

Do methane seeps support distinct macrofaunal assemblages? Observations on community structure and nutrition from the northern California slope and shelf

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ABSTRACT: Although the conspicuous epifauna of reducing environments are known to exhibit strong morphological, physiological, and nutritional adaptations for life in these habitats, it is less clear whether infaunal organisms do so as well. We examined metazoan macrofauna from methane-seep sediments on the northern California slope (500 to 525 m depth) and from seep and non-seep sediments at 3 locations on the shelf (31 to 53 m depth) to determine whether the community structure and nutritional sources of seep infauna were distinct from those in non-seep, margin sediments. Seep macrofauna consisted mainly of normal slope and shelf species found in productive settings. Several macrofaunal taxa, such as *Capitella* sp., *Diastylopsis dawsoni*, and *Synidotea angulata*, exhibited a preference for seeps. Other taxa, such as the amphipods *Rhepoxynius abronius* and *R. daboius*, avoided seeps. Species richness of shelf macrofauna, evaluated by rarefaction and diversity indices (H' and J'), generally did not differ in seep and non-seep sediments. Similarly, stable isotopic composition ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) of active seep and non-seep macrofauna did not differ at the 3 shelf sites. Stable isotopic analyses of calcareous material confirmed the presence of methane-influenced pore waters at the slope study site. At one slope clam bed, macrofaunal $\delta^{13}\text{C}$ signatures were lower and $\delta^{15}\text{N}$ values were higher than at another clam bed, in inactive slope sediments and shelf sites. However, only 1 of 14 macrofaunal taxa (a dorvilleid polychaete) exhibited isotopic evidence of chemosynthetic nutritional sources. At these sites, seep influence on the ecology of continental margin infauna appears spatially limited and relatively subtle. At their current level of activity, the northern California slope and shelf seeps appear to function as ephemeral, small-scale disturbances that are not sufficiently persistent to allow chemosynthesis-based trophic specialization by most infauna. Rather, we suggest that many of the infauna inhabiting these seep sediments are shelf and slope species preadapted to organic-rich, reducing environments.

KEY WORDS: Macrofauna · Macrobenthos · Methane cold seep · Sulfide · Stable isotope · $\delta^{13}\text{C}$ · $\delta^{15}\text{N}$ · Chemoautotrophy · Diversity · Eel River margin

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INTRODUCTION

Seafloor sediments provide varied environments for sediment-dwelling macrofauna (infauna). Because the

physical and chemical properties of the sediments can strongly influence resident animals (McCall & Tevesz 1982), processes that change these properties can potentially exert strong influence on infaunal communities. One such process is the venting of methane, and consequent microbially mediated oxidation, which is

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coupled with sulfate reduction in anaerobic environments (Beauchamp et al. 1989, Masuzawa et al. 1992). Since discovery of the first methane seeps (Paull et al. 1984), seep-like environments have been found in varied settings, including subduction zones, transform faults, mass wasting sites (Hovland & Judd 1988, Sibuet & Olu 1998), pockmarks (Dando et al. 1991, 1994), and around dead marine mammals (Smith et al. 1998). These sites are characterized by the presence of reduced sulfides and methane, limited oxygen within sediments, high microbial biomass (Guezennec & Fiala 1996), and often a characteristic epibiota that includes symbiont-bearing clams, vestimentiferan tube worms and sometimes mussels or gastropods (Hovland & Judd 1988, Sibuet & Olu 1998). During the past decade, a large number of sites venting cold, methane-rich fluids have been discovered along the eastern and western Pacific margins. Sites of fluid flow in near-surface Pacific sediments include the Nankai Trough and Japan Trench (Boulegue et al. 1987a,b, Dron et al. 1987, Sibuet et al. 1988, Gamo et al. 1992), Gulf of Alaska (Suess et al. 1998), Oregon subduction zone (Han & Suess 1986, Kulm et al. 1986, Suess & Whiticar 1989), northern California slope (Brewer et al. 1997, Yun et al. 1999), Monterey Bay (Barry et al. 1996, 1997), accretionary prisms off Costa Rica (Zuleger et al. 1995, 1996) and Barbados (Olu et al. 1996b, 1997), and the Peruvian margin (Olu et al. 1996a).

Most reports of seep fauna have focused on the larger, surface-dwelling organisms (megafauna) (reviewed in Sibuet & Olu 1998) but there are several reports of smaller infauna (Table 1); only a few of these examined infaunal community structure. Megafauna and macrofauna of methane seeps and pockmarks have been studied most thoroughly in shallow waters of the Santa Barbara margin (Davis & Spiess 1980, Montagna et al. 1989), the North Sea (Dando et al. 1991, 1994, Jones 1993, 1996) and the Skagerrak (Dando et al. 1994). General patterns emerging from these studies suggest that densities of macrofauna living in seep environments may be elevated or reduced relative to non-seep conditions. In all instances where this was examined, dominance was high and species diversity was relatively low, relative to surrounding sediments. Several megafaunal or meiofaunal taxa at seeps belong to genera or families known to bear symbionts. Examples include pogonophorans, thyasirid, lucinid and vesicomyid clams, and various gutless nematodes (Table 1).

Analyses of the natural, stable isotopic compositions of tissues ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^{34}\text{S}$) have been used as a means to determine food sources in organisms inhabiting reducing environments (e.g., Paull et al. 1985, Brooks et al. 1987, Cary et al. 1989, Kennicutt et al. 1989, Schmaljohann et al. 1990, Conway et al. 1994). The

stable isotopic compositions ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) of carbonate skeletal material from deep-sea organisms can also be indicative of ambient temperature and chemistry conditions (Van Dover & Fry 1989, Sen Gupta & Aharon 1994). Large depletions of $\delta^{13}\text{C}$ (–30 to –70‰) in the tissues of organisms, such as vestimentiferans, bivalves and gastropods, have been proposed to indicate methanotrophy or sulfide oxidation by symbionts in seep and vent taxa (Paull et al. 1985, Brooks et al. 1987, Van Dover & Fry 1989). However, comparable isotopic signatures may be acquired from consumption of free-living chemosynthetic bacteria (e.g., *Beggiatoa* or *Thioploca*), or by predation on animals with endosymbionts. Plankton detrital matter and terrestrially derived organic matter are other possible food sources for continental margin seep faunas.

This paper examines the metazoan macrofauna within shelf and slope seep sediments on the Eel River margin of northern California, USA, and for the shelf assemblages, draws comparisons with non-seep faunas. The following questions are addressed: (1) Do sites of methane seepage support macrofaunal assemblages distinct from those in non-seep sediments with respect to composition and diversity? and (2) Do methane seep macrofauna derive nutrition from different sources than non-seep macrofauna? Specifically, do seep infauna utilize chemosynthetically fixed organic matter? This latter question was addressed using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses.

METHODS

Macrofauna were sampled from northern California methane seeps located on the continental slope at 500 to 525 m depth during October 1997 and on the shelf at 31 to 53 m depth during October 1998 (Fig. 1). This margin is a dynamic environment subject to extensive, rapid deposition of flood-derived terrestrial sediment, episodic seismic activity characteristic of convergent margins, intense, winter-storm-induced sediment re-suspension, and migration of subsurface gases and pore fluids that alter surface morphology and redistribute sediments (Alexander & Simoneau 1999, Yun et al. 1999). Seep samples from the slope site were collected in 5 distinct *Calyptogena pacifica* clam beds (40° 47.08' N, 124° 35.68' W) and nearby inactive areas (40° 47.12' N, 124° 35.61' W) with tube cores (8.3 cm inner diameter, 10 to 15 cm deep) using the ROV 'Scorpio' and Sea Cliff submersible. Macrofauna were examined from 6 clam bed cores, and from 2 cores in sediments away from clam beds (Table 2). Seep and non-seep sediments were sampled at 3 shelf sites: 1 north of the Eureka Harbor (Site A, 50 to 53 m deep, 40° 49.87' N, 124° 15.95' W) and 2 south of the Harbor

Table 1. Summary of infaunal studies (megafauna, macrofauna and meiofauna) in seep environments. PAH: polyaromatic hydrocarbon

Location	Depth (m)	Seep type	Major epifaunal feature	Faunal observations	Source
Santa Barbara, USA	16	Hydrocarbon	<i>Beggiatoa</i> mats	72% of species and 90% of individuals shared with non-seep sites 60% of spp. had higher densities at seeps, especially tubificid oligochaetes Dominance and diversity similar to outside seeps More deposit feeders, fewer carnivores at seeps Nematodes dominate seep meiofauna (85%)	Davis & Spies (1980) Montagna et al. (1989)
Flower Garden, Gulf of Mexico, USA	70	Brine, sulfides	<i>Beggiatoa</i> mats	Meiofauna dominated by gnathostomulida, platyhelminthes, aschelminthes, and amphipods Fauna distinct from non-seep sites, but densities similar Nematodes show higher dominance, body elongation	Powell & Bright (1981) Powell et al. (1983) Jensen (1986)
Gulf of Mexico, USA	350–2200	Hydrocarbon/methane Ammonia	Microbial mats, tube worms, clams, mussels	Lucinid, thyasirid clams associated with lithified sediments to 65 cm deep. PAH present in tissues $\delta^{13}\text{C}$ varies—multiple C sources	MacDonald et al. (1990) Wade et al. (1989) Brooks et al. (1987)
Barbados Prism	1000–2000	Methane seeps		Maldanidae, Echiura, Sipuncula Polyplacophora	Olu et al. (1996b)
Barbados Prism	6800	Methane seeps		Maldanidae, Chaetopteridae, Ampharetidae, meiofauna up to 11 000 ind. 10 cm ⁻²	Olu et al. (1997)
Guaymas Basin, Gulf of California, Mexico	2020	Hydrocarbon/hydrothermal venting (hot)	<i>Beggiatoa</i> mats, <i>Calyptogena pacifica</i>	High densities, low spp. richness Patchy faunal distributions Dorvilleid polychaetes dominate Also, ampharetid <i>Amphisamytha</i> , trochid gastropods, <i>Exallopus</i> , <i>Nuculana</i>	Grassle et al. (1985)
Florida Escarpment, USA	3300	Brine, methane, sulfides	<i>Beggiatoa</i> , tube worms, mussels, gastropods	3 cores taken—some species also present in Pacific vents (<i>Amphisamytha</i> , <i>Nicomache</i> , <i>Hesiospira</i>)	Petrecca & Grassle (1987) Cary et al. (1989) Paul et al. (1984)
Hatsuchima Seep, Japan	1170	Methane seep	<i>Calyptogena soyae</i>	Meiofauna abundance at seep similar to control Nematodes less diverse at seep Maldanids <i>Nicomache</i> present <i>N. ohta</i> has <i>Beggiatoa</i> -like filaments	Shirayama & Ohta (1990) Miura & Hashimoto (1991)
Nankai Trough, Japan Trench,	3830 5900	Methane seep	3 spp. <i>Calyptogena</i> <i>C. phaseoliformis</i>	Serpulids associated with clams Tubicolous polychaetes in mudstone, caprellids Caprellid amphipods and tubicolous polychaetes near clams	Juniper & Sibuet (1987)
Kashima Seamount, Japan	5640		<i>C. phaseoliformis</i>		
Laurentian Fan	3850	Methane, sulfides	<i>Calyptogena</i>	<i>Thyasira</i> , <i>Solemya</i> , pogonophorans, <i>Spirobranchia</i> , galatheid crabs	Petrecca & Grassle (1987)
North Sea	115	Methane seep Pockmarks	<i>Beggiatoa</i>	Taxa with chemosynthetic symbionts including <i>Thyasira</i> , <i>Astomonema</i> , <i>Siboglinium</i> Polychaetes rare, but many non-seep taxa present Macrofaunal dominance high, diversity low Nematodes dominated meiofauna	Dando et al. (1991) Jensen et al. (1992)
Kattegat, Denmark	10	Bubbling reefs (carbonate) Sandy seeps	<i>Cancer pagurus</i> <i>Homarus vulgaris</i> <i>Metridium senile</i>	Reduced densities of nematodes, oligochaetes and polychaetes relative to nearby control sites Infauna concentrated in upper 2 cm Symbiont bearing nematodes to 22 cm <i>Leptonemella aphanothecae</i>	
Skaggerak, Denmark	300	Methane seep		Pogonophorans form 63% of infauna. Also, <i>Paramphinome</i> , <i>Abra</i> , <i>Nucula</i> , <i>Amphiura</i>	Dando et al. (1994)
Monterey Bay, USA	906	Cold seep	<i>Beggiatoa</i> , <i>Thioploca</i> sp. mats <i>Calyptogena</i> sp.	Nematodes dominant Nematode and ciliate biovolume and density higher at seep than control sites Largest body diameter at seeps	Buck & Barry (1998)

