

ECOLOGY OF COLD SEEP SEDIMENTS: INTERACTIONS OF FAUNA WITH FLOW, CHEMISTRY AND MICROBES

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Abstract Cold seeps occur in geologically active and passive continental margins, where pore waters enriched in methane are forced upward through the sediments by pressure gradients. The advective supply of methane leads to dense microbial communities with high metabolic rates. Anaerobic methane oxidation presumably coupled to sulphate reduction facilitates formation of carbonates and, in many places, generates extremely high concentrations of hydrogen sulphide in pore waters. Increased food supply, availability of hard substratum and high concentrations of methane and sulphide supplied to free-living and symbiotic bacteria provide the basis for the complex ecosystems found at these sites. This review examines the structures of animal communities in seep sediments and how they are shaped by hydrologic, geochemical and microbial processes. The full size range of biota is addressed but emphasis is on the mid-size sediment-dwelling infauna (foraminiferans, metazoan meiofauna and macrofauna), which have received less attention than megafauna or microbes.

Megafaunal biomass at seeps, which far exceeds that of surrounding non-seep sediments, is dominated by bivalves (mytilids, vesicomysids, lucinids and thyasirids) and vestimentiferan tube worms, with pogonophorans, cladorhizid sponges, gastropods and shrimp sometimes abundant. In contrast, seep sediments at shelf and upper slope depths have infaunal densities that often differ very little from those in ambient sediments. At greater depths, seep infauna exhibit enhanced densities, modified composition and reduced diversity relative to background sediments. Dorvilleid, hesionid and ampharetid polychaetes, nematodes, and calcareous foraminiferans are dominant. There is extensive spatial heterogeneity of microbes and higher organisms at seeps. Specialized infaunal communities are associated with different seep habitats (microbial mats, clam beds, mussel beds and tube worms aggregations) and with different vertical zones in the sediment. Whereas fluid flow and associated porewater properties, in particular sulphide concentration, appear to regulate the distribution, physiological adaptations and sometimes behaviour of many seep biota, sometimes the reverse is true. Animal-microbe interactions at seeps are complex and involve symbioses, heterotrophic nutrition, geochemical feedbacks and habitat structure.

Nutrition of seep fauna varies, with thiotrophic and methanotrophic symbiotic bacteria fueling most of the megafaunal forms but macrofauna and most meiofauna are mainly heterotrophic. Macrofaunal food sources are largely photosynthesis-based at shallower seeps but reflect carbon fixation by chemosynthesis and considerable incorporation of methane-derived C at deeper seeps. Export of seep carbon appears to be highly localized based on limited studies in the Gulf of Mexico.

Seep ecosystems remain one of the ocean's true frontiers. Seep sediments represent some of the most extreme marine conditions and offer unbounded opportunities for discovery in the realms

of animal-microbe-geochemical interactions, physiology, trophic ecology, biogeography, systematics and evolution.

Introduction

Ecosystems known as cold seeps are found where reduced sulphur and methane emerge from seafloor sediments without an appreciable temperature rise. Cold seep environments are among the most recently discovered marine habitats; the first such system was found just 20 yr ago, on the Florida Escarpment in the Gulf of Mexico (Paull et al. 1984). Initial exploration of this seep and others in the Gulf of Mexico revealed communities dominated by symbiont-bearing tube worms, mussels and clams, often belonging to genera found earlier at hydrothermal vents. Since that discovery, large numbers of cold seeps have been identified in a broad range of tectonic settings, on both passive and active continental margins (Sibuet & Olu 1998, Kojima 2002). Many fossil seeps have been discovered (or reinterpreted) as well (Figure 1) (Campbell et al. 2002).

Most biological studies of cold seeps have focused on large, symbiont-bearing megafauna (vestimentiferan tube worms, mytilid mussels, vesicomyid clams), or on microbiological processes. Major reviews of megafaunal community structure at methane seeps have been prepared by Sibuet & Olu (1998), Sibuet & Olu-LeRoy (2002) and Tunnicliffe et al. (2003), and by Kojima (2002) for western Pacific seeps. Seep microbiology is reviewed in Valentine & Reeburgh (2000), Hinrichs & Boetius (2002) and Valentine (2002). Detailed understanding of the sediment-animal-microbe interactions at seeps has only just begun to emerge, along with new discoveries related to anaerobic methane oxidation.

The present review addresses the communities of organisms that inhabit cold seep sediments, focusing on soft-bodied, mid-size organisms (e.g., macrofauna and meiofauna) and on the nature of their interaction with biogeochemical processes. To fully understand the ecology of cold seep sediment-dwellers it is necessary to understand the environmental conditions at a scale that is

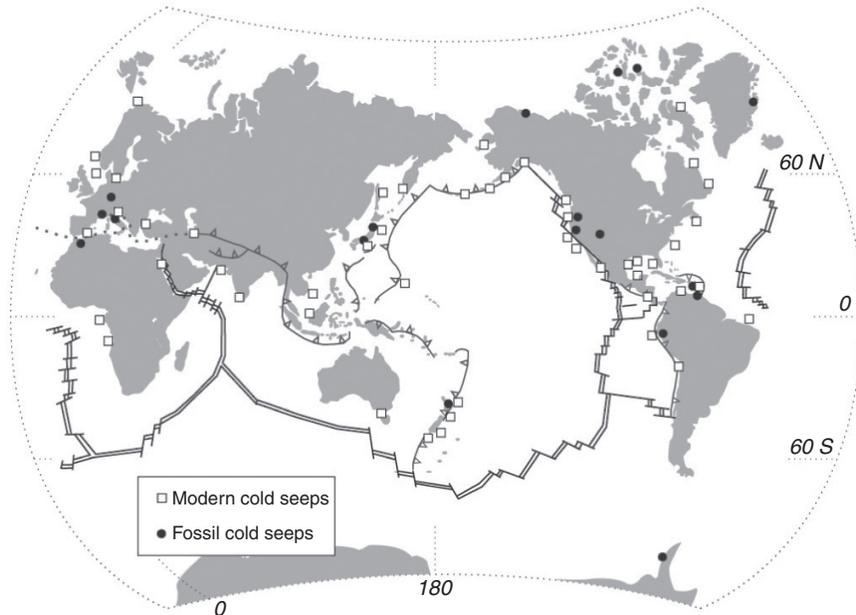


Figure 1 Distribution of modern and fossil cold seeps. (Modified from Campbell et al. 2002)

relevant to the organisms. To this end the review briefly considers the different types of cold seeps, patterns of fluid flow and aspects of their sediment geochemistry that are most likely to influence animals. The role of microbial activity in shaping the geochemical environment is discussed as is how this environment regulates the distribution and lifestyles of animals on different spatial scales. In this context the review describes the geochemical links to faunal abundance, composition, nutrition and behaviour, focusing on organisms and processes that occur within seep sediments. Because the large (megafaunal) seep organisms influence the sediment environment, providing physical structure and modulating geochemistry through oxygenation (pumping) and ion uptake activities, relevant features of the epibenthic megafauna are also included. The study of animal-sediment interactions at cold seeps is unquestionably still in its infancy. Where appropriate, those classes of organism-sediment interactions that are relatively unknown, but could yield interesting insights if researched further, are highlighted.

Forms of seepage and global distribution

Cold seeps are among the most geologically diverse of the reducing environments explored to date. They are widespread, occurring in all continental margin environments (tectonically active and passive) and even inland lakes and seas. It is safe to say that probably only a small fraction of existing seafloor seeps have been discovered, because new sites are reported every year. Seep communities (with metazoans) are known from depths of <15 m (Montagna et al. 1987) to >7,400 m in the Japan Trench (Fujikura et al. 1999).

Tunnicliffe et al. (2003) briefly review the major processes known to form seeps. These processes include compaction-driven overpressuring of sediments due to sedimentary overburden and/or convergent plate tectonics, overpressuring from mineral dehydration reactions and gas hydrate dynamics. Fluids exiting overpressured regions migrate along low permeability pathways such as fractures and sand layers or via mud diapirs. Cold seeps are commonly found along fractures at the crests of anticlines, on the faces of fault and slump scarps where bedding planes outcrop and along faults associated with salt tectonics at passive margins. Formation and dissociation of gas hydrate outcrops also can drive short-term, small-scale variation in chemosynthetic communities in the Gulf of Mexico (MacDonald et al. 2003). Seep ecosystems may be fuelled by a variety of organic hydrocarbon sources, including methane, petroleum, other hydrocarbon gasses and gas hydrates, which are only stable below about 500 m (Sloan 1990). All of these sources are ultimately of photosynthetic origin because they are generated from accumulations of marine or terrestrial organic matter.

