33)	2.67 (1.45)	0.00 (0)
Maladanidae				
Unid. maldanid	0.67 (0.33)	0.33 (0.33)	1.00 (0.58)	0.00 (0)
Opheliidae				
Unid. opheliid	0.00 (0.00)	1.00 (1)	1.00 (0.58)	0.20 (0.2)
Spionidae				
spionidae spp.	0.00 (0.00)	1.00 (0.58)	1.67 (1.67)	0.20 (0.2)
Prionospio spp.	0.33 (0.33)	0.00 (0)	0.33 (0.33)	0.00 (0)
Hesionidae				
Unid. hesionid	0.33 (0.33)	0.67 (0.67)	0.00 (0)	0.00 (0)
Cirratulidae				
Unid. cirratulid	1.00 (0.58)	0.33 (0.33)	2.00 (0.58)	0.60 (0.4)
cirratulid (?)	0.00 (0.00)	1.33 (1.33)	2.00 (1.53)	0.40 (0.24)
Capitellidae				
Unid. capitellid (?)	0.00 (0.00)	0.67 (0.33)	0.33 (0.33)	0.20 (0.2)
Sabellidae				
Unid. sabellid	0.00 (0.00)	0.33 (0.33)	0.00 (0)	0.00 (0)

Table 3. Continued.

	vesicomyid clam bed	pogonophoran field	non-seep – slope	non-seep – mudmount
Depth (m)	3267	3283	3302–10	3165–90
Syllidae				
Unid. syllid	0.00 (0.00)	0.67 (0.33)	0.00 (0)	0.00 (0)
Syllidae (?)	0.00 (0.00)	0.00 (0)	0.33 (0.33)	0.20 (0.2)
Phyllodocidae				
Unid. phyllodocid	0.00 (0.00)	0.00 (0)	0.33 (0.33)	0.60 (0.4)
Nereididae				
Unid. nereidid	0.00 (0.00)	0.00 (0)	0.00 (0)	0.20 (0.2)
undetermined family				
Unid. polychaete	0.67 (0.67)	0.67 (0.33)	1.00 (0)	0.00 (0)
Arthropoda				
Crustacea				
Cumacea				
Unid. cumacean	0.00 (0.00)	1.00 (1)	0.67 (0.33)	0.40 (0.4)
Isopoda				
Unid. isopod	0.33 (0.33)	1.33 (0.67)	1.67 (1.2)	0.00 (0)
Tanaidacea				
Unid. tanaid	3.00 (1.73)	5.00 (4)	3.33 (0.88)	1.20 (0.49)
Amphipoda				
Unid. gammarid	0.33 (0.33)	1.67 (1.67)	0.33 (0.33)	2.80 (1.02)
Mollusca				
Bivalvia				
Unid. bivalve	1.00 (0.58)	1.33 (0.67)	0.33 (0.33)	0.80 (0.49)
Acharax sp.	0.00 (0.00)	0.33 (0.33)	0.00 (0)	0.00 (0)
Gastropoda				
Gastropod sp. A	0.00 (0.00)	9.33 (9.33)	0.00 (0)	0.00 (0)
Gastropod sp. B	0.00 (0.00)	1.33 (1.33)	0.00 (0)	0.00 (0)
Gastropod spp.	0.00 (0.00)	8.33 (7.84)	0.00 (0)	0.00 (0)
Aplacophora				
Unid. aplacophoran	0.33 (0.33)	1.00 (0.58)	0.33 (0.33)	0.00 (0)
Scaphopoda				
Unid. scaphopod	0.00 (0.00)	2.67 (1.76)	0.67 (0.33)	0.00 (0)
Echinodermata				
Ophiuroidea				
Unid. ophiuroid	0.00 (0.00)	0.33 (0.33)	0.00 (0)	0.40 (0.24)
Nemertinea				
Unid. nemertean	0.00 (0.00)	5.33 (4.37)	1.00 (0.58)	0.20 (0.2)
Cnidaria				
Anthozoa				
Unid. anthozoan	0.00 (0.00)	0.33 (0.33)	0.00 (0)	0.00 (0)
Hydroidea				
Unid. hydrozoan (?)	0.00 (0.00)	1.00 (1)	0.00 (0)	0.00 (0)
Sipunculida				
Unid. sipunculid	0.33 (0.33)	0.00 (0)	0.33 (0.33)	0.20 (0.2)
Undetermined phylum				
unidentified sp. a	0.00 (0.00)	0.33 (0.33)	0.00 (0)	0.00 (0)
total macrofauna	15.33 (4.81)	52.67 (12.67)	29.00 (1)	15.60 (4.91)

Values are expressed as mean (1 SE).