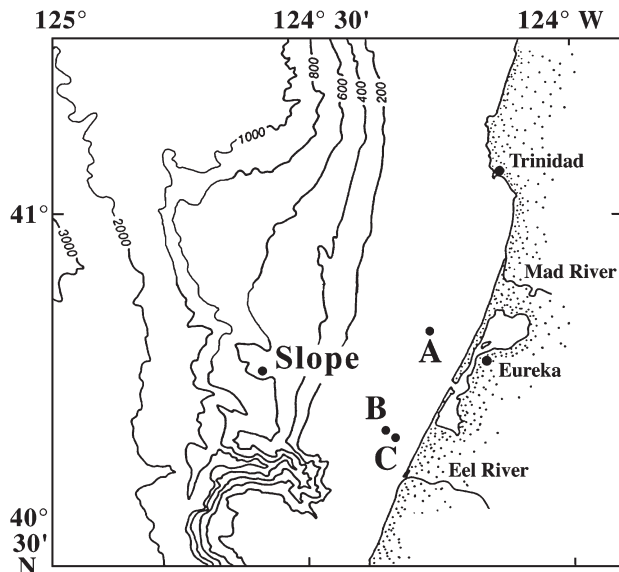


Fig. 1. Location of sampling stations on the northern California shelf and slope, USA

(Site B, 40 to 43 m deep, 40° 42.22' N, 124° 22.35' W; Site C, 31 to 37 m deep, 40° 41.83' N, 124° 21.37' W). Shelf sediments were sampled by the Delta submersible's slurp device and by shipek grabs deployed from the surface on the RV 'McGaw' (Table 2). The slurp and shipek samples collected the upper 6 to 8 cm of sediment, but were considered non-quantitative for analytical purposes.

On board ship, shipek samples were designated as seep samples if sediments were black and smelled sulfidic. They were considered non-seep samples if they were brown or tan and did not smell of sulfide. Five of the shipek samples appeared to be transitional between seep and non-seep sediments (gray sediments, slight sulfide smell). These were discarded from the analysis. Slurp samples were designated as seep samples if the scientist in the submersible viewed black surface sediments and methane bubbles emerging from the collection site.

The occurrence of methane seeps is well documented for the study sites (Brewer et al. 1997, Yun et al. 1999). They are oriented along deep-rooted structures in the accretionary wedge (e.g., faulted anticlines) (K. Brown pers. comm.). Although modern wood debris is ubiquitous in near-surface sediments on the Eel River margin, it is refractory. Degradation of ancient terrestrial detritus is the likely methane source on the shelf, while methane hydrates are the probable source of the observed sulfidic sediments and bubbles on the slope (Brewer et al. 1997).

On board ship, macrofauna samples were sieved on a 0.3 mm mesh and the material retained was preserved in 8% buffered formaldehyde and seawater. In the laboratory, macrofauna were sorted from sediments, counted, and identified to the lowest taxon possible. Macrofaunal diversity was examined using rarefaction analyses (Hurlbert 1971), the information index ($H' \log_2$), and evenness (J') with the software Biodiversity Pro (McAleece et al. 1997). Species count data were pooled within each station and treatment for the rarefaction analyses. Differences among sites and between seep versus non-seep sediments were examined for species composition and isotopic signatures with 1-way ANOVA or with *t*-tests using JMP® software. Proportions were arcsine-transformed prior to analysis. Multivariate analyses of community composition were performed by multidimensional scaling (MDS) and analysis of similarities (ANOSIM) (on uniform numbers of replicates) using Primer software (Clarke & Warwick 1994). Multivariate analyses were conducted on species proportions because the shipek and slurp samples did not allow accurate density estimates.

At both shelf and slope sites, some macrofauna were sorted live on board ship, counted, identified and frozen in liquid nitrogen for subsequent analyses of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Table 2). Isotopic analyses were conducted using a Finnigan ConFlo II continuous flow system and a Fisons NA1500 elemental analyzer. Prior to combustion, all samples were acidified with 1% PtCl_2 to remove carbonates.

Surface sediments from the slope and each shelf site (0 to 2 cm deep) were frozen on board ship for later

Table 2. Number of samples examined for macrofauna on the northern California shelf and slope and number of individuals assayed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

	Slurp		Shipek grab		Tube cores		Isotopic analyses (no. of ind.)	
	Seep	Non-seep	Seep	Non-seep	Seep	Inactive	Seep	Non-seep
Site A (50 m deep)	5	2	3	3	0	0	20	11
Site B (40 m deep)	4	4	6	6	0	0	2	2
Site C (35 m deep)	0	2	6	33	0	0	19	15
Slope (500 m deep)	0	0	0	0	6	2	19	7

analyses of sand, carbonate, and organic carbon and nitrogen content. Percent sand ($>63\ \mu\text{m}$) and silt and clay ($<63\ \mu\text{m}$) were determined by wet sieving homogenized sediments through a $63\ \mu\text{m}$ screen, drying the sediments at 80°C for 48 h, and weighing the fractions. Organic C and N contents were analyzed on freeze dried sediments using a Perkin-Elmer CHN analyzer after removing inorganic carbonate through dissolution in 10% HCl. Bottom water was collected in a Niskin bottle by the ROV Scorpio or Delta submersible from within 2 m of the sediment surface for oxygen analysis. Samples were preserved in volumetric flasks with MnCl_2 and NaOH/NaI at sea and returned to the Scripps Institution of Oceanography for analysis of oxygen concentration on a modified Technicon AA-II continuous flow analyzer.

RESULTS

Site descriptions

Active venting of methane bubbles, visible at the sea surface and on the seabed, was observed in the 3 shelf areas sampled. Methane seepage was widespread but patchy, with discoloration of sediments (indicating sulfidic patches) on scales of decimeters to a meter. Storms during the cruise produced bottom disturbances and bedload transport over the entire study area, preventing sampling by the Delta submersible on some days. No microbial mats or typical seep epifauna were evident. Sediments often were rippled and swell troughs were present. No carbonate concretions were visible on the surface. Epifaunal flatfish, decapods, and cnidarians were abundant at Site A. Mysids, isopods and small flatfish were visible at Sites B and C.

On the slope, dense aggregations of the clam *Calypptogena pacifica* were observed in beds ca 15 to $100\ \text{cm}^2$, often with a mix of living and dead shells. The distribution of clam beds suggested that seepage occurred in patches over at least $1\ \text{km}^2$ of seafloor. Sea pens, the sea star *Rathbunaster californicus*, and the cnidarian *Anthomastus ritteri* were common throughout the area, though the cnidarians were absent in clam beds. Although sediments contained fine mud and did not appear to be current swept, tidal forcing generated strong, periodic bottom currents. Boulder-sized outcrops of authigenic carbonate were observed, with smaller carbonate nodules present within sediments. Rapid venting of methane bubbles was observed in a 2 m diameter depression at ca 520 m. Venting of seep fluids is indicated by pore-water profiles in 10 to 23 cm deep cores from 3 slope clam beds (clam beds 2, 3 and 4). These profiles revealed upward advection of slightly more saline, and Ca- and Mg-

depleted fluids (J. Gieskes unpubl. data). However, compositional changes were relatively small, indicating that upward moving fluids mixed substantially with seawater prior to reaching the sediment-water interface.

Bottom-water and sediment properties

Bottom-water oxygen concentrations were higher on the shelf (2.74 to $2.95\ \text{ml l}^{-1}$) than at the slope site ($0.76 \pm 0.02\ \text{ml l}^{-1}$), which was at the upper boundary of the oxygen minimum zone (Table 3). Sediments at all sites were relatively coarse grained, but were markedly sandier at the 2 shallowest sites (B and C; 84 to 95% sand), than at Site A (63% sand) or the slope site (69% sand) (Table 3). Correspondingly, sediment organic C content was low ($<1\%$) at all sites, but was slightly higher in the finer-grained areas (Table 3). No marked differences in sand content or organic matter content were evident between seep and non-seep sediments within a site.

Macrofaunal composition

Shelf settings

A total of 1269, 892, and 925 infaunal animals (excluding mysids) were examined from shelf Sites A, B, and C, respectively. Most of the macrofaunal species collected from the shelf seeps also were present in nearby non-seep sediments (Table 4). The assemblage collected at both seep and non-seep sites was typical for sandy shelf environments. Dominant taxa included the isopod *Tecticeps convexus*, the amphipod *Rhepoxyanius daboius*, the cumacean *Diastylopsis dawsoni*, the gastropod *Astyris gausapata*, and the polychaetes *Nephtys californiensis*, *N. cornuta*, *Lumbrineris* sp., *Amaeana occidentalis*, *Scoletoma tetraura*, *Magelona sacculata*, and *Mediomastus* spp. (Table 4).