Understanding of the different sources and forms of seep systems continues to grow as new seep settings are encountered. Interactions between hydrothermal venting, methane seepage and carbonate precipitation have led to several new constructs in both shallow (Michaelis et al. 2002, Canet et al. 2003) and deep water (Kelly et al. 2001). New settings may be discovered where spreading ridges (e.g., Chile Triple Junction) or seamounts (e.g., Aleutian Archipelago) encounter subduction zones, or when seepage occurs within oxygen minima (Schmaljohann et al. 2001, Salas & Woodside 2002). Mass wasting from earthquakes, tsunamis or turbidity currents may generate or expose reduced sediments and yield seep communities as well (e.g., Mayer et al. 1988).

The seepage, emission and escape of reduced fluids results in a broad range of geological and sedimentary constructs (Table 1, Judd et al. 2002). The most conspicuous manifestation of seepage is bubbles escaping from the sea bed. These bubbles may be visualized (i.e., by eye, film or video) or are evident as acoustical plumes observed through echo sounding. Topographic depressions (pockmarks) sometimes result from escaping gas but topographic highs (mounds, mud volcanoes, mud diapirs) may also be raised by seeping gas and are equally common. In karst formations, hypogenic caves may form by acid fluid intrusion (Forti et al. 2002). Precipitates of gas hydrate

Table 1 Geological constructs and features associated with cold seeps

Feature	Description	Fluid flux	Examples	References
Direct indicators				
Gas seepage	Gas bubbles escaping from the sea bed visible to the eye or evident as acoustical plumes observed through echo sounding, side scan sonar or high frequency seismic systems.	High	Mediterranean Sea, Gulf of Mexico	e.g., Coleman & Ballard 2001, Sassen et al. 2004
Microbial mat	Often formed of filamentous sulphide oxidizers. Common taxa include <i>Beggiatoa</i> , <i>Thioploca</i> , <i>Thiothrix</i> .	Moderate	Most seeps	Hovland 2002
Pockmarks	Shallow seabed depressions formed by fluid escape.		North Sea	Dando et al. 1991
Authigenic carbonate platforms	Formed by microbial activity in presence of methane seepage.	Moderate	Gulf of Mexico, Oregon margin, Mediterranean Sea	
Carbonate mounds	Precipitates up to 300 m high associated with fossil venting.		Porcupine Bight, Rockall Trough, Irish Sea, NE Atlantic Ocean Margin, Gulf of Mexico	van Weering et al. 2003
Bioherms	Reef-like communities associated with presence of shallow gas or seepage.	Low	Cascadia Subduction Zone	Bohrmann et al. 1998
Mud volcanoes	Volcano-shaped structure of mud that has been forced above the normal surface of the sediment, usually by escaping gas.	High	Costa Rica margin, Mediterranean Sea	Sassen et al. 2001, Charlou et al. 2003
Mud diapir, ridges	Positive seabed features composed of sediment raised by gas (smaller than mud volcanoes). May form elongate ridges.		Gulf of Mexico	Sassen et al. 2003
Gas hydrates	Crystalline, ice-like compound composed of water and methane gas, will form mounds.	Moderate	Gulf of Mexico	MacDonald et al. 1994, Sassen et al. 2001
Hypogenic caves	Karst formations formed by acidic fluids ascending from depth.	Low	Romania, Italy	Forti et al. 2002, Sarbu et al. 2002
Indirect indicators				
Bright spots	High amplitude negative phase reflections in digital seismic data.			
Acoustic turbidity	Chaotic seismic reflections indicative of gas presence.			
Gassy cores	Sediment cores found to have high gas content.			

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Table 1 (continued) Geological constructs and features associated with cold seeps

Feature	Description	Fluid flux	Examples	References
Faulting	Major scarps may be sites of exposed venting or seepage.			
Deep water coral reefs	May occur at sites of fossil venting, associated with carbonate mounds.	Low or none	Norwegian corals, Storegga margin	Hovland & Risk, 2003
Oil slicks	Evident from satellite or aerial imagery.		Gulf of Mexico	Sassen et al. 1993

Definitions after Judd et al. 2002.

and authigenic carbonate can form mounds, platforms or other structures. Much of the carbonate precipitation is now understood to be microbially mediated (Barbieri & Cavalazzi 2004). Mats of filamentous bacteria and bioherms (reefs or aggregations of clams, tubeworms or mussels) provide biological evidence of seepage. Indirect indicators include bright spots, acoustic turbidity, gas chimneys, scarps, gassy cores and possibly deep-water coral reefs (Table 1).

Significant methane reservoirs are generally found in areas of high organic content (i.e., in sediments underlying upwelling areas characterized by high primary productivity in the water column). When the supply of other oxidants becomes depleted in deeper sediments, CO₂ becomes the most important oxidant for the decomposition of organic material coupled to methane production. In geologically active areas, methane-enriched fluids formed by the decomposition of organic matter in deeper sediment layers are forced upward and the advective flow provides a high supply of methane emanating as dissolved or free gas from the sea floor. Under low temperature and high pressure, methane hydrates are formed as ice-like compounds consisting of methane gas molecules entrapped in a cage of water molecules. An increase in temperature or decrease in pressure leads to dissolution of hydrate, yielding high methane concentrations that are dissolved in the surrounding and overlying pore waters or emerge to the overlying water. Methane may originate from decaying organic matter (e.g., sapropel) or by thermogenic degradation of organic matter, with fluid circulation within sediments bringing it to the surface (Coleman & Ballard 2001).

Substrata

Seeps are typically considered to be soft sediment ecosystems, at least during initial stages of formation. Sediments may consist of quartz sand, carbonate sands, turbidites of terrestrial origin, fine grained muds or clays. However, carbonate precipitates are commonly associated with both active and fossil cold seeps and provide a source of hard substratum in an otherwise soft matrix (Bohrmann et al. 1998, Barbieri & Cavalazzi 2004). Methane-based cold seep communities are reported from exposed oceanic basement rock on the Gorda Escarpment at 1600 m (Stakes et al. 2002). In Monterey Bay, Stakes et al. (1999) have documented carbonate pavements (flat platforms), circular chimneys (cemented conduits), doughnut-shaped rings (cm to m in size) and veins in basement rock. Less structured carbonate pebbles, rocks and soft concretions are distributed haphazardly throughout sediments of many cold seep sites (e.g., Bohrmann et al. 1998) and are clearly visible in x-radiographs (Figure 2). Comparable interspersion of hard substrata with fine-grained sediments is evident on the Peru margin where phosphorite pebbles are common, and on seamounts where basalt fragments are common. Dense assemblages of crabs dwell at methane ‘jacuzzis’ on phosphorite hardgrounds on the upper Peru slope (R. Jahnke, personal communication).

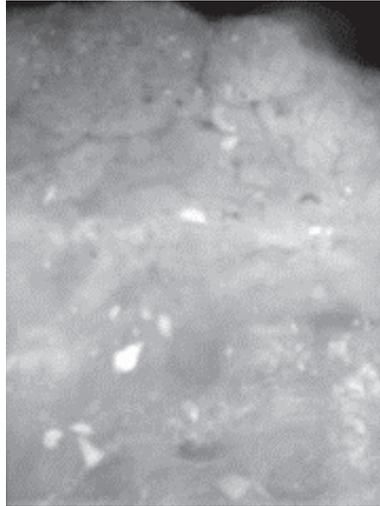


Figure 2 X-radiograph of seep sediments from the Gulf of Alaska (2,200 m), showing carbonate concretions, which are higher density than surrounding sediments and appear as white reflectors. Image width = 9.5 cm.

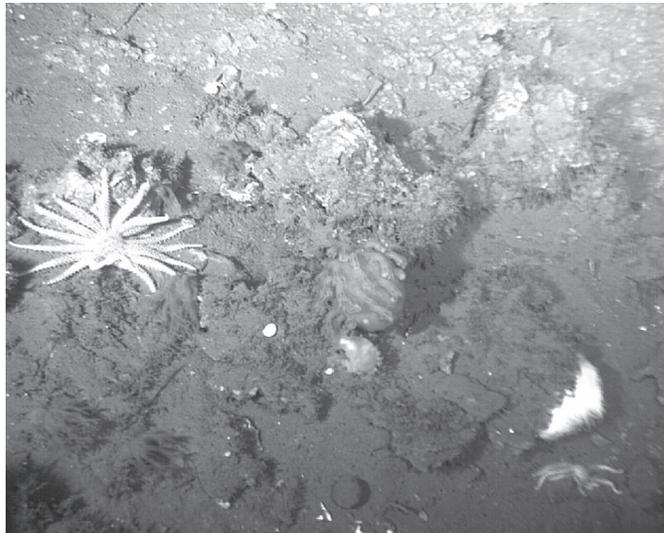


Figure 3 Photograph of animals on carbonate outcrops on the Eel River margin (500 m). *Anthomastus ritterii*, *Rathbunaster californicus* and an unidentified sponge are the large taxa visible. Image width ~75 cm.