Of the 201 taxa observed on the shelf, 55 were found exclusively in seep patches and 59 were found exclusively in non-seep sites (Table 4). Seven taxa were found exclusively in seep sediments at 2 of the 3 shelf sites: *Atylus tridens*, *Cheirimedeia zotea*, Lampropidae, *Photis brevipes*, *Spiochaetopterus costarum*, *Synidotea angulata*, and *Tubulanus polymorphus*. Many of these were single collections from a site, however, and probably do not reflect real habitat preferences. *Cheirimedeia zotea* ($t_{74} = 1.97$, $p = 0.053$) and *Synidotea angulata* ($t_{74} = 2.44$, $p = 0.017$), however, exhibited significant seep preference. *Capitella* sp. was the only taxon found exclusively in seep sediments at each of the 3 shelf sites, and was absent in

Table 3. Bottom-water oxygen and sediment properties on the northern California margin. n = 1 where no standard error (SE) is given

		Bottom-water dissolved oxygen (ml l ⁻¹)	Grain size (%)		CaCO ₃ (%)	Org C (%)	Org N (%)	C:N
			Sand	Silt and clay				
Site A (50 m deep)		2.95						
Seep	Mean		62.5	37.5	10.6	0.76	0.05	15.2
	SE							
	n							
Non-seep	Mean		–	–	–	–	–	–
	SE							
	n							
Site B (40 m deep)		–						
Seep	Mean		83.7	16.3	8.4	0.37	0.02	16.4
	SE				(2.3)	(0.02)	(0.02)	
	n				2	2	2	
Non-seep	Mean		93.2	6.8	8.0	0.31	0.01	30.5
	SE				(1.4)	(0.02)	(0.01)	
	n				3	3	3	
Site C (35 m deep)		2.74						
Seep	Mean		94.9	5.1	11.0	0.31	0.01	22.7
	SE				(0.5)	(0.03)	(0.01)	
	n				4	4	4	
Non-seep	Mean		89.2	10.8	7.7	0.33	0.03	10.4
	SE				(1.6)	(0.02)	(0.02)	
	n				3	3	3	
Slope (500 m deep)								
Seep	Mean	0.76	59.9	40.1	12.4	0.97	0.06	16.8
	SE	(0.02)	(3.0)	(3.0)	(0.7)	(0.00)	(0.01)	
	n	9	2	2	2	2	2	

non-seep sediments ($t_{74} = 2.57$, $p = 0.012$). The cumaceans *Diastylopsis dawsoni* ($t_{74} = 3.45$, $p < 0.001$) and other Lampropidae ($t_{74} = 1.96$, $p = 0.054$) were present in non-seep sediments but were proportionally better represented in seep settings. In addition, mysids were observed to concentrate over black patches emitting methane bubbles at Sites B and C. The mysids were abundant in slurp samples but rarely appeared in shipek grabs. Because they were demersal rather than infaunal, they were not included in the community analyses.

Although numerous species were collected in greater numbers outside of seeps, only the amphipods *Rhepoxynius abronius* ($t_{74} = 2.77$, $p = 0.007$) and *R. daboius* ($t_{74} = 3.62$, $p < 0.001$) were proportionally more abundant in non-seep than seep sediments.

Multidimensional scaling of macrofaunal assemblage data indicated significant compositional differences among the 3 shelf Sites A, B, and C, and between shelf and slope communities (Fig. 2) (ANOSIM all pairwise comparisons $p < 0.001$). Within each shelf site, comparisons of seep and non-seep faunas by sampling gear type (slurp or shipek) revealed no differences (Fig. 3) (ANOSIM Site A: shipek $p = 0.800$, slurp

$p = 0.333$; Site B: shipek $p = 0.383$, slurp $p = 0.314$; Site C: shipek $p = 0.412$).

Slope settings

Most of the infaunal species present in cores from 4 *Calypptogena pacifica* beds were characteristic of Pacific, North American continental margin sediments (Blake & Scott 1997) (Table 5). Annelids were the dominant taxon, comprising about two-thirds of the seep infaunal collections. The most common species at both seep and non-seep sites were *Mediomastus californiensis*, *Levinsenia gracilis*, *Nephtys cornuta*, and various tanaids, amphipods, and ophiuroids. We observed potential differences in faunal abundance and biomass within and among clam beds (Table 6). The core from the most sulfidic sediments (clam bed 5) yielded infaunal densities 2.25 to 5 times higher than those in other clam patches or non-seep sediments (Table 6). Species or groups such as *Ophryotrocha* sp., oligochaetes, pyramidellid and other bivalves, amphipods and tanaids were more abundant or exclusively present in seep sediments, but the small number of inactive sediment sam-

Table 4. Counts and proportions of infaunal species in seep and non-seep shelf sediments, northern California margin. See Table 2 for the sample types and numbers. Prop. = Proportion

Species	Site A				Site B				Site C			
	Non-seep		Seep		Non-seep		Seep		Non-seep		Seep	
	Total	Prop.	Total	Prop.	Total	Prop.	Total	Prop.	Total	Prop.	Total	Prop.
Cnidaria												
Hydroid	0	0.000	0	0.000	0	0.000	1	0.002	0	0.000	0	0.000
<i>Obelia</i> sp.	0	0.000	2	0.002	0	0.000	0	0.000	0	0.000	0	0.000
Anemone	0	0.000	0	0.000	1	0.002	1	0.002	6	0.007	0	0.000
<i>Scolanthus</i> sp. A	0	0.000	1	0.001	0	0.000	0	0.000	0	0.000	0	0.000
Edwardsid ? sp.	3	0.010	0	0.000	0	0.000	0	0.000	0	0.000	0	0.000
Platyhelminthes												
Turbellaria	0	0.000	0	0.000	0	0.000	0	0.000	1	0.001	0	0.000
Polycladida	0	0.000	1	0.001	0	0.000	0	0.000	0	0.000	0	0.000
Platyhelminthes sp. A	0	0.000	1	0.001	0	0.000	0	0.000	1	0.001	0	0.000
Nemertea												
Nemertea	1	0.003	4	0.004	1	0.002	0	0.000	1	0.001	1	0.012
<i>Cerebratulus</i> sp.	1	0.003	0	0.000	0	0.000	0	0.000	1	0.001	0	0.000
<i>Lineus bilineatus</i>	0	0.000	1	0.001	0	0.000	0	0.000	0	0.000	0	0.000
<i>Tubulanus polymorphus</i>	0	0.000	1	0.001	0	0.000	1	0.002	0	0.000	0	0.000
Annelida												
<i>Amaeana occidentalis</i>	6	0.021	20	0.020	31	0.064	15	0.037	8	0.009	0	0.000
<i>Ampharete arctica</i>	1	0.003	0	0.000	0	0.000	0	0.000	1	0.001	0	0.000
<i>Ampharete finmarchica</i>	0	0.000	0	0.000	0	0.000	0	0.000	6	0.007	0	0.000
<i>Ampharete labrops</i>	0	0.000	0	0.000	0	0.000	12	0.029	0	0.000	0	0.000
Ampharetidae juvenile	0	0.000	16	0.016	1	0.002	0	0.000	0	0.000	0	0.000
<i>Aphelochaeta</i> sp.	2	0.007	2	0.002	0	0.000	0	0.000	0	0.000	0	0.000
<i>Aphrodita refulgida</i>	0	0.000	0	0.000	0	0.000	0	0.000	1	0.001	0	0.000
<i>Apopriospio pygmaea</i>	0	0.000	0	0.000	0	0.000	0	0.000	7	0.008	4	0.049
<i>Aricidea (Acmira) catherinae</i>	1	0.003	4	0.004	0	0.000	1	0.002	2	0.002	0	0.000
<i>Aricidea (Allia) antennata</i>	0	0.000	0	0.000	0	0.000	1	0.002	0	0.000	0	0.000
<i>Aricidea pseudoarticulata</i>	0	0.000	0	0.000	0	0.000	0	0.000	1	0.001	0	0.000
<i>Boccardia</i> sp.	0	0.000	0	0.000	1	0.002	0	0.000	0	0.000	0	0.000
<i>Capitella</i> sp.	0	0.000	2	0.002	0	0.000	16	0.039	0	0.000	3	0.037
Capitellidae	0	0.000	5	0.005	1	0.002	1	0.002	0	0.000	0	0.000
<i>Chaetozone cf. hartmanae</i>	30	0.105	0	0.000	0	0.000	0	0.000	0	0.000	0	0.000
<i>Chaetozone columbiana</i>	0	0.000	12	0.012	0	0.000	0	0.000	0	0.000	0	0.000
<i>Chaetozone</i> sp.	0	0.000	11	0.011	0	0.000	0	0.000	1	0.001	0	0.000
<i>Chaetozone</i> sp. A	4	0.014	7	0.007	0	0.000	1	0.002	20	0.024	2	0.025
Cirratulidae	1	0.003	4	0.004	3	0.006	1	0.002	1	0.001	0	0.000
<i>Cossura</i> sp.	1	0.003	1	0.001	0	0.000	0	0.000	0	0.000	0	0.000
<i>Decamastus gracilis</i>	4	0.014	9	0.009	1	0.002	4	0.010	0	0.000	0	0.000
<i>Dipolydora cardalia</i>	0	0.000	0	0.000	0	0.000	1	0.002	0	0.000	0	0.000
<i>Dipolydora</i> sp. juvenile	0	0.000	1	0.001	0	0.000	0	0.000	0	0.000	0	0.000
<i>Drilonereis</i> sp. A	6	0.021	0	0.000	0	0.000	0	0.000	0	0.000	0	0.000
<i>Eteone cf. brigittae</i>	0	0.000	0	0.000	0	0.000	1	0.002	0	0.000	0	0.000
<i>Eteone cf. spilotus</i>	3	0.010	0	0.000	1	0.002	0	0.000	1	0.001	0	0.000
<i>Eteone</i> sp.	0	0.000	0	0.000	1	0.002	0	0.000	0	0.000	0	0.000
<i>Eteone spilotus</i>	0	0.000	9	0.009	0	0.000	0	0.000	0	0.000	0	0.000
Euclymeninae	0	0.000	1	0.001	0	0.000	0	0.000	0	0.000	0	0.000
<i>Glycera cf. convoluta</i>	0	0.000	0	0.000	0	0.000	1	0.002	3	0.004	0	0.000
<i>Glycera nana</i>	7	0.024	10	0.010	0	0.000	0	0.000	1	0.001	0	0.000
<i>Glycera</i> sp. A	1	0.003	0	0.000	0	0.000	0	0.000	0	0.000	0	0.000
Glyceridae/Goniadidae	0	0.000	1	0.001	0	0.000	0	0.000	0	0.000	0	0.000
<i>Glycinde armigera</i>	1	0.003	4	0.004	1	0.002	0	0.000	2	0.002	0	0.000
<i>Glycinde</i> sp.	1	0.003	2	0.002	0	0.000	0	0.000	0	0.000	0	0.000
<i>Goniada maculata</i>	1	0.003	1	0.001	1	0.002	0	0.000	2	0.002	1	0.012
<i>Goniada</i> sp.	1	0.003	0	0.000	0	0.000	0	0.000	0	0.000	0	0.000
<i>Harmothoinae</i> sp. A juvenile	0	0.000	0	0.000	1	0.002	0	0.000	1	0.001	0	0.000
<i>Hesionella</i> sp.	0	0.000	0	0.000	0	0.000	1	0.002	5	0.006	0	0.000
<i>Hesionella</i> sp. A	0	0.000	1	0.001	0	0.000	0	0.000	2	0.002	0	0.000
<i>Heteromastus filobranchus</i>	15	0.052	18	0.018	0	0.000	3	0.007	0	0.000	0	0.000
<i>Heteromastus</i> sp.	2	0.007	1	0.001	0	0.000	0	0.000	0	0.000	0	0.000
<i>Lanassa</i> sp. juvenile	0	0.000	1	0.001	0	0.000	0	0.000	0	0.000	0	0.000
<i>Lanassa venusta</i>	0	0.000	1	0.001	0	0.000	0	0.000	0	0.000	0	0.000
<i>Laonice cirrata</i>	4	0.014	4	0.004	0	0.000	0	0.000	0	0.000	0	0.000
<i>Leitoscoloplos pugettensis</i>	9	0.031	56	0.057	15	0.031	14	0.034	31	0.037	1	0.012
<i>Levinsenia gracilis</i>	1	0.003	1	0.001	0	0.000	0	0.000	0	0.000	0	0.000
<i>Levinsenia oculata</i>	0	0.000	1	0.001	0	0.000	0	0.000	0	0.000	0	0.000
<i>Levinsenia</i> sp. juvenile	0	0.000	2	0.002	0	0.000	0	0.000	0	0.000	0	0.000
<i>Listriolobus</i> sp.	1	0.003	0	0.000	0	0.000	0	0.000	0	0.000	0	0.000
Lumbrineridae	0	0.000	1	0.001	0	0.000	0	0.000	0	0.000	0	0.000
<i>Lumbrineris californiensis</i>	0	0.000	0	0.000	1	0.002	0	0.000	6	0.007	0	0.000
<i>Lumbrineris latreilli</i>	0	0.000	0	0.000	2	0.004	2	0.005	0	0.000	0	0.000