While a number of invertebrate taxa attach to carbonates (Figure 3), there have been no community descriptions of carbonate-associated or carbonate-burrowing seep taxa — either the epifauna or endolithofauna. In contrast, extensive programs have been developed to catalogue the species diversity associated with carbonate mounds and coral reefs in the North Atlantic and Gulf of Mexico. Sibuet et al. (1988) note the occurrence of *Calyptogena* species on a broad range of substrata in the Japan Trench, including sediments, mudstone, gravel, talus and vertical rock ledges. In surveying 50 sites, however, they observed that large colonies develop only on sediments and

mudstones and suggest that these substrata promote greater lateral transport of rising pore fluids, enhancing the area suitable for the clams.

Distribution

Modern (active) seeps have been reported from all oceans of the world except the polar regions (Figure 1). Many seeps are known from active subduction zones in the Pacific Ocean, along the margins of Alaska, Oregon, California, Central America, Peru, Japan and New Zealand (reviewed in Sibuet & Olu 1998, Sibuet & Olu-LeRoy 2002, Kojima 2002). Particularly well-studied regions include the Nankai Trough and Sagami Bay off Japan, the Aleutian Trench, Hydrate Ridge off Oregon, the Eel River margin and Monterey Bay in northern California, the Costa Rica Prism, the Peru margin, the Barbados Prism, and the Florida Escarpment in the Gulf of Mexico (see reviews by Sibuet & Olu 1998, Sibuet & Olu-LeRoy 2002). Seismic documentation of bottom simulating reflectors indicative of hydrates on the Chile margin (Morales 2003) and dredged seep bivalves (Stuardo & Valdovinos 1988, Sellannes et al. 2004) indicate the existence of many more (as yet unlocated) seeps in subduction settings. Hydrocarbon cold seeps abound in the Gulf of Mexico from depths of 400–3500 m and include petroleum seeps, gas hydrate seeps and recently discovered tar deposits (Sassen et al. 1993, 1999, MacDonald et al. 2004). Other types of seeps are documented in the NE and NW Atlantic Ocean (Mayer et al. 1988, Van Dover et al. 2003), Mediterranean Sea (Charlou et al. 2003), Northern Indian Ocean (Schmaljohann et al. 2001) and off east and west Africa, and Brazil from shelf to rise depths.

Geochemical settings

It is the upward transport of methane (or other hydrocarbons) that provides the ultimate carbon and/or energy source for microorganisms. High sulphide concentrations resulting from high rates of sulphate reduction coupled to anaerobic methane oxidation provide the energy for sulphide oxidizing free-living and symbiotic bacteria. Other reduced compounds such as H_2 , NH_4^+ , Fe^{2+} and Mn^{2+} (Tunnicliffe et al. 2003) may be associated with increased microbial activity. Methane concentrations in the upper sediment layers vary with organic content of the underlying deep sediment, the nature and magnitude of upward flow and the transport of methane-laden pore water. Concentrations range widely from micromolar to millimolar concentrations (Van Dover 2000), with values up to 10 mM recorded in sediments from the Florida Escarpment (Chanton et al. 1991) and up to ~20 mM in Eel River and Hydrate Ridge sediments. Methane concentration also varies among microhabitats (Treude et al. 2003). Typically methane is rapidly oxidized; oxidation in anoxic sediments is apparently coupled to sulphate reduction in some areas (Orphan et al. 2001 a,b, Hinrichs et al. 1999, Boetius et al. 2000, Treude et al. 2003), yielding exceptionally high concentrations of H_2S . Total hydrogen sulphide concentrations of up to 20–26 mM have been documented at upper slope seeps on the Oregon and California margins (Sahling et al. 2002, Levin et al. 2003, Ziebis unpublished data). Decay of organic matter can also yield high sulphide concentrations, thus similar sulphide profiles may occur around whale or wood falls (Smith & Baco 2003).

The millimolar sulphide concentrations found in seep sediments are much higher than the low micromolar concentrations characteristic of non-seep sediments. Sulphide is extremely toxic to most animals even at low concentrations (Bagarinao 1992, Somero et al. 1989). The consequences of this for development of seep infaunal communities will be discussed below. Typically, sulphide does not persist in most sediments; it becomes complexed and is removed as FeS and pyrite (Whiticar et al. 1995) or is sequestered in gas hydrates.

Fluid flow

Nature

Fluid flow is thought to control the distribution and abundance of seep benthos by regulating the availability of reduced compounds (Barry et al. 1997, Olu et al. 1997, Sahling et al. 2002, Tunnicliffe et al. 2003, Levin et al. 2003). Flow is expressed through permeable substrata, faults, cracks, scarps, slumps, erosion and outcropping, with sediment cover and manganese crusts sometimes acting to block discharge. Seeping fluids include hypersaline brines, petroleum, sediment pore waters, recirculating sea water and sometimes groundwater. Only in the last decade have rates and patterns of fluid flow at seeps been quantified with measurements on the sea floor (e.g., Tryon et al. 2001). Most measurements are relatively short-term (i.e., weeks or less) but some long-term records reveal complex patterns of advective outflow, inflow and variable fluid chemistry (e.g., Tryon et al. 2002). Measurements suggest that a range of dynamic processes influence the expression of flow at the sediment-water interface. These include gas-expulsion driven pumping (with aqueous entrainment), buoyancy-driven fracturing of overlying sediments, changes in permeability due to gas injection and gas hydrate formation, non-stationary flow conduits, tidally-driven flow oscillations and formation and dissolution of gas bubbles (Tryon et al. 1999, 2002).

Rates

Rates of fluid flow within sediments have been estimated by (a) combining oxygen flux with vent fluid analysis (Wallmann et al. 1997), (b) geophysical estimates of dewatering based on sediment porosity reduction (von Huene et al. 1998), (c) comparison of flux rate of fluid tracers into a bottom chamber with flow meter data (Suess et al. 1998), (d) direct measurement of outflow by tracer dilution (Tryon et al. 2001) and visual observations (Olu et al. 1997) and (e) application of thermal models (Olu et al. 1996b, Henry et al. 1992, 1996). Early measurements of fluid flow rates ranged from low values of $10 \text{ l m}^{-2} \text{ d}^{-1}$ (Alaska margin $>5000 \text{ m}$, Suess et al. 1998) up to $>1700 \text{ l m}^{-2} \text{ d}^{-1}$ on the Oregon margin (Linke et al. 1994), with intermediate values off Peru ($440 \text{ l m}^{-2} \text{ d}^{-1}$; Linke et al. 1994; Olu et al. 1996a) but it is now believed that these values are too high (Luff & Wallmann 2003). Within a single region, such as the Bush Hill seeps in the northern Gulf of Mexico, flow can be highly variable over short periods, e.g., $1 \text{ mm yr}^{-1} - 6 \text{ m yr}^{-1}$ (Tryon & Brown 2004).

Spatial variation and relation to biology

Where flow measurements have been made in relation to biological features, there appears to be a somewhat predictable relationship. Downward directed flow (inflow) and oscillatory flows are common features of vesicomid clam bed sediments off Oregon (Tryon et al. 2001) and California (Levin et al. 2003). Observations of *Calyptogena* beds in the Barbados Prism suggest shallow convective circulation in the upper few metres (Olu et al. 1997). Oscillatory flow may produce optimal conditions for clams by injecting seawater sulphate into the sediments, bringing it into contact with methane. Microbial reduction of sulphate to hydrogen sulphide, which is needed to fuel clam symbionts, is tied to methane oxidation (Boetius et al. 2000). Net outflow in clam beds may be limited.