Table 4 (continued)

Species	Site A				Site B				Site C			
	Non-seep		Seep		Non-seep		Seep		Non-seep		Seep	
	Total	Prop.	Total	Prop.	Total	Prop.	Total	Prop.	Total	Prop.	Total	Prop.
<i>Lumbrineris</i> sp.	9	0.031	141	0.144	21	0.043	16	0.039	20	0.024	0	0.000
<i>Magelona berkeleyi</i>	0	0.000	1	0.001	0	0.000	0	0.000	2	0.002	0	0.000
<i>Magelona hartmanae</i>	0	0.000	0	0.000	0	0.000	0	0.000	7	0.008	0	0.000
<i>Magelona sacculata</i>	0	0.000	0	0.000	8	0.017	10	0.025	68	0.081	11	0.136
<i>Magelona</i> sp. A	0	0.000	1	0.001	0	0.000	0	0.000	0	0.000	0	0.000
<i>Malmgreniella scriptoria</i>	0	0.000	0	0.000	25	0.052	9	0.022	1	0.001	0	0.000
<i>Mediomastus ambisetus</i>	9	0.031	75	0.076	5	0.010	1	0.002	0	0.000	0	0.000
<i>Mediomastus californiensis</i>	9	0.031	0	0.000	0	0.000	0	0.000	0	0.000	0	0.000
<i>Mediomastus</i> spp.	0	0.000	102	0.104	15	0.031	2	0.005	0	0.000	1	0.012
<i>Melina oculata</i>	0	0.000	1	0.001	0	0.000	0	0.000	0	0.000	0	0.000
<i>Myriochele gracilis</i>	1	0.003	1	0.001	0	0.000	0	0.000	0	0.000	0	0.000
<i>Myriochele oculata</i>	0	0.000	2	0.002	0	0.000	0	0.000	0	0.000	0	0.000
<i>Myriochele</i> sp.	1	0.003	0	0.000	0	0.000	0	0.000	0	0.000	0	0.000
<i>Myriochele</i> sp. M	1	0.003	0	0.000	0	0.000	0	0.000	0	0.000	0	0.000
<i>Naineris ? dendritica</i>	0	0.000	0	0.000	0	0.000	0	0.000	1	0.001	0	0.000
Nephtyidae	0	0.000	1	0.001	0	0.000	1	0.002	10	0.012	0	0.000
<i>Nephtys caecoides</i>	0	0.000	0	0.000	2	0.004	2	0.005	6	0.007	0	0.000
<i>Nephtys californiensis</i>	4	0.014	11	0.011	48	0.099	16	0.039	158	0.187	15	0.185
<i>Nephtys cornuta</i>	11	0.038	87	0.089	5	0.010	3	0.007	0	0.000	0	0.000
<i>Nephtys ferruginea</i>	2	0.007	7	0.007	0	0.000	0	0.000	0	0.000	0	0.000
Nereididae	0	0.000	0	0.000	1	0.002	0	0.000	0	0.000	0	0.000
<i>Nereis</i> sp. A	0	0.000	0	0.000	0	0.000	2	0.005	0	0.000	0	0.000
<i>Notomastus</i> cf. <i>lineatus</i>	0	0.000	0	0.000	9	0.019	2	0.005	3	0.004	2	0.025
<i>Notomastus</i> sp.	0	0.000	3	0.003	5	0.010	0	0.000	0	0.000	0	0.000
<i>Ophelina acuminata</i>	1	0.003	1	0.001	0	0.000	0	0.000	0	0.000	0	0.000
<i>Orbinia johnsoni</i>	0	0.000	0	0.000	0	0.000	0	0.000	1	0.001	0	0.000
Orbiniidae	1	0.003	3	0.003	1	0.002	1	0.002	2	0.002	0	0.000
Paraonidae	0	0.000	6	0.006	0	0.000	2	0.005	3	0.004	0	0.000
<i>Paraprionospio pinnata</i>	3	0.010	9	0.009	0	0.000	0	0.000	0	0.000	0	0.000
<i>Pholoe glabra</i>	2	0.007	5	0.005	0	0.000	0	0.000	0	0.000	0	0.000
<i>Phyllochaetopterus prolifica</i>	0	0.000	0	0.000	0	0.000	3	0.007	0	0.000	0	0.000
<i>Phyllodoce longipes</i>	1	0.003	0	0.000	0	0.000	0	0.000	0	0.000	0	0.000
<i>Phylo felix</i>	0	0.000	0	0.000	13	0.027	2	0.005	6	0.007	0	0.000
<i>Podarkeopsis glabrus</i>	0	0.000	3	0.003	3	0.006	12	0.029	3	0.004	0	0.000
<i>Polycirrus</i> sp.	0	0.000	0	0.000	0	0.000	0	0.000	0	0.000	1	0.012
Polynoidae	0	0.000	5	0.005	0	0.000	0	0.000	0	0.000	0	0.000
Polynoidae sp. A	0	0.000	0	0.000	1	0.002	0	0.000	0	0.000	0	0.000
<i>Praxillella pacifica</i>	0	0.000	5	0.005	0	0.000	0	0.000	0	0.000	0	0.000
<i>Prionospio (Minuspio) lighti</i>	3	0.010	14	0.014	1	0.002	1	0.002	3	0.004	0	0.000
<i>Prionospio (P.) steenstrupi</i>	3	0.010	2	0.002	0	0.000	0	0.000	1	0.001	0	0.000
<i>Prionospio (P.)</i> sp. A	0	0.000	6	0.006	1	0.002	0	0.000	1	0.001	2	0.025
<i>Prionospio</i> spp.	0	0.000	6	0.006	0	0.000	2	0.005	1	0.001	0	0.000
<i>Proceraea</i> sp.	0	0.000	1	0.001	0	0.000	0	0.000	0	0.000	0	0.000
Scaleworm	0	0.000	5	0.005	0	0.000	0	0.000	2	0.002	0	0.000
<i>Scalibregma inflatum</i>	4	0.014	1	0.001	0	0.000	0	0.000	0	0.000	0	0.000
<i>Scolecipis</i> sp.	0	0.000	0	0.000	0	0.000	0	0.000	2	0.002	0	0.000
<i>Scoletoma tetraura</i>	20	0.070	19	0.019	19	0.039	5	0.012	22	0.026	1	0.012
<i>Sigalion spinosus</i>	0	0.000	0	0.000	0	0.000	0	0.000	4	0.005	0	0.000
Sigalionidae	0	0.000	0	0.000	2	0.004	0	0.000	6	0.007	0	0.000
<i>Sphaerosyllis ranuncululus</i>	0	0.000	5	0.005	0	0.000	0	0.000	0	0.000	0	0.000
<i>Spiochaetopterus costarum</i>	0	0.000	1	0.001	0	0.000	1	0.002	0	0.000	0	0.000
Spionidae	0	0.000	1	0.001	0	0.000	0	0.000	0	0.000	0	0.000
<i>Spiophanes berkeleyorum</i>	3	0.010	11	0.011	2	0.004	1	0.002	2	0.002	1	0.012
<i>Spiophanes bombyx</i>	0	0.000	0	0.000	1	0.002	0	0.000	26	0.031	5	0.062
<i>Sternaspis fossor</i>	6	0.021	7	0.007	0	0.000	0	0.000	0	0.000	0	0.000
<i>Streptosyllis</i> cf. <i>minuta</i>	0	0.000	0	0.000	0	0.000	0	0.000	8	0.009	0	0.000
<i>Trochochaeta multisetosa</i>	8	0.028	16	0.016	0	0.000	0	0.000	0	0.000	0	0.000
Mollusca												
Epitoniidae	0	0.000	1	0.001	0	0.000	0	0.000	0	0.000	0	0.000
<i>Astyris gausapata</i>	15	0.052	18	0.018	26	0.054	39	0.096	4	0.005	0	0.000
<i>Nassarius mendicus</i>	0	0.000	11	0.011	0	0.000	1	0.002	1	0.001	0	0.000
<i>Olivella pycna</i>	0	0.000	1	0.001	3	0.006	1	0.002	34	0.040	13	0.160
<i>Odostomia</i> sp.	0	0.000	1	0.001	0	0.000	0	0.000	0	0.000	0	0.000
<i>Turbonilla</i> sp.	0	0.000	2	0.002	0	0.000	0	0.000	0	0.000	0	0.000
Bivalve	0	0.000	0	0.000	0	0.000	1	0.002	0	0.000	0	0.000
<i>Axinopsida serricata</i>	1	0.003	8	0.008	1	0.002	2	0.005	1	0.001	0	0.000
<i>Rocheffortia tumida</i>	23	0.080	10	0.010	1	0.002	0	0.000	1	0.001	0	0.000
<i>Macoma carlottensis</i>	0	0.000	0	0.000	1	0.002	0	0.000	3	0.004	0	0.000
<i>Macoma nasuta</i>	0	0.000	2	0.002	0	0.000	0	0.000	4	0.005	0	0.000
<i>Tellina modesta</i>	0	0.000	1	0.001	2	0.004	0	0.000	9	0.011	1	0.012
<i>Gadila aberrans</i>	2	0.007	2	0.002	0	0.000	0	0.000	0	0.000	0	0.000

Table 4 (continued)