Microbial mat-covered sediments support more consistent outflow of altered fluids on the Oregon margin (Tryon & Brown 2001, Tryon et al. 2002), northern California margin (Tryon et al. 2001, Levin et al. 2003) and in the Gulf of Mexico (Tryon & Brown 2004). Studies at Hydrate Ridge suggest that orange or reddish mats develop on sediments with stronger flow than non-pigmented (white) mats (M.D. Tryon, personal communication). Olu et al. (1997) document biological differences between vents and seeps on Barbados mud volcanoes. In contrast to the results

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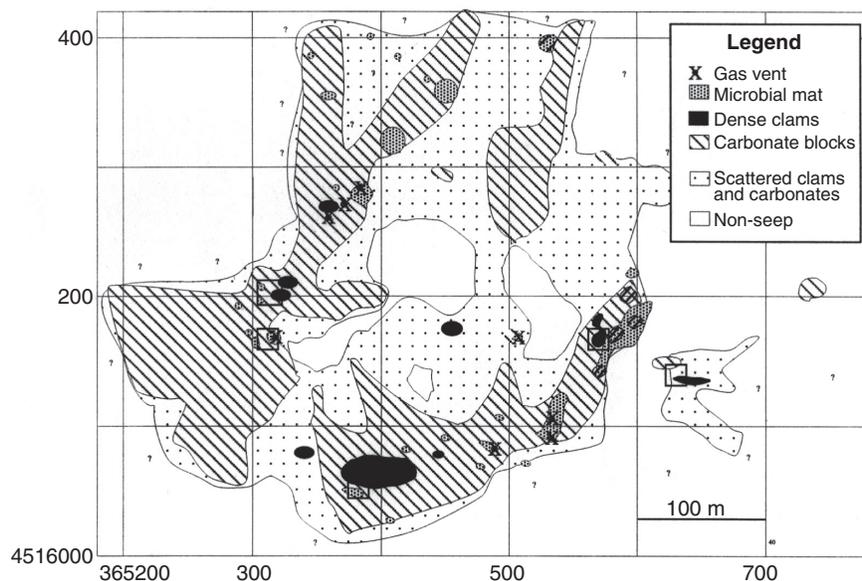


Figure 4 Map illustrating heterogeneity of clam bed, microbial mat, scattered clam, carbonate and non-seep habitats on the Eel River margin. (Map by K. Brown and M. Tryon, modified from Levin et al. 2003). Axes are in metres. Area shown is approximately 600 × 400 m.

described above, they found that vents with highly focused outflow of 10 cm s^{-1} support dense clams, whereas seepages, with low, diffuse flow were associated with dispersed clams and bacterial mats. However, all of these seeps were associated with thermal gradients that are not evident in other seep habitats. It should be noted that biological manifestations of flow are ephemeral, and significant flow has been documented where there is no biological indication of seepage on the surface (Tryon & Brown 2004). Excessively rapid fluid expulsion or soupy, unconsolidated mud is likely to create too unstable a system to support seep animals (Olu et al. 1997).

Current evidence suggests that spatial heterogeneity in flux rates is, in part, the result of heterogeneity in permeability. The small number of flow measurements made within any one seep site is insufficient to reconstruct the spatial patterns of flow. However, it is clear from large differences in direct measurements made by instruments placed only a few metres apart, that fluid flow can vary on spatial scales of centimetres to metres. This variability leads to a patchy distribution of biological communities (Tryon & Brown 2001). A rough interpretation of recent flow histories in two dimensions and indication of the spatial scales of patchiness may be derived from the mapped distribution of biological community types (e.g., Figure 4). The number, size, and proximity of different patch types within a region has implications for the dynamics of organisms that must disperse, locate and colonise these habitats.

Temporal variation

Flow records reveal transience on times scales of hours to months with variation coinciding with tidal, lunar or much longer cycles (Carson & Sreaton 1998). High-frequency variation due to tidal forcing has been observed off Oregon (Linke et al. 1994, Tryon & Brown 2001) and Alaska (Tryon et al. 2001). Longer-term changes in permeability (e.g., through formation of gas hydrate or infilling and outfilling of subsurface gas reservoirs) may drive changing amplitudes of flow oscillations. On the Eel River margin, even microbial mat sites with net outflow were observed to have periods of

several months with little or no flow (Levin et al. 2003). Pulsed expulsion events with short-term flow up to 6 m yr^{-1} have been documented (e.g., Bush Hill) and may be synchronous over 10s of metres (Tryon & Brown 2004). In contrast to hydrothermal vent ecosystems, where changes in biological activities have been directly correlated with increases and decreases in venting (Geistdoerfer et al. 1995, Shank et al. 1998), there have been no studies that document the local rise and decline of seep communities in direct relation to temporal changes in flow. It is believed that regional patterns of fluid flow may persist for 1000 or more years (Tunnicliffe et al. 2003, Roberts & Carney 1997), maintaining biological activity in certain areas for extended periods. The chemistry of vesicomid clam shells may prove to be good meso-timescale tracers of fluid flow. Ba/Ca profiles in *Calyptogena kilmeri* in Monterey Bay indicate 1–2 yr periods of enhanced barium, possibly reflecting rainfall driven inputs of groundwater from the Monterey Formation on land. Reduced $\delta^{18}\text{O}$ values that correspond to elevated Ba concentrations are consistent with this hypothesis (Torres et al. 2001). Even longer time scales may drive the accumulations and release of methane, gas hydrate, brines and petroleum (e.g., Kennett et al. 2000).

There is little information about how most fauna respond to temporal variation in availability of methane, sulphide and other porewater constituents that result from variability in fluid flow at seeps. One might expect to see behavioural and physiological adaptations that either limit short-term exposure to toxic compounds or enhance access to required compounds. These could be cyclic, such as pumping activities tied to tidal cycles. Functional responses such as small-scale migration are likely because some seep taxa are clearly mobile (Figure 5). Vertical movements within the sediment column may occur, whereas some taxa may cease pumping or feeding in response to hostile conditions. Species of *Calyptogena* are known to survive periods of reduced or halted fluid flow and variable sulphide concentrations (Sibuet & Olu 1998). Numerical responses, including reproduction, recruitment and colonization, and succession, are expected, and are probably rapid in selected, opportunistic taxa. If lunar, seasonal or longer-scale forcing imparts predictable variation in availability of methane or sulphide, reproductive cycles may be entrained. Functional responses,

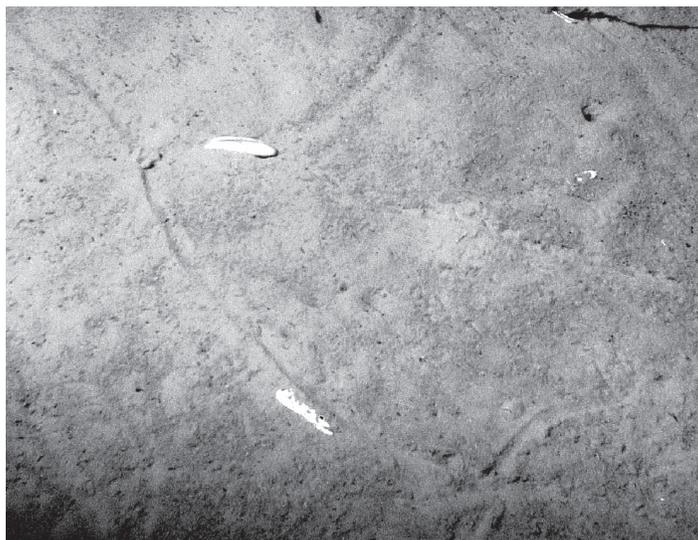


Figure 5 *Calyptogena phaseoliformis* shown moving with trails (drag marks) as evidence. The clams, which normally occur in dense aggregations, are probably searching for new sources of sulphide. Kodiak Seep, Gulf of Alaska, 4,445 m. Clams are ~12–15 cm long.

including changes in diet as reflected by carbon and nitrogen isotopic signatures, have been detected by experimentally moving mussels between seep sites (Dattagupta et al. 2004).

The variability of fluid flow and attendant sediment microbial activities in space and time raises the following questions about biological responses.

- (1) Do species life histories (generation time, reproductive cycles, dispersal abilities) reflect temporal variation in resource availability (i.e., reduced compounds)? How do species cope with temporary cessation of flow or expulsion events that raise sulphide concentrations to toxic levels?
- (2) Are there successional stages that mirror development, input and breakdown of fluid flow? Does succession involve alteration of substratum properties (e.g., Hovland 2002)? Succession of major bivalve taxa was hypothesized by Olu et al. (1996b) for diapiric domes of the Barbados prisms, with vesicomid clams colonizing soft sediments first, two *Bathymodiolus* species recruiting later as the sediment becomes lithified and fluid flow increases and, finally, a decline in fauna as metre-high blocks occlude fluid expulsion.
- (3) Does mixotrophy (e.g., involving ingestion and symbionts or multiple symbionts) allow species to adapt to variable fluid flow conditions?

To obtain answers to these questions, researchers will need to make coordinated, *in situ* biological, geochemical, microbiological and hydrogeological measurements over extended periods.

Sediment microbiology

The geochemical environments described above reflect the products of microbial metabolic processes — most significantly methanogenesis, sulphate reduction, methane oxidation and sulphide oxidation. Cold-seep biota rely largely on oxidation of reduced sulphur and methane by microorganisms for nutrition, and possibly even on nitrogen fixation. Seep microbiology is a burgeoning field that cannot be examined in detail in this review. Only basic microbial features and processes likely to influence higher organisms are considered here.

Methane at cold seeps can be biogenic (microbial) or thermogenic in origin. Ratios of $^{13}\text{C}/^{12}\text{C}$ differ between the mechanisms, with biogenic methane having much lighter $\delta^{13}\text{C}$ signatures. In diffusion-controlled anoxic sediments, all of the methane produced by methanogenesis is oxidized at the methane/sulphate transition zone and never reaches bottom waters (Valentine 2002). At seeps, methane-laden pore water is transported towards the sediment surface and the high supply of methane leads to higher rates of Anaerobic Oxidation of Methane (AOM) in surface sediments. For gas-hydrate bearing sediments on Hydrate Ridge off the coast of Oregon it has been shown that AOM also represents an important methane sink in the surface sediments, consuming between 50 and 100% of the methane transported by advection (Treude et al. 2003). In the Eel River Basin, a large fraction of methane is transported to the water column (Ziebis et al. 2002) and is oxidized in the deeper part of the water column (Valentine et al. 2001).

AOM is carried out by two or more groups of archaea — the ANME-1 (Michaelis et al. 2002), ANME-2 (Boetius et al. 2000) and possibly ANME-3. They typically live in syntrophic consortia with sulphate-reducing bacteria in the *Desulfosarcina/Desulfococcus* and *Desulfobulbu* groups (Orphan et al. 2002, Knittel et al. 2003), although the exact nature of the interactions is poorly understood (reviewed in Valentine 2002, Widdel et al. 2004). The overall reaction involves oxidation of methane and reduction of sulphate, leading to the formation of bicarbonate and hydrogen sulphide:



The exact mechanisms and the intermediates involved in this reaction are not yet known.

Use of Fluorescent In Situ Hybridization (FISH) has revealed that the consortia may have many forms: they can grow in a shell-like construct with an inner core of archaea surrounded by bacteria, the archaea and bacteria may be randomly distributed throughout clusters, the two may grow separately in dense microcolonies or cells may grow individually without partners (Widdel et al. 2004, Orphan et al. 2004). The activities of the consortia increase the alkalinity of pore waters, thus facilitating the precipitation of carbonate minerals, mainly aragonite (Valentine 2002). In contrast, aerobic methane oxidation, a process which occurs in the presence of oxygen and leads to production of CO_2 , a weak acid, causes the dissolution of carbonates.

Some methanogens are apparently capable of oxidizing methane to CO_2 (Zehnder & Brock 1979) but reverse methanogenesis does not seem to be a general property of methanogens (Valentine 2002). However, genome-based observations suggest that genes associated with methane production are present in ANME-1 and some ANME-2 methanotrophs (Hallam et al. 2004).

Gene sequencing, the use of oligonucleotide targeting probes, and lipid biomarker analysis indicate that the community structure of microorganisms involved in anaerobic methane oxidation is complex, and involves very diverse assemblages of archaea and bacterial lineages, occurring in many configurations and geometries (Orphan et al. 2004). Tremendous microscale heterogeneity in isotopic signatures of microbes, perhaps related to physiological state or local fluid chemistry, has been revealed by use of FISH with Secondary Ion Mass Spectrometry (SIMS) (Orphan et al. 2001b, 2004).

Microbial metabolic rates also vary with meso-scale habitat features; bacterial mats and different types of clam beds within a single region exhibit different rates of AOM and sulphate reduction (SR) that correspond to fluid flow regimes (Orphan et al. 2004, Treude et al. 2003). For example, at Hydrate Ridge, average rates of AOM were nearly 2 times higher in bacterial mats ($99 \text{ mmol m}^{-2} \text{ d}^{-1}$) than *Calyptogenia* fields ($56 \text{ mmol m}^{-2} \text{ d}^{-1}$), and 47 times higher than in *Acharax* fields ($2.1 \text{ mmol m}^{-2} \text{ d}^{-1}$) (Treude et al. 2003). Sulphate reduction rates showed great variance within the habitats and appeared to be higher in *Calyptogenia* fields ($64 \text{ mmol m}^{-2} \text{ d}^{-1}$) than *Beggiatoa* mats ($32 \text{ mmol m}^{-2} \text{ d}^{-1}$). In the Eel River Basin, depth-integrated (0–15 cm) AOM rates were an order of magnitude lower but showed a similar difference between habitats: $0.9 \text{ mM m}^{-2} \text{ d}^{-1}$ in bacterial mat covered sediments compared with $0.6 \text{ mM m}^{-2} \text{ d}^{-1}$ in *Calyptogenia* beds (Ziebis et al. 2002). Methane concentrations were 20 times higher in the microbial mat habitats than in clam beds. The highest Eel River AOM rates also co-occurred with highest sulphate reduction rates in the microbial mat habitats ($2.6 \text{ mM m}^{-2} \text{ d}^{-1}$) compared with lower SR rates in clam beds ($0.9 \text{ mM m}^{-2} \text{ d}^{-1}$) and non-seep habitats ($0.3 \text{ mM m}^{-2} \text{ d}^{-1}$).

High rates of anaerobic methane oxidation coupled to sulphate reduction generate high microbial biomass that, upon cell death, can provide a significant supply of methane-derived carbon to the sediment microbial community. Heterotrophic bacteria may play an important role in transferring this carbon to higher-order consumers, where it is expressed as light $\delta^{13}\text{C}$ ratios (Levin & Michener 2002). There is evidence that remineralization of sedimentary organic matter might be inhibited in seep sediments, emphasizing the importance of methane as a carbon source (Hinrichs et al. 2000).

Microbial mats form near the surface of seep sediments where there is persistent outflow of reduced fluids and a source of oxygen (Tryon & Brown 2001) (Figure 6A,B). Mat distributions can be highly patchy over scales of metres, indicating localized fluid flow, and the patches can be small (Figure 4). Microbial mats usually comprise a mixture of taxa, with biomass dominated by large filamentous sulphide-oxidizing bacteria (*Beggiatoa*, *Thioploca*, *Arcobacter*, *Thiothrix*). Seep microbial mats typically appear to be white, yellow or orange. Coloured pigmentation may be

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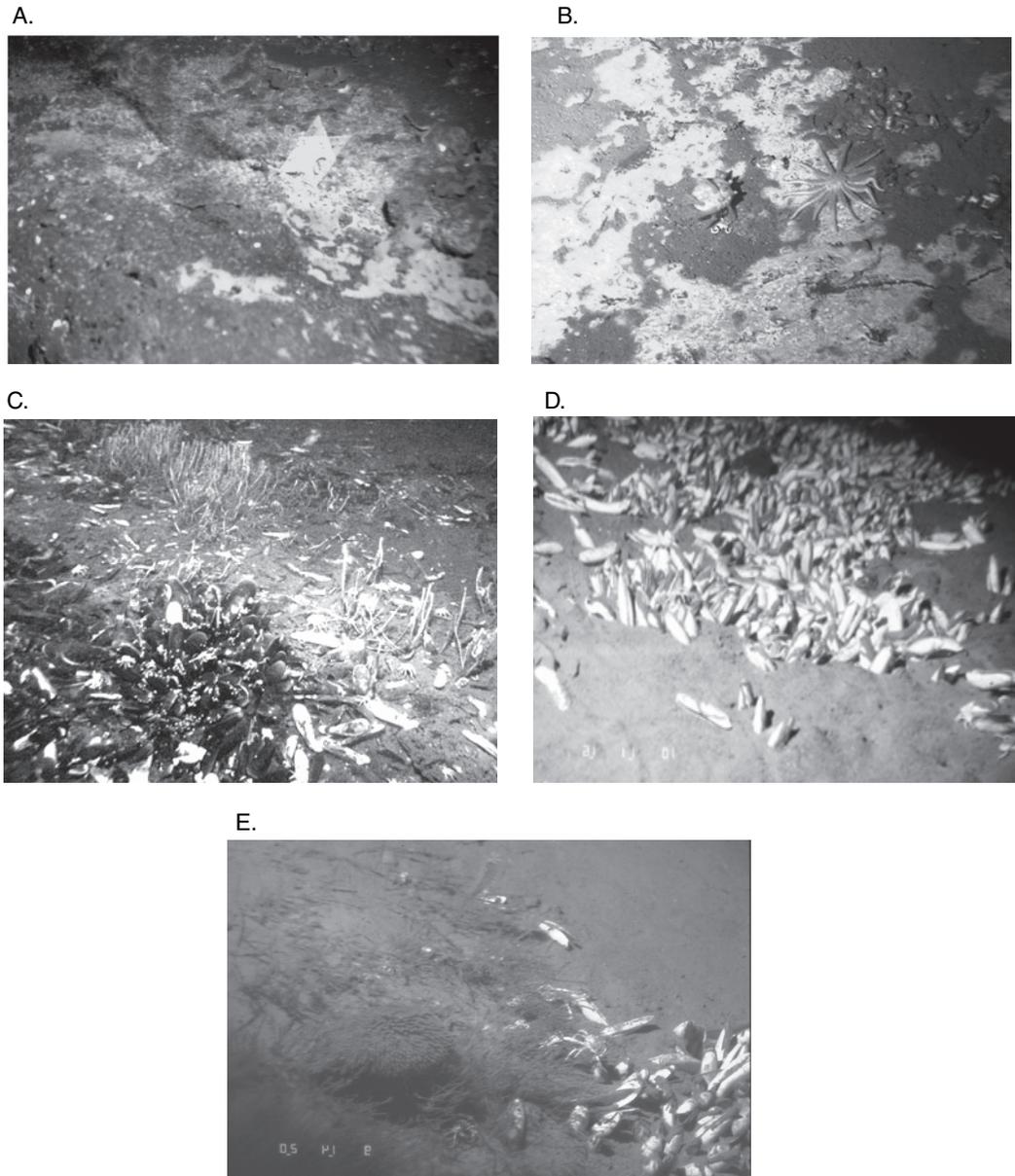