Species	Site A				Site B				Site C			
	Non-seep		Seep		Non-seep		Seep		Non-seep		Seep	
	Total	Prop.	Total	Prop.	Total	Prop.	Total	Prop.	Total	Prop.	Total	Prop.
Mytilidae	0	0.000	1	0.001	0	0.000	0	0.000	0	0.000	0	0.000
<i>Solemya reidi</i>	0	0.000	2	0.002	0	0.000	0	0.000	0	0.000	0	0.000
<i>Yoldia seminuda</i>	1	0.003	0	0.000	0	0.000	0	0.000	0	0.000	0	0.000
<i>Yoldia</i> sp.	0	0.000	1	0.001	0	0.000	0	0.000	0	0.000	0	0.000
Crustacea												
<i>Ampelisca agassizi</i>	0	0.000	0	0.000	0	0.000	0	0.000	1	0.001	0	0.000
<i>Ampelisca careyi</i>	1	0.003	3	0.003	10	0.021	3	0.007	32	0.038	1	0.012
Amphipod unidentified	0	0.000	0	0.000	2	0.004	0	0.000	3	0.004	0	0.000
<i>Argissa hamatipes</i>	0	0.000	1	0.001	0	0.000	0	0.000	0	0.000	0	0.000
<i>Atylus tridens</i>	0	0.000	1	0.001	0	0.000	1	0.002	0	0.000	0	0.000
<i>Cheirimedeia zotea</i>	0	0.000	3	0.003	0	0.000	3	0.007	0	0.000	0	0.000
<i>Dyopedos</i> sp.	0	0.000	0	0.000	1	0.002	0	0.000	0	0.000	0	0.000
<i>Eohaustorius sencillus</i>	0	0.000	0	0.000	0	0.000	0	0.000	2	0.002	0	0.000
<i>Ericthonius brasiliensis</i>	0	0.000	0	0.000	8	0.017	17	0.042	0	0.000	0	0.000
<i>Foxiphalus obtusidens</i>	0	0.000	0	0.000	0	0.000	0	0.000	5	0.006	0	0.000
<i>Foxiphalus xiximeus</i>	0	0.000	0	0.000	25	0.052	0	0.000	0	0.000	0	0.000
Gammaridea	0	0.000	0	0.000	0	0.000	0	0.000	3	0.004	0	0.000
<i>Gammaropsis thompsoni</i>	0	0.000	5	0.005	3	0.006	9	0.022	0	0.000	0	0.000
Isaeidae	0	0.000	0	0.000	0	0.000	2	0.005	0	0.000	0	0.000
<i>Majoxiphalus major</i>	0	0.000	0	0.000	3	0.006	0	0.000	4	0.005	0	0.000
<i>Microjassa bousfieldi</i>	0	0.000	0	0.000	1	0.002	0	0.000	0	0.000	0	0.000
<i>Neoschyrocerus claustris</i>	0	0.000	0	0.000	0	0.000	1	0.002	0	0.000	0	0.000
Oedicerotidae	0	0.000	0	0.000	0	0.000	2	0.005	0	0.000	0	0.000
<i>Pachynus barnardi</i>	1	0.003	0	0.000	0	0.000	0	0.000	0	0.000	0	0.000
<i>Pacifocolodes spinipes</i>	0	0.000	0	0.000	2	0.004	2	0.005	3	0.004	0	0.000
<i>Photis brevipes</i>	0	0.000	1	0.001	0	0.000	1	0.002	0	0.000	0	0.000
<i>Photis parvidons</i>	0	0.000	0	0.000	1	0.002	0	0.000	6	0.007	0	0.000
<i>Photis</i> sp.	0	0.000	0	0.000	0	0.000	10	0.025	1	0.001	0	0.000
Phoxocephalidae	1	0.003	5	0.005	16	0.033	2	0.005	31	0.037	5	0.062
<i>Pleusymtes</i> sp.	0	0.000	0	0.000	0	0.000	2	0.005	0	0.000	0	0.000
<i>Protomeдея prudens</i>	0	0.000	1	0.001	0	0.000	0	0.000	0	0.000	0	0.000
<i>Protomeдея</i> sp. juvenile	1	0.003	0	0.000	0	0.000	0	0.000	0	0.000	0	0.000
<i>Rhepoxynius abronius</i>	5	0.017	2	0.002	12	0.025	0	0.000	15	0.018	0	0.000
<i>Rhepoxynius daboius</i>	2	0.007	3	0.003	19	0.039	1	0.002	59	0.070	0	0.000
<i>Rhepoxynius homocuspoidatus</i>	0	0.000	0	0.000	1	0.002	0	0.000	6	0.007	0	0.000
<i>Rhepoxynius lucubrans</i>	0	0.000	0	0.000	1	0.002	0	0.000	0	0.000	0	0.000
<i>Rhepoxynius stenodes</i>	0	0.000	1	0.001	0	0.000	3	0.007	4	0.005	0	0.000
<i>Rhepoxynius vigitegus</i>	0	0.000	0	0.000	0	0.000	0	0.000	1	0.001	0	0.000
<i>Synchelidium</i> sp.	0	0.000	0	0.000	3	0.006	1	0.002	2	0.002	0	0.000
<i>Tiron biocellata</i>	0	0.000	7	0.007	1	0.002	5	0.012	0	0.000	0	0.000
<i>Westwoodilla caecula</i>	2	0.007	0	0.000	0	0.000	0	0.000	0	0.000	0	0.000
<i>Diastylis quadruplicata</i>	0	0.000	0	0.000	1	0.002	1	0.002	0	0.000	0	0.000
<i>Diastylis santamariensis</i>	1	0.003	0	0.000	0	0.000	0	0.000	0	0.000	0	0.000
<i>Diastylopsis dawsoni</i>	11	0.038	42	0.043	3	0.006	10	0.025	7	0.008	4	0.049
<i>Eudorella pacifica</i>	3	0.010	2	0.002	0	0.000	0	0.000	0	0.000	0	0.000
Lampropidae	0	0.000	2	0.002	0	0.000	1	0.002	0	0.000	0	0.000
<i>Mesolamprops dillonensis</i>	0	0.000	0	0.000	1	0.002	0	0.000	0	0.000	0	0.000
<i>Cragon alaskensis</i>	0	0.000	0	0.000	0	0.000	3	0.007	0	0.000	0	0.000
<i>Eualus pusiolus</i>	0	0.000	1	0.001	1	0.002	1	0.002	0	0.000	0	0.000
<i>Lissocragon stylirostris</i>	0	0.000	0	0.000	1	0.002	0	0.000	2	0.002	0	0.000
<i>Pagurus armatus</i>	0	0.000	0	0.000	2	0.004	0	0.000	0	0.000	0	0.000
<i>Pinnixa franciscana</i>	1	0.003	0	0.000	0	0.000	0	0.000	0	0.000	0	0.000
<i>Pinnixa occidentalis</i>	0	0.000	0	0.000	0	0.000	0	0.000	1	0.001	0	0.000
<i>Edotia sublittoralis</i>	0	0.000	0	0.000	0	0.000	0	0.000	1	0.001	0	0.000
Isopod unidentified	0	0.000	0	0.000	0	0.000	2	0.005	0	0.000	0	0.000
<i>Munnogonium tillerae</i>	3	0.010	2	0.002	1	0.002	0	0.000	0	0.000	1	0.012
<i>Pleurogonium californiense</i>	0	0.000	0	0.000	1	0.002	0	0.000	0	0.000	0	0.000
<i>Synidotea angulata</i>	0	0.000	2	0.002	0	0.000	5	0.012	0	0.000	0	0.000
<i>Synidotea</i> sp. juvenile	0	0.000	0	0.000	2	0.004	1	0.002	15	0.018	0	0.000
<i>Tecticeps convexus</i>	2	0.007	19	0.019	71	0.147	98	0.240	67	0.079	3	0.037
<i>Uromunna ubiquita</i>	0	0.000	0	0.000	0	0.000	3	0.007	0	0.000	0	0.000
Sipunculida												
Sipuncula juvenile	0	0.000	1	0.001	0	0.000	0	0.000	1	0.001	0	0.000
Echinodermata												
<i>Amphiodia urtica</i>	1	0.003	6	0.006	5	0.010	2	0.005	33	0.039	2	0.025
<i>Lovenia cordiformis</i>	0	0.000	0	0.000	0	0.000	0	0.000	1	0.001	0	0.000
Hemichordata												
Enteropneusta	0	0.000	0	0.000	1	0.002	0	0.000	0	0.000	0	0.000
Chaetognatha												
Chaetognath	0	0.000	26	0.026	0	0.000	0	0.000	0	0.000	0	0.000
Total	287		982		484		408		844		81	

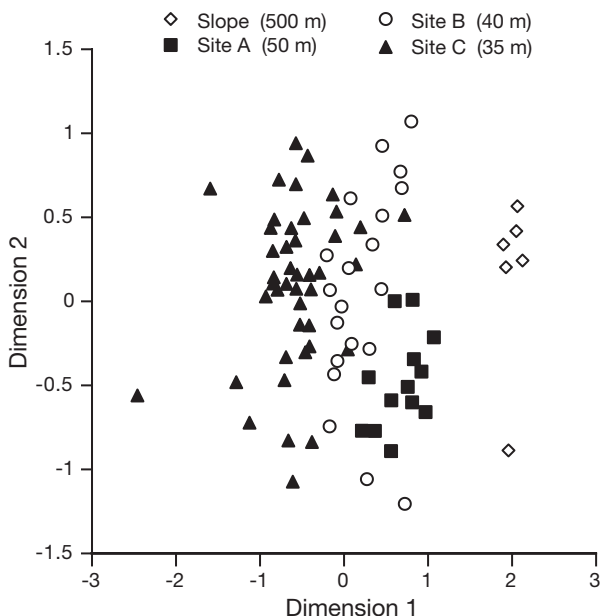


Fig. 2. Nondimensional MDS plot of macrofauna from sediments (seep and non-seep combined) at shelf Sites A, B, C, and from the slope on the northern California margin, USA. Stress value is 0.21

ples prevents conclusive statements about seep preference. A species accumulation curve for the slope macrofauna (Biodiversity Pro, 25 randomizations) suggests that 6 samples are insufficient to fully characterize the seep fauna.

Macrofaunal diversity

Rarefaction analyses, conducted to normalize species richness estimates for samples of different size, suggest there were few within-site differences in species richness between seep and non-seep sediments (Fig. 4). On average, diversity was relatively high at all sites. Information (H' [\log_2], range 3.8 to 5.2) and evenness indices (J' , range 0.76 to 0.87), exhibited greater differences among shelf sites than between seep and non-seep sediments within a site (Table 7). Diversity was remarkably similar at all shelf and slope sites except in Site C seep sediments, where species richness appeared lower (Fig. 4, Table 7). Here 3 species, *Magelona sacculata*, *Nephtys californiensis*, and *Olivella pycna*, comprised 48% of the macrofauna.

Macrofaunal nutrition

Seep and non-seep infauna exhibited similar $\delta^{13}C$ and $\delta^{15}N$ signatures within each of the 3 shelf stations (Table 8). Mean $\delta^{13}C$ values ranged from -17 to -19,

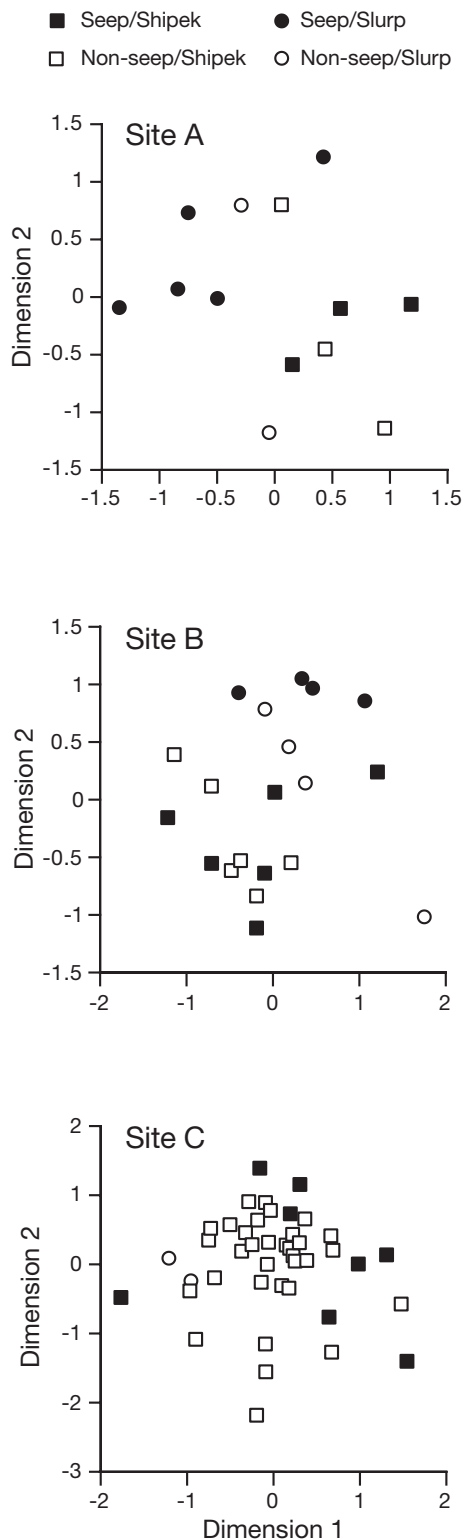


Fig. 3. Nondimensional MDS plot of macrofauna from seep and non-seep sediments at Sites A (50 m deep), B (40 m deep), and C (35 m deep) on the northern California shelf, USA. Samples taken by submersible suction (slurp) and shipek grab from the surface are indicated. Stress values are 0.14 for Site A, 0.14 for Site B, and 0.21 for Site C