Figure 6 (A) microbial mats at Hydrate Ridge, Oregon, Cascadia margin (590 m); (B) microbial mats on the Eel River margin, 500 m; (C) typical seep biota: vestimentiferan tubeworms (*Escarpia*) and mytilid mussels (*Bathymodiolus*) with epibiotic gastropods (*Bathynnerita*), Florida Escarpment, 3,290 m; (D) vesicomid clams (*Calyptogena phaseoliformis*) and galatheid crabs at the Kodiak Seep, Gulf of Alaska, 4,445 m; (E) pogonophorans, vesicomid clams, and an unidentified cnidarian at the Kodiak Seep, Gulf of Alaska, 4,440 m.

associated with sulphide oxidation activity level (Nikolaus et al. 2003). Despite the harsh geochemical conditions (e.g., high sulphide levels) associated with microbial mats, they support a diverse assemblage of micro-, meio- and macrofauna (Buck & Barry 1998, Bernhard et al. 2001, Levin et al. 2003, Robinson et al. 2004).

Epifauna and megafauna

Abundance, composition and characteristics

Community descriptions exist for a wide number of cold seeps (reviewed in Sibuet & Olu 1998, Van Dover 2000, Kojima 2002). At most seeps in the Pacific and Atlantic Oceans, vestimentiferan tube worms (now recognized to be polychaetes), bathymodiolid mussels, and vesicomid clams (Figure 6C,D) form most of the biomass. As a result, biological research has focused extensively on these groups. Common vestimentiferan genera at seeps include *Lamellibrachia*, *Escarpia* and *Alaysia*.

There are at least 11 species of seep mussels, most in the subfamily Bathymodiolinae, genus *Bathymodiolus*. Where present, they can often form extensive beds, similar to *Mytilus* beds on rocky shorelines. Their absence at some seeps off Japan and in the northeastern Pacific is noteworthy but the reasons are not known. *Bathymodiolus* species may partition the environment by substratum and fluid flow. Of the two species found on the Barbados prism, one species, with both sulphide- and methane-oxidizing symbionts, prefers soft sediment where flow is more diffuse and the other, with only methanotrophic symbionts, occurs on hard, carbonate substratum where fluid flows and methane concentrations are higher (Olu et al. 1996b).

Seep clams are usually members of the family Vesicomidae, and are the most pervasive of large seep taxa, with a presence at most seeps (Sibuet & Olu 1998, Kojima 2002) (Figure 6D). There are many species in the genera *Calyptogena* and *Vesicomya* (Goffredi et al. 2003), and in the Pacific it is not unusual for two or three species to co-occur at seeps (Barry et al. 1997, Kojima 2002). Like the mussels, they can attain high densities (up to 1000 ind m⁻² — Japan trenches, Peru) and biomass (10–30 kg m²) (Hashimoto et al. 1989, Olu et al. 1996a) with single fields covering areas up to 7000 m² (Olu et al. 1996a, 1997). The clams are often aligned linearly along geological structures at the base of steps, in depressions or in cracks (Suess et al. 1998). *Calyptogena phaseoliformis* (now referred to the genus *Ectaegena*) in the Aleutian Trench (Suess et al. 1998), Japan Trench (6,180–6,470 m, Fujioka & Murayama 1992) and Ryukyu Trench (5,800 m, Kato et al. 1999) and *Calyptogena fossajaponica* (6600–6800 m, Kojima et al. 2000b) have the deepest distributions.

The large sizes of the tubeworms (up to 2 m, Bergquist et al. 2003), mussels (up to 36 cm, Van Dover et al. 2003) and clams (up to 18.6 cm, Olu et al. 1996b) at seeps are a result of symbiont-supported chemoautotrophic nutrition. Each of the species hosts either sulphide-oxidizing symbionts (Fiala-Médioni et al. 1993), methanotrophic symbionts (Childress et al. 1986) or both (Fisher et al. 1993). They typically have a reduced gut and exhibit little reliance on photosynthetically fixed organic matter raining down from the surface, although the mussels are known to feed.

At some seeps the typical taxa may be absent and thyasirid, solemyid and lucinid bivalves, perviate and monoliferan pogonophoran worms, and trochid or buccinid gastropods may be dominant (Suess et al. 1998, Callender & Powell 2000). Lucinids are reported as dominant at 290–330 m on the Kanesu no Se Bank above the Nankai Trough (*Mesolinga soliditesta*, Okutani & Hashimoto 1997), and in the eastern Mediterranean Sea (1700 m, *Lucinoma kazani* n.sp., Salas & Woodside 2002), in the Gulf of Mexico, Green Canyon and Garden Banks (513–754 m, *Lucinoma* sp., Callender & Powell 2000).

Infaunal thyasirids are dominant at both shallow seeps (North Sea, Dando et al. 1991; Sea of Okhotsk at 750–800 m (*Conchocera bisecta*), Kuznetsov et al. 1989) and at the deepest chemo-synthetic seep known (7330–7430 m in the Japan Trench (*Maorithyas hadalis*), Fujikura et al. 1999, Okutani et al. 1999). They have also been reported from Barbados (Olu et al. 1996a), the Gulf of Mexico (MacDonald et al. 1990) and the Laurentian Fan (Mayer et al. 1988). There are fossil thyasirid biofacies in the shallow Gulf of Mexico (Callender & Powell 1997, 2000).

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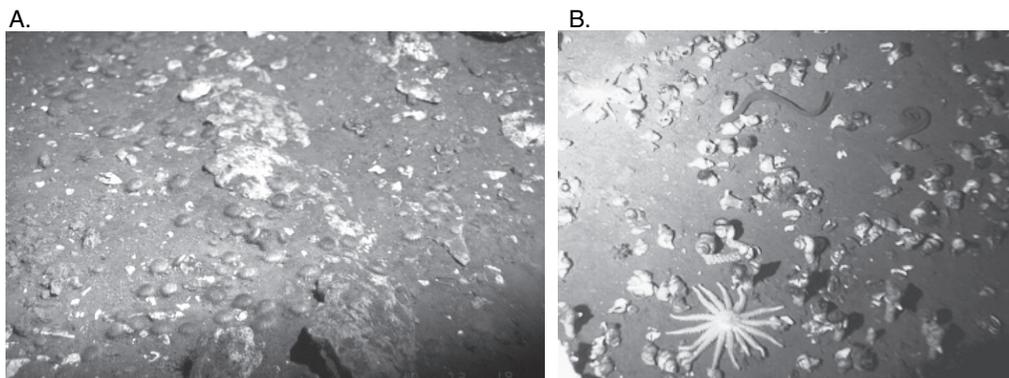


Figure 7 (A) carbonate slabs with aggregations of the urchin *Allocentrotus fragilis*. Hydrate Ridge, Oregon, 590 m; urchin diameter ~5 cm; (B) aggregations of moribund gastropods (*Neptunia* sp.) with egg cases, gastropod length ~8 cm. Also in the picture are hagfish and the asteroid *Rathbunaster californicus*. April 2001, Eel River margin, 500 m.