Table 5. Macrofaunal densities (per 54 cm² core) in *Calyptogena pacifica* beds and inactive sediments on the Eel River margin slope

Clam bed species	Clam bed 2	Clam bed 3a	Clam bed 3b	Clam bed 4a	Clam bed 4b	Clam bed 5	Average	Percentage	Inactive #1	Inactive #2	Average	Percentage
Annelida												
Polychaeta												
Ampharetidae												
Ampharetinae sp. B	1	1	0	0	0	1	0.5	0.007	2	0	1.0	0.017
Ampharetinae (juvenile)	0	0	0	0	0	1	0.2	0.002	0	0	0.0	0.000
Ampharetidae (unidentified)	0	0	0	2	0	0	0.3	0.005	0	1	0.5	0.008
Amplictenidae												
<i>Pectinaria</i> (unidentified)	0	1	0	0	0	0	0.2	0.002	0	1	0.5	0.008
Capitellidae												
<i>Mediomastus californiensis</i>	6	3	10	7	18	27	11.8	0.177	10	8	9.0	0.151
Cirratulidae												
<i>Aphelochoeta</i> sp. A	0	0	1	0	0	0	0.2	0.002	0	0	0.0	0.000
<i>Aphelochoeta</i> (unidentified)	0	0	1	0	0	0	0.2	0.002	0	0	0.0	0.000
<i>Chaetozone commensalis</i>	0	2	0	0	0	0	0.3	0.005	0	0	0.0	0.000
<i>Chaetozone</i> sp. A	0	0	0	0	0	0	0.0	0.000	0	3	1.5	0.025
<i>Chaetozone</i> (juvenile)	0	0	0	0	0	1	0.2	0.002	0	0	0.0	0.000
<i>Monticellina</i> sp. A	0	0	2	0	0	0	0.3	0.005	0	2	1.0	0.017
<i>Tharyx</i> -complex (unidentified)	0	0	0	1	0	2	0.5	0.007	0	0	0.0	0.000
Cirratulid shell-dweller	0	0	0	0	0	1	0.2	0.002	0	0	0.0	0.000
Cirratulidae (juvenile)	0	0	0	0	1	2	0.5	0.007	0	0	0.0	0.000
Cirratulidae (unidentified)	0	0	1	0	0	4	0.8	0.012	0	0	0.0	0.000
Cossuridae												
<i>Cossura</i> sp. A	0	4	0	0	0	0	0.7	0.010	3	0	1.5	0.025
<i>Cossura</i> sp. B	0	0	0	0	0	0	0.0	0.000	1	0	0.5	0.008
<i>Cossura</i> (unidentified)	3	0	1	0	3	5	2.0	0.030	0	2	1.0	0.017
Dorvilleidae												
<i>Dorvillea</i> sp. A	0	0	0	0	0	0	0.0	0.000	0	3	1.5	0.025
<i>Ophryotrocha</i> sp. A	0	0	1	0	3	9	2.2	0.032	0	0	0.0	0.000
<i>Parougia</i> sp. A	0	0	0	0	1	0	0.2	0.002	0	0	0.0	0.000
Flabelligeridae												
<i>Flabelligeridae</i> sp. A	0	0	0	0	0	0	0.0	0.000	1	0	0.5	0.008
Glyceridae												
<i>Hemipodus</i> sp. A	0	0	1	0	0	0	0.2	0.002	0	0	0.0	0.000
Goniadidae												
<i>Glycine</i> nr. <i>armigera</i>	1	0	0	0	1	0	0.3	0.005	0	0	0.0	0.000
Hesionidae												
<i>Gyptis lobatus</i>	0	0	0	0	0	0	0.0	0.000	0	1	0.5	0.008
<i>Hesionidae</i> sp. A	0	0	0	1	0	0	0.2	0.002	0	0	0.0	0.000
<i>Hesionidae</i> sp. B	0	2	0	1	0	0	0.5	0.007	1	0	0.5	0.008
Lumbrineridae												
Lumbrineridae sp. A	0	0	0	0	0	0	0.0	0.000	1	0	0.5	0.008
Lumbrineridae (unidentified)	1	0	0	0	0	0	0.2	0.002	0	0	0.0	0.000
Lumbrineridae (juvenile)	0	0	0	0	1	0	0.2	0.002	0	0	0.0	0.000
Maldanidae												
Maldanidae sp. A	0	0	0	1	0	4	0.8	0.012	0	1	0.5	0.008
<i>Rhodine bitorquata</i>	0	2	0	0	0	0	0.3	0.005	0	0	0.0	0.000
Nephtyidae												
<i>Nephtys cornuta</i>	6	9	0	2	2	7	4.3	0.065	3	8	5.5	0.092
Orbiniidae												
Orbiniidae (juvenile)	0	0	0	0	4	0	0.7	0.010	0	0	0.0	0.000
Oweniidae												
<i>Myriochele oculata</i>	0	0	0	2	0	0	0.3	0.005	0	0	0.0	0.000
<i>Myriochele</i> sp. A	1	0	0	0	0	0	0.2	0.002	0	0	0.0	0.000
Paraonidae												
<i>Cirrophorus branchiatus</i>	4	4	1	0	0	0	1.5	0.022	3	1	2.0	0.034
<i>Levinsenia gracilis</i>	6	4	3	4	2	14	5.5	0.082	16	3	9.5	0.160
<i>Levinsenia</i> nr. <i>gracilis</i>	0	0	1	0	0	0	0.2	0.002	0	0	0.0	0.000
Phyllodoceidae												
<i>Eteone</i> sp. A	0	1	0	0	0	0	0.2	0.002	0	0	0.0	0.000
<i>Eulalia?</i> <i>tubiformis</i>	0	0	0	0	0	1	0.2	0.002	0	0	0.0	0.000
<i>Phyllodoce</i> cf. <i>groenlandica</i>	0	1	0	0	0	0	0.2	0.002	0	0	0.0	0.000
<i>Eumida/Eulalia?</i> n. sp.	0	0	1	0	0	0	0.2	0.002	0	0	0.0	0.000
Phyllodoceidae (unidentified)	0	0	0	0	0	0	0.0	0.000	0	1	0.5	0.008
Pilargidae												
<i>Ancistrosyllis</i> sp. A	0	0	0	0	0	1	0.2	0.002	0	0	0.0	0.000
Polynoidae												
<i>Halosydna johnsoni</i>	2	0	0	0	0	0	0.3	0.005	0	0	0.0	0.000
Spionidae												
<i>Prionospio (Minuspio)</i> sp. A	0	0	0	0	0	0	0.0	0.000	3	1	2.0	0.034
<i>Prionospio</i> (unidentified)	1	0	0	1	0	0	0.3	0.005	0	0	0.0	0.000
<i>Spiophanes</i> (unidentified)	0	0	0	0	1	0	0.2	0.002	0	0	0.0	0.000

Table 5 (continued)

Clam bed species	Clam bed 2	Clam bed 3a	Clam bed 3b	Clam bed 4a	Clam bed 4b	Clam bed 5	Average	Percentage	Inactive #1	Inactive #2	Average	Percentage
Syllidae												
<i>Exogone</i> sp. A	0	0	0	0	1	1	0.3	0.005	0	1	0.5	0.008
<i>Eusyllinae</i> sp. A	0	0	0	0	0	3	0.5	0.007	0	1	0.5	0.008
<i>Syllinae</i> sp. A (juvenile)	0	0	0	0	0	1	0.2	0.002	0	0	0.0	0.000
Syllidae (unidentified)	0	0	1	0	0	0	0.2	0.002	0	0	0.0	0.000
Terebellida	0	0	1	0	0	0	0.2	0.002	0	0	0.0	0.000
Terebellidae												
Amphitritinae?	0	0	0	0	0	3	0.5	0.007	0	2	1.0	0.017
Trichobranchidae												
<i>Terebellides</i> sp.	0	0	0	0	0	1	0.2	0.002	0	0	0.0	0.000
Unknown sp. B	0	0	0	0	0	1	0.2	0.002	0	0	0.0	0.000
Unidentified	0	0	0	0	1	0	0.2	0.002	0	1	0.5	0.008
Oligochaeta												
Oligochaeta sp. A	0	0	0	0	0	3	0.5	0.007	0	0	0.0	0.000
Oligochaeta sp. B	0	0	0	0	0	1	0.2	0.002	0	0	0.0	0.000
Oligochaeta sp. C	2	0	1	1	0	0	0.7	0.010	0	0	0.0	0.000
Oligochaeta sp. D	2	0	0	0	3	0	0.8	0.012	0	0	0.0	0.000
Oligochaeta sp. E	0	0	0	0	0	0	0.0	0.000	1	0	0.5	0.008
Other vermes												
Nemertea	1	2	1	1	0	3	1.3	0.020	3	0	1.5	0.025
Turbellaria	0	0	0	0	0	1	0.2	0.002	0	0	0.0	0.000
Crustacea												
Amphipoda												
Gammaridea												
<i>Ampelisca</i> spp.	0	0	0	1	0	0	0.2	0.002	0	0	0.0	0.000
<i>Listriella</i> cf. <i>eriopisa</i>	1	0	1	0	6	7	2.5	0.037	1	5	3.0	0.050
Corophioidea												
<i>Gammaropsis</i> (<i>Podoceroopsis</i>) <i>ocellata</i>	0	1	6	1	2	5	2.5	0.037	3	0	1.5	0.025
<i>Protomedea</i> sp. A	0	1	0	0	1	1	0.5	0.007	1	0	0.5	0.008
<i>Photis</i> sp. A	0	0	0	0	0	1	0.2	0.002	0	0	0.0	0.000
<i>Corophioidea</i> (unidentified)	0	0	0	0	0	1	0.2	0.002	0	0	0.0	0.000
Isopoda												
Pleurogoniidae	0	0	0	0	0	2	0.3	0.005	1	0	0.5	0.008
Eurycopidae	0	1	0	0	0	0	0.2	0.002	0	0	0.0	0.000
Cumacea												
Bodotriidae												
Bodotriidae sp. A	0	0	1	0	0	0	0.2	0.002	0	0	0.0	0.000
Diastylidae												
<i>Diastylis pellucida</i>	0	1	0	0	0	0	0.2	0.002	1	0	0.5	0.008
Nannastacidae												
<i>Campylaspis rufa</i>	1	0	0	1	0	1	0.5	0.007	0	0	0.0	0.000
Tanaidacea												
Tanaidacea sp. A	2	6	3	1	5	25	7.0	0.105	1	4	2.5	0.042
Mollusca												
Aplacophora												
Aplacophora sp. A	1	0	0	0	0	0	0.2	0.002	0	3	1.5	0.025
Bivalvia												
<i>Calyptogena</i> sp. A	0	0	0	0	4	0	0.7	0.010	0	0	0.0	0.000
Lucinidae sp. A	1	0	1	0	0	0	0.3	0.005	0	1	0.5	0.008
Lucinidae sp. B	1	0	0	0	0	0	0.2	0.002	0	0	0.0	0.000
Bivalvia sp. A	0	0	0	0	1	0	0.2	0.002	0	0	0.0	0.000
Bivalvia sp. B	0	1	0	0	0	0	0.2	0.002	0	0	0.0	0.000
Gastropoda												
Archaeogastropoda sp. A	0	0	0	0	0	1	0.2	0.002	0	0	0.0	0.000
<i>Lirobittium paganicum</i>	0	0	0	1	0	0	0.2	0.002	0	0	0.0	0.000
Pyramidellidae sp. B (<i>Fargoa</i> ?)	0	0	0	0	7	0	1.2	0.017	0	0	0.0	0.000
<i>Oenopota</i> sp. A	0	0	0	0	0	1	0.2	0.002	0	0	0.0	0.000
<i>Opisthobranchia</i> spp.	4	0	0	0	0	2	1.0	0.015	0	0	0.0	0.000
Gastropoda (unidentified)	0	1	0	1	2	0	0.7	0.010	0	0	0.0	0.000
Scaphopoda	0	0	1	0	0	0	0.2	0.002	0	2	1.0	0.017
Miscellaneous												
Hydroid	0	0	0	0	0	0	0.0	0.000	0	0	0.0	0.000
Ophiuroidea	2	3	1	2	0	11	3.2	0.047	2	5	3.5	0.059
Total macrofauna	50	51	42	32	70	156	66.8		58	61	59.5	