Pogonophorans form dense fields at seeps on the Hakon Mosby Mud Volcano (*Sclerolinum*, *Oligobrachia*, Pimenov et al. 1999), in the Gulf of Alaska (*Spirobrachia*, Suess et al. 1998, Levin & Michener 2002) and occasionally in the Gulf of Mexico (3234 m, R.S. Carney, personal communication). Other seep epifauna include bresiliid shrimp, cladorhizid and hymedesmid sponges (Olu et al. 1997), serpulids, pennatulids and caprellid amphipods (Olu et al. 1996b) and galatheid crabs (though these may be vagrants *sensu* Carney 1994). Shrimp (family Bresiliidae) are much less common at seeps than vents and have been documented only at seeps in the Gulf of Mexico, Florida, Barbados and Blake Ridge. Sponges with methanotrophic bacterial symbionts are abundant on Barbados mud volcanoes where they occur in bushes up to 2 m in diameter (Olu et al. 1997). Gas hydrate mounds in the Gulf of Mexico provide a specialized substratum for the ice worm *Hesiocaeca methanicola*, which burrows into the deposits.

Occasionally non-seep species will exhibit enhanced densities in the vicinity of deep-water seeps. Aggregations of holothurians (*Scotoplanes*, *Peniagone*) and large tubicolous polychaetes were documented by Sibuet et al. (1988) at the Japan Trench and Kashima Seamount seep sites. Holothurians aggregate on the flanks of hydrate and tar mounds in the Gulf of Mexico (MacDonald et al. 2003, 2004). At upper-slope depths off Oregon and California dense aggregations of sea urchins (Figure 7A), buccinid gastropods (Figure 7B), cnidarians (Figure 3) and asteroids occur on or near seeps (Levin, unpublished data).

Zonation, distribution and geochemistry

Concentric (circular) zonation of fauna has been noted by Sahling et al. (2002) at Hydrate Ridge in Oregon, by Barry et al. (1997) and Rathburn et al. (2003) in Monterey Bay and by Olu et al. (1997) at mud volcanoes near the Barbados accretionary prism. Central areas with methane-rich fluid mud or strong flows are devoid of fauna or covered by bacterial mats. These areas are surrounded by different species of clams. At 'Extrovert Cliffs' in Monterey Bay (960 m water depth), 2-m diameter seep patches consisted of a dark gray bacterial mat encircled by a yellow bacterial mat, which was surrounded by *Calyptogena* clams (Figure 8, Rathburn et al. 2003). Barry et al. (1997) document different sulphide preferences in different *Calyptogena* species from this region. Similar concentric structures were observed at Hydrate Ridge (770 m) on the Oregon margin, where mounds several metres in diameter contain mats of sulphur bacteria surrounded by two



Figure 8 Seep 'ring' consisting of bacterial mats in the core (~45 cm) and a concentric ring of vesicomid clams (1 m diameter) Extrovert Cliffs, Monterey Bay, 960 m. (Photo copyright 2000, Monterey Bay Research Aquarium.)

species of vesicomid clams (*Calyptogena pacifica*, *C. kilmeri*), which were encircled by the solemyid *Acharax*. The biological zones coincided with changes in the porewater hydrogen sulphide and alkalinity and in oxygen penetration (Sahling et al. 2002). The lowest oxygen penetration and highest sulphide concentrations were associated with bacterial mats; greater oxygen penetration and lower sulphide levels were associated with clam beds (Rathburn et al. 2003, Levin et al. 2003). Off Peru, the spatial distribution of *Calyptogena* clam beds was strongly linked to features such as joints, scars and screes related to slope instabilities, which are likely to conduct or expose sulphide (Olu et al. 1996a).

MacDonald et al. (2003) note that vestimentiferan tube worms in the Gulf of Mexico are abundant at upper slope depths (<1000 m) and at the base of the slope (>2500 m) but not in the middle (1000–2000 m). They propose that gas hydrates fuel the shallow systems but are more stable with less flux of hydrocarbons at mid depths, and that the deepest communities are fueled by another source unrelated to gas hydrates.

Epifauna as sources of habitat heterogeneity

Seep tubeworms, mussels and clams typically serve as 'ecosystem engineers' that generate extensive habitat complexity both above and below ground. Their tubes, shells and byssus threads support a myriad of smaller taxa (Carney 1994, Bergquist et al. 2003, Turnipseed et al. 2003). There are epizoots on shells and tubes, and byssus-thread associates. Common among these are gastropods in the families Neolepetopsidae, Provannidae and Pyropeltidae, actinians, dorvilleid and scale polychaetes. Each of the large dominant seep species also supports specialized commensal taxa including nautiliniellid (Miura & Laubier 1990) and phyllodocid polychaetes (E. Hourdes, personal observation) as well as bivalves (*Acesta* sp., C. Young, in preparation). Sponge and serpulid thickets (worms 20 cm long, thickets of 20–30 ind m²) also introduce habitat complexity at seeps (Olu et al. 1996b, 1997) but their associated faunas have not been studied.

Vestimentiferans support a rich community of associated invertebrates above and below the sediment surface (Bergquist et al. 2003). In the Gulf of Mexico, *Lamellibrachia cf. luymesii* and *Seepiophila jonesi* form hemispherical ‘bushes’ that are several metres high and wide. A collection of seven of these bushes yielded 66 species of which 18 are considered to be endemic (Bergquist et al. 2003) and five (four bivalves and a sponge) appear to harbor symbionts. The most abundant taxa within Gulf of Mexico tubeworm aggregations are gastropods (*Bathynnerita*, *Provanna*), shrimp (*Alvinocaris*), mussels (*Bathymodiolus*), crabs (*Munidopsis*), nemertean, polychaetes (*Harmothoe*, sabellids), amphipods (*Orchomene* and *Stephonyx* sp.) and sipunculans (*Phalascosoma*). Densities of many taxa increase with habitat complexity, measured as tubeworm density, but decline with age of the tubeworm aggregation. Increasing patch age leads to a decline in primary producers (symbiont-bearing taxa) and increasing importance of secondary and higher predators, as well as non-endemic species. Species richness also increases with patch size, tube surface area and vestimentiferan biomass.

Successional changes corresponding to aggregation composition and age may be driven by environmental factors, especially sulphide. Order of magnitude declines in biomass and density of associated fauna in older aggregations may reflect indirect effects of diminishing sulphide production (Bergquist et al. 2003). Similar results have been obtained for tubeworm associates at hydrothermal vents on the Juan de Fuca Ridge. Tubeworm aggregation complexity and successional stage (driven by venting) had a strong influence on the numbers of species and composition (Tsurumi & Tunnicliffe 2003). It appears that species richness of tubeworm aggregations is lower at vents than seeps (only 37 taxa were found among 350,000 specimens), with gastropods and polychaetes dominant (Tsurumi & Tunnicliffe 2003).

Diversity of mussel bed associates has been assessed quantitatively in the Gulf of Mexico and on the Blake Ridge at depths of 2500–3600 m (Turnipseed et al. 2003). These habitats shared only four species. Blake Ridge mussel beds contain numerous chirodotid holothurians, deposit-feeding sipunculans and alvinocarid shrimp (similar to *Alvinocaris muricola*). Smaller taxa included chaetopterid, maldanid and capitellid polychaetes, as well as nematodes (Van Dover et al. 2003). Large predators are galatheid crabs, octopus, fishes and anemones. Comparison of mussel-bed fauna at the Gulf of Mexico and Blake Ridge seep sites to those of four hydrothermal vents revealed species richness nearly 2 times greater at seeps than vents (Turnipseed et al. 2003).

Beds of vesicomyid clams are a feature of many seeps throughout the oceans. Typically the clams nestle within the upper few centimetres of sediments and the associated clam bed fauna is more of a sediment community than is the case for vestimentiferan and mussel bed assemblages, which may occur on carbonate or biogenic substrata (Van Dover et al. 2003). Although clam aggregations exist at most seeps, there has been limited quantitative sampling of associated fauna. Influence of seep clams on associated infauna is discussed later in the section on macrofauna.

Seep infauna

Foraminifera

Interest in Foraminifera at methane seeps stems largely from the potential use of their carbonate tests as indicators of historical methane flux (Wefer et al. 1994, Rathburn et al. 2000, 2003, Stott et al. 2002, Hill et al. 2003). Release of methane hydrates (clathrates) has been implicated as a forcing mechanism for climate warming in the late Quaternary (Kennett et al. 2000). Therefore most research has focused on the stable carbon isotopic composition of tests, which exhibit negative spikes in the presence of methane in pore waters (Rathburn et al. 2000, Hill et al. 2003).