Table 6. Density and biomass of macrofauna (>0.3 mm) in seep and inactive sediments on the northern California margin (500 m deep). *Calyptogena pacifica* are excluded. a and b: separate cores from the same clam bed

Clam bed:	Seep								Inactive			
	Bed 2	Bed 3a	Bed 3b	Bed 4a	Bed 4b	Bed 5	Mean	SE	Site 1	Site 2	Mean	SE
Ind. m ⁻²	9365	9552	7867	5994	13111	29219	12518	3475	10863	11425	11444	140.48
Biomass, g m ⁻²												
Annelida	3.36	7.83	5.82	4.32	8.25	37.91	11.25	5.39	8.95	57.40	33.18	12.11
Other	2.95	2.07	3.88	17.81	3.13	45.51	12.56	7.02	1.51	0.90	1.20	0.15
Total	6.31	9.90	9.70	22.13	11.38	83.43	23.81	12.12	10.47	58.29	34.38	11.96

consistent with a marine phytoplankton-based food chain. There was little evidence of lighter $\delta^{13}\text{C}$ signatures that would indicate chemosynthetically derived food sources in shelf sediments. However, some of the capitellids, *Mediomastus*, *Heteromastus* and *Capitella* sp., and polychaetes in the genera *Nephtys* and *Sternaspis*, exhibited lower $\delta^{13}\text{C}$ values (-19.2 to -23.0) than other infauna (Table 8). $\delta^{15}\text{N}$ values were quite variable, probably reflecting a range of trophic levels, but did not differ among shelf sites.

Of the 19 infaunal invertebrates examined isotopically from clam beds on the slope, those from clam bed 1 exhibited lighter $\delta^{13}\text{C}$ signatures (-24.6 ± 1.1) (Fig. 5) than those for individuals from clam bed 2 (-19.9 ± 0.3), or inactive sediments (-18.6 ± 0.6) ($F_{2,25} = 12.93$, $p < 0.001$). Macrofauna from clam beds 1 and 2 had lighter average $\delta^{13}\text{C}$ signatures than those from shelf sites ($F_{3,95} = 43.3$, $p < 0.001$). A single dorvilleid polychaete, *Dorvillea* sp., had a very light $\delta^{13}\text{C}$ signature (-33.5), suggestive of chemoautotrophic symbionts or selective feeding on free-living chemoautotrophic bacteria. $\delta^{15}\text{N}$ values were variable (Fig. 5), but did not differ among clam beds and inactive sediments. However, $\delta^{15}\text{N}$ values were considerably greater for slope macrofauna from the 2 clam beds

and inactive slope sediments (Fig. 5) than for shelf macrofauna (Table 8) ($F_{3,95} = 25.2$, $p < 0.001$).

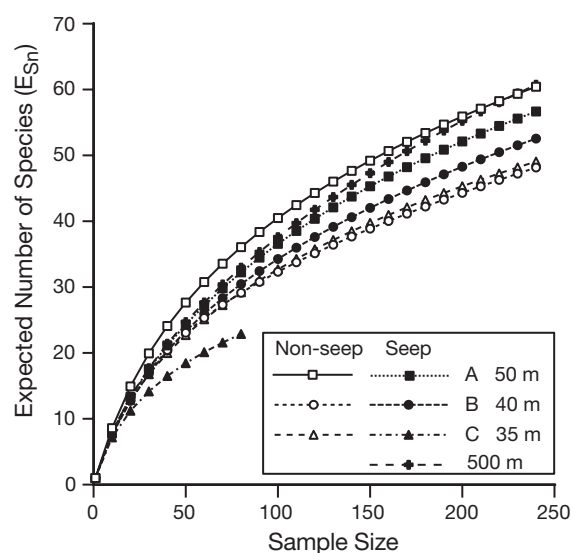


Fig. 4. Rarefaction curves showing expected number of macrofaunal species (≥ 0.3 mm) for a given sample size (no. of ind.) in pooled samples (seep vs non-seep) from 4 locations on the northern California margin

Table 7. Diversity indices of shelf and slope macrofauna on the northern California margin. Data are for pooled cores unless otherwise indicated. **Average of 6 cores

	Site A		Site B		Site C		Slope		
	Seep	Non-seep	Seep	Non-seep	Seep	Non-seep	Seep	Inactive site 1	Inactive site 2
Information index H' (\log_2)	5.02	5.22	4.66	4.80	3.85	4.76	4.95 (3.83)**	3.45	3.89
Evenness J'	0.76	0.87	0.77	0.79	0.85	0.76	0.79 (0.85)**	0.81	0.85
Rank 1 dominance (%)	14.4 ^a	10.5 ^b	24.0 ^c	14.7 ^c	18.5 ^d	18.7 ^d	17.7 ^e	27.6 ^f	13.1 ^e
Most abundant species:	^a <i>Lumbrineris</i> sp.		^d <i>Nephtys californiensis</i>		^e <i>Mediomastus californiensis</i>			^f <i>Levinsenia gracilis</i>	
	^b <i>Chaetozone hartmanae</i>		^c <i>Tecticeps convexus</i>						

Table 8. Stable isotopic signatures of northern California shelf macrofauna

Species	$\delta^{13}\text{C}$						$\delta^{15}\text{N}$					
	Site A		Site B		Site C		Site A		Site B		Site C	
	Seep	Non-seep	Seep	Non-seep	Seep	Non-seep	Seep	Non-seep	Seep	Non-seep	Seep	Non-seep
Annelida												
Capitellidae												
<i>Capitella complex</i>			-19.6		-16.4				8.2		7.6	
Capitellidae (unidentified)		-16.3						9.4				
<i>Heteromastus filobranchus</i>	-18.1						8.6					
<i>Heteromastus filobranchus</i>	-17.9						8.5					
<i>Mediomastus</i> sp.	-19.2						8.2					
<i>Notomastus</i> cf. <i>lineatus</i>					-23.0						8.7	
Lumbrineridae												
<i>Lumbrineris</i> sp. A	-17.8	-17.6					11.2	11.5				
<i>Lumbrineris</i> sp. A	-17.6	-17.5					11.3	11.5				
Magelonidae												
<i>Magelona sacculata</i>					-15.7	-17.8					21.5	8.6
<i>Magelona sacculata</i>						-16.4						10.6
Nephtyidae												
<i>Nephtys californiensis</i>					-18.9	-19.2					8.3	10.4
<i>Nephtys californiensis</i>					-19.6	-17.0					11.5	9.3
<i>Nephtys cornuta</i>	-19.6	-21.6					8.0	7.1				
Orbiniidae												
<i>Leitoscoloplos</i> sp.	-17.3						9.2					
<i>Leitoscoloplos pugettensis</i>					-20.6	-17.1					10.3	7.9
<i>Leitoscoloplos pugettensis</i>						-17.0						7.9
Polycirrinae												
<i>Amaeana</i> sp.				-16.6						8.8		
<i>Amaeana</i> sp.				-17.2						8.6		
Spionidae												
<i>Paraprionospio pinnata</i>	-16.8	-17.4					11.5	10.0				
<i>Paraprionospio pinnata</i>	-16.8						11.3					
<i>Spiophanes berkeleyorum</i>	-19.8				-17.4		11.1					8.5
<i>Spiophanes bombyx</i>					-17.4						8.9	
Sternaspidae												
<i>Sternaspis fossor</i>	-18.9	-18.3					7.1	7.3				
<i>Sternaspis fossor</i>	-19.2						7.1					
Trochochaetidae												
<i>Trochochaeta multisetosa</i>	-18.1						11.1					
<i>Trochochaeta</i> sp.		-17.6						8.8				
Mollusca												
Columbellidae												
<i>Astyris gausapata</i>	-17.0	-18.0					11.5	7.8				
Lasaeidae												
<i>Rochefortia tumida</i>		-19.3						9.2				
Olividae												
<i>Olivella pycna</i>					-19.3	-17.7					8.7	9.3
<i>Olivella pycna</i>					-17.8	-18.6					9.0	8.7
<i>Olivella pycna</i>						-19.8						8.8
Tellinidae												
<i>Macoma nasuta</i>	-18.9						7.5					
<i>Macoma nasuta</i>	-17.9						7.7					
Arthropoda												
Diastylidae												
<i>Diastylopsis dawsoni</i>		-17.4						7.9				
<i>Diastylopsis dawsoni</i>		-17.1						8.0				
<i>Diastylopsis dawsoni</i>					-17.3						8.6	
<i>Diastylopsis dawsoni</i>					-16.6						8.4	
<i>Diastylopsis dawsoni</i>					-18.0						7.2	
Mysidae	-15.8						9.6					
Mysidae	-16.3						9.2					
Phoxocephalidae					-19.9	-16.6					10.5	11.5
Phoxocephalidae					-20.1	-18.3					10.4	11.6
Sphaeromatidae												
<i>Tecticeps convexus</i>			-17.8		-17.9	-16.9		7.5			8.5	9.8
<i>Tecticeps convexus</i>					-17.6						8.2	
Caridea	-15.1						10.8					
Caridea	-15.0						10.7					
Echinodermata												
Ophiuroidea												
Ophiuroidea					-15.9	-17.3					11.5	7.5
Ophiuroidea					-15.2	-17.3					11.3	7.6
Nemertina												
Nemertea												
					-16.4						8.6	
Mean	-17.7	-18.0	-18.7	-16.9	-18.1	-17.6	9.6	9.0	7.8	8.7	9.9	9.2
SE	0.3	0.4	0.9	0.3	0.5	0.3	0.4	0.5	0.4	0.1	0.7	0.3

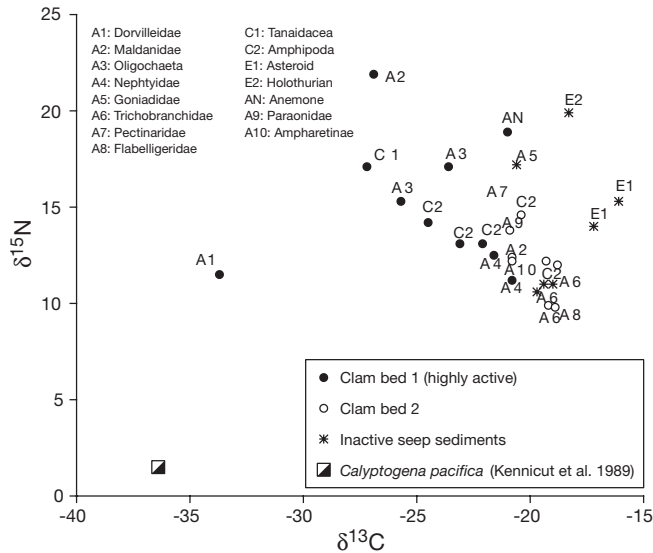


Fig. 5. Dual isotope plot of infaunal invertebrate isotopic signatures from 3 locations at ca 500 m deep on the northern California margin. A = annelid, C = crustacean, E = echinoderm

DISCUSSION

Is there evidence for specialization among seep macrofauna?

Shelf

The few existing studies comparing seep to non-seep macrofauna have yielded varied results that differ with setting and taxon (Table 1). At shelf depths, hydrocarbon seeps (Davis & Spies 1980, Montagna et al. 1989) methane pockmarks (Dando et al. 1991, 1994), and 'bubbling reef' sediments (Jensen et al. 1992) support many taxa typical of non-seep settings. Some seep specialists with chemosynthetic symbionts are present in these environments, but they are usually megafaunal (pogonophorans and thyasurid bivalves) or meiofaunal (nematodes). The northern California shelf and slope faunas characterized in this study do not appear to differ substantially from nearby non-seep assemblages. The most common infaunal taxa were present in both seep and non-seep sediments. Our data suggest that some rarer forms may select for or against seep settings on the shelf (Table 4), but confirmation of habitat preferences would require additional collections. Like Vanreusel et al.'s (1997) multivariate comparisons of hydrothermal vent and non-vent nematode genera, we found greater similarity of macrofaunal communities in seep and non-seep sediments compared within shelf sites (A, B, or C) than among seep faunas at different sites (Fig. 2, Table 4). We speculate that shelf

environmental properties such as flow, particle size or localized terrestrial inputs can have greater influence on infaunal community composition than methane seepage.

The regular presence of *Capitella* sp. in shelf seep sediments, and their absence in our non-seep samples, is consistent with known sulfide tolerances for the genus (Thiermann et al. 1997, Gamenick et al. 1998a,b). *Capitella* may cue to sulfides during settlement (Cuomo 1985) or may require sulfidic conditions for maximal growth (Tsutsumi 1997). However, *Capitella* never comprised more than 5% of the shelf seep assemblage, and was absent in seeps on the slope (Table 4). Amphipods in the genus *Rhepoxynius* are sensitive to sulfides (Knezovich et al. 1996). Their apparent avoidance of seeps on the northern California shelf is consistent with this behavior. At Site A, the most quiescent and fine-grained of the shelf sites, the dominant taxa *Lumbrineris* sp., *Mediomastus* spp., and *Nephtys cornuta* together comprised >41% of the seep fauna but only 13% of the non-seep fauna. These deposit-feeding taxa, capable of responding to sediment enrichment, contribute to higher dominance in seep than non-seep sediments.

Slope

The infaunal assemblage at the 500 m seep site was generally characteristic of North American upper slope sediments (Lissner et al. 1988, Hyland et al. 1991). Exceptions were the vesicomid *Calyptogena pacifica* and lucinid bivalves, which are symbiont-bearing and characteristic of seep or oxygen minimum zone sediments (Sibuet & Olu 1998, Levin et al. 2000). Together the polychaetes *Mediomastus* spp. and *Levinnesia gracilis* comprised over 25% of the infauna. *Mediomastus* spp. are typical of non-seep sediments, but usually occur at shallower depths than 500 m (Lissner et al. 1988). Smith et al. (1998) studied infaunal community composition beneath and near another deep-water reducing environment, at whale falls in the Santa Catalina Basin (1240 m). As in the present study, they found little evidence of specialization on enrichment or sulfides.

Quantitative macrofaunal density estimates were available in the present study only for slope seep sediments. The average macrofaunal density at the 500 m seep (12 518 ind. m⁻²), was typical of bathyal margins of the Atlantic (Blake & Grassle 1994), Pacific (Lissner et al. 1988, Hyland et al. 1991, Vetter & Dayton 1998) and Indian Oceans (Levin et al. 1997, 2000). Density differences among cores from different northern California clam beds could reflect differing levels of seepage in each bed. Clam bed 5, with high densities of

Mediomastus spp. and dorvilleids, appeared more active than the other clam beds. Unfortunately, no pore-water profiles were available to confirm this. Other investigators have reported elevated densities of meiofauna (Buck & Barry 1998) and macrofauna (Davis & Spies 1980) at seeps.

Reduced macrofaunal diversity at methane seeps might be expected if sediments were physiologically stressful or were organically enriched settings (Levin & Gage 1998). Reduced macrofaunal diversity has been reported from North Sea pockmarks (115 m) (Dando et al. 1991) and from hydrothermal settings in the Galapagos, at 21° N (2600 to 2700 m, Grassle et al. 1985) and in the Aegean Sea (5 to 10 m, Thiermann et al. 1997). Vanreusel et al. (1997) noted reduced species diversity and greater dominance in nematode assemblages at hydrothermal vents in the North Fiji Basin. We did not observe any diversity reduction in most northern California shelf seep patches, except at Site C (35 m) (Fig. 4, Table 7). Hydrocarbon seeps off Santa Barbara (16 m) also did not exhibit reduced macrofaunal diversity (Montagna et al. 1989).

Do seep infauna exhibit nutritional specialization?

Food sources for the shelf and slope infauna on the northern California margin may include phytoplankton-based organic matter, terrestrial material deposited by Eel River flood events, and chemosynthetically derived organic matter. Marine phytoplankton in productive coastal waters typically have $\delta^{13}\text{C}$ signatures between -15 and -23 at temperate latitudes (Fry & Wainright 1991) and approximately -19 on the Eel River slope (Leithold & Hope 1999). Organic matter from the Eel River has a $\delta^{13}\text{C}$ value of about -25 (Leithold & Hope 1999), whereas invertebrates with symbiotic sulfur oxidizing or methane consuming bacteria may have $\delta^{13}\text{C}$ signatures of -30 to -70 (Brooks et al. 1987, Conway et al. 1994). Based on average $\delta^{13}\text{C}$ values, which are between -17 and -19 (Table 8), shelf faunas of both seep and non-seep sediments appear to rely primarily on phytoplankton-based organic matter. This occurs despite the fact that terrestrial debris (twigs and wood chips) was visible in most sediment samples.

The absence of strong chemosynthetic contribution to nutrition of benthos appears to be a widespread feature of shallow water seeps and vents. Carbon isotopic studies of macrofauna in a North Sea methane seep revealed most fauna with $\delta^{13}\text{C}$ signatures between -16 and -20 , indicating little nutritional contribution of methane-derived carbon or sulfur oxidation (Dando et al. 1991). Similar results were obtained for epifauna on carbonates produced at seeps in the Kattegat (10 to

12 m, Jensen et al. 1992). Tissues of benthic fishes and crustaceans at a 132 m methane seep off Oregon exhibited detectable but very minor contributions of seep-associated C and N (Juhl & Taghon 1993). The lesser dependence on chemoautotrophic-based food sources exhibited by shallow-water seep macrofauna, relative to those at deep-water seeps (Conway et al. 1994), may result from the greater availability of photosynthetically produced food in shallow water.

On the Eel River margin, isotopic signatures of the slope fauna (Fig. 5) differ from those on the shelf (Table 8). The lighter $\delta^{13}\text{C}$ and higher $\delta^{15}\text{N}$ values for the slope organisms suggest one or more of the following scenarios: (1) organics derived from Eel River flood deposits may be a significant dietary component of infauna, (2) sulfur oxidizing or methanotrophic bacteria may be of nutritional importance in combination with a phytoplankton-based diet, and (3) the organic matter is derived from heavy, upwelled nitrogen, or is extensively reworked before reaching the slope, creating high $\delta^{15}\text{N}$ values. Approximately 5% of the annual Eel River sediment discharge accumulates on the slope between 450 and 600 m (Alexander & Simoneau 1999), providing a ready source of lighter carbon and recycled nitrogen. Only a dorvilleid polychaete and presumably the clam *Calyptogena pacifica* (analyzed from this region by Kennicutt et al. 1989) exhibited the light $\delta^{13}\text{C}$ values characteristic of chemosynthesis-based nutrition. However, the lighter $\delta^{13}\text{C}$ of clam bed 1 infauna (Fig. 5) may indicate some reliance by other taxa on chemosynthetic bacteria. Overall, the slope observations suggest that there are nutritional differences among species, among seep sites (clam beds) on scales of 10s of meters, and between inactive and active sites.

Conclusions

Information about macrofaunal composition, density, diversity and trophic pathways suggests that methane seeps on the northern California continental shelf and slope do not support macrofaunal assemblages that are highly distinct from the ambient faunas. On the shelf, seep patches are small and may be ephemeral due to frequent, storm-induced disturbance and shifting of methane vent sites. Shelf seeps appear to be inhabited by a subset of the ambient shelf fauna that is tolerant of sulfidic conditions. The absence of typical seep epifauna (vesicomyid clams, vestimentiferan or pogonophoran tubeworms, and bacterial mats) suggests that the shelf seep habitats sampled were too small or short lived for trophic specialization to occur among infauna. In addition, the high mobility of many shelf organisms, particularly the crustaceans, might reduce the likelihood that they will remain localized within seep

patches. Our sampling took place just following a major storm that resuspended bottom sediments on the shelf. Bacterial mats have been observed at Site B during summer by other investigators (Orange et al. 1997, Orange et al. pers. comm.).

The slope seep macrofauna exhibited typical upper bathyal densities, taxonomic composition, and diversity patterns. A similar result has been obtained for foraminifera sampled at our same slope study site (Rathburn et al. 2000). The seeps support several macrofaunal species that utilize either symbiotic or free-living chemosynthetic bacteria. However, the majority of infaunal taxa are carnivores or deposit feeders that probably utilize mainly terrestrial or marine organic matter of photosynthetic origin.

It would be premature to generalize these findings to other seep environments. Shelf and shallow bathyal faunas regularly encounter patches of disturbed, stressed or sulfidic sediments in non-seep circumstances, such as beneath large-animal or plant falls (Stockton & DeLaca 1982, Smith et al. 1998) or within oxygen minimum zones (Gallardo et al. 1995, Levin & Gage 1998). Thus, at least some bathyal and shelf taxa may be preadapted to the geochemical conditions associated with seeps. Abyssal faunas, however, may be less likely to experience sulfidic or hypoxic conditions in the absence of seepage or venting. As a result, we predict that physiological, trophic, and morphological specialization, as well as shifts in community structure, are potentially more likely among seep infauna on the continental rise and abyss.

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