Communities

Much of the research on foraminiferan community composition and its relation to environmental factors at seeps has been done in the Gulf of Mexico (Sen Gupta et al. 1997, Robinson et al. 2004), in central and northern California (Stakes et al. 1999, Rathburn et al. 2000, 2003, Bernhard et al. 2001) and off Japan (Akimoto et al. 1994). Species characteristic of shallow (120 m) methane seeps in the Santa Barbara Basin off California include *Bolivina tumida*, *Epistominella pacifica*, *Oridorsalis umbonatus* and *Uvigerina peregrina*. It has been proposed that the first of these occurs mainly during periods of high methane flux in the Santa Barbara Basin (Hill et al. 2003). These same genera are common at seeps further north in California (Rathburn et al. 2000, Bernhard et al. 2001), off Japan (Akimoto et al. 1994) and in the Gulf of Mexico (Sen Gupta et al. 1997, Robinson et al. 2004). Central and northern California seeps also support high densities of *Chilostomella*, *Globobulimina*, *Nonionella*, *Cassidulina* and *Textularia* (Bernhard et al. 2001, Rathburn et al. 2003). Biogeographic variation is evident. Gulf of Mexico and Atlantic (Blake Ridge) seep sediments have high densities of *Fursenkoina complanata*. *Brizalina earlandi* and *Praeglobobulimina ovata* were also present in both oceans. Significant compositional differences between Alaminos Canyon and Blake Ridge seeps were due to higher densities of *Epistominella exigua*, *Nodellum membranaceum* and *Tiloculina* sp. in the Alaminos assemblage (Robinson et al. in press). Notably, there have been no seep endemics identified among Foraminifera; most seep genera are also characteristic of other low-oxygen, organic-rich settings (Bernhard et al. 2001, Rathburn et al. 2000, 2003).

Foraminiferan densities at seeps on the California margin are within the range reported from non-seep sediments (275–1,382 50 cm⁻³ in the upper 1 cm) but may be reduced locally (Bernhard et al. 2001, Rathburn et al. 2000, 2003). Some species may be more abundant in seeps than in adjacent habitats (Akimoto et al. 1994, Bernhard et al. 2001). However, Foraminifera at Gulf of Mexico seeps appear to exhibit lower densities than reported from the Pacific (Robinson et al. 2004). Broad-scale density enhancements have not been observed for foraminiferan assemblages, as they have for bacteria, some other protists, nematodes and clams (see citations in Bernhard et al. 2001) and lower biovolume has been reported for Monterey seeps (Buck & Barry 1998). Robinson et al. (2004) showed that Foraminifera make up only 15% of the total community at seeps in the Gulf of Mexico and on Blake Ridge, with unexpectedly low densities in some cores with bacterial mats (*Beggiatoa* and *Arcobacter*).

There is little information about seep effects on diversity. A study based on only a few cores in Alaminos Canyon, Gulf of Mexico, suggests that diversity is reduced in seep sediments relative to non-seep sediments (Robinson et al. 2004). Vertical distribution of Foraminifera varies with seepage, although the majority of seep species are considered 'infaunal' (*sensu* Rathburn & Corliss (1994)). This designation is correlated with tolerance of low-oxygen, organic-rich conditions (Rathburn et al. 2000). Infaunal foraminiferan species exhibited different maximum depths of occurrence in different habitats (bacterial mats vs. clam beds) and even in different clam beds (Rathburn et al. 2000, 2003), with subsurface peaks (sometimes more than one) between 2 and 4 cm.

At Monterey seeps, cytoplasm-containing specimens occupying sediments with H₂S concentrations >16 mM, suggest remarkable tolerance for sulphide in some species (Rathburn et al. 2003). Further research is needed to determine whether foraminiferan distributions reflect responses to geochemical, microbial or biological features of the seep sediments.

Foraminiferan adaptations to seep conditions do not resemble those of their metazoan counterparts. Bernhard et al. (2001), examining a limited number of specimens, did not find symbionts in Monterey seep Foraminifera, despite their presence in four common foraminiferan species in bacterial mats from non-seep sites in the Santa Barbara Basin (Bernhard et al. 2000). The presence of peroxisomes complexed with endoplasmic reticulum and the association of ectobiotic bacteria could aid survival in toxic seep environments but their functions in this capacity are not known (Bernhard et al. 2001).

Indicators of methane seepage

Although several studies have documented light $\delta^{13}\text{C}$ signatures in tests of methane seep Foraminifera, they are typically far less negative than the surrounding pore waters (and more similar to sea water), suggesting some regulatory behaviour. Even in sediments with known high methane flux, carbon isotopic signatures of foraminiferan tests can be highly variable (Sen Gupta & Aharon 1994, Sen Gupta et al. 1997, Hill et al. 2003, Rathburn et al. 2003, Martin et al. 2004). It is likely that this high variability is unique to seeps (non-seep signatures are very stable) and could be exploited as a seep system marker. Foraminifera from Santa Barbara seeps exhibit a range of $\delta^{13}\text{C}$ values from -0.09‰ to -20.13‰ (Hill et al. 2003), with lighter signatures closer to sources of venting and among infaunal species dwelling deeper in the sediment (e.g., *Bolivina tumida*). At Monterey seeps, test isotopic differences are observed among clam beds at comparable water depths, and species dwelling at different depths in the sediment. Deep infaunal taxa (*Globobulimina pacifica*) have lighter $\delta^{13}\text{C}$ values than shallow infaunal and transitional taxa and these have lighter signatures than epifaunal species (Rathburn et al. 2003). This difference mirrors a similar but less dramatic pattern observed in non-seep sediments. Understanding the dietary habits of seep Foraminifera could shed light on their distributions and test signatures. Diets could be determined from organic analyses of isotope and lipid biomarker signatures but these have not been examined for seep Foraminifera.

Scientists are not yet at a point where test isotopic composition can be translated into a quantitative measure of methane release. They may be nearing the ability to place methane release events in time (Behl & Kennett 1996, Kennett et al. 2000, 2003), although interpretations of ancient seepage based on the isotopic composition of fossil Foraminifera remain controversial (Stott et al. 2002, Cannariato & Stott 2004). Differences between signatures of tests of living individuals present near the surface and fossil tests from 6–20 cm depth in the sediment column have been attributed to influence of temporal variation in methane flux on porewater DIC signatures (Rathburn et al. 2000). Foraminiferan test signatures may be better detectors of diffusive methane flux than larger organisms such as clams, which integrate over a broader range of conditions. Examination of fossil Foraminifera from seeps, however, has revealed evidence of diagenetic alteration, such as carbonate overgrowth, which significantly alters the carbon isotopic signature (Martin et al. 2004, Cannariato & Stott 2004). A challenge has been to distinguish the influences of organic matter degradation, vital effects (McCorkle et al. 1990), foraminiferan diet, and diagenetic alteration from locally varying porewater methane on test signatures. Ingested methanotrophic and sulphide-oxidizing bacteria can provide a significant source of isotopically light carbon. No chemosynthetic symbiotic bacteria have been identified in methane seep Foraminifera to date but they could ultimately turn out to be a source of light $\delta^{13}\text{C}$ signatures.

Metazoan meiofauna

There are only a few investigations of metazoan meiofauna at cold seeps but these cover a variety of environments, water depths and geographic regions (Table 2). Rarely do seep meiofaunal studies go beyond bulk measurement of abundance, biomass or major taxa to examine patterns of species composition or diversity.

Abundance and composition

No clear response of metazoan meiofaunal abundance to seep conditions emerges from the existing research, although several studies find estimates of density or volume to be 2–5 times higher than in nearby control sediments. Enrichments of meiofauna have been observed at shallow hydrocarbon

Table 2 Meiofauna at methane seeps

Seep type and depth	Density	% Nematodes	% Harpacticoids	Nematode: copepod ratio	Other information	References
Hydrocarbon, 15 m, shelf	Nematodes: 2.42 × 10 ⁶ m ⁻² 1.31 × 10 ⁶ m ⁻² 1.41 × 10 ⁶ m ⁻²	88 76 78	6.9 13.5 10.9	40.1 12.5 9.7	Harpacticoids unaffected Link between harpacticoids and microalgae, nematodes and bacteria	Montagna et al. 1987, 1989
Methane, 906 m clam field	Higher biovolume in seep than control for nematodes and ciliates, not for forams, euglenoids, allogromiids). Nematodes: 9–307 cm ² Nematode density elevated at seeps (179 ± 184 cm ⁻²) vs. control (82 ± 52) (2.2× higher). 1.5 to 1.6 times higher meiofauna density at seep than control				High incidence of symbiotic relationships among euglenoids and ciliates with bacteria. No difference in length: diameter relationship in seep vs. control nematodes. Largest body diameter nematodes were from seeps.	Buck & Barry 1998
Clam bed habitat, 1170 m, (63 μ)*		94% in centre of bed 60% near edge		188 centre 4.2 edge	Kinorhynch and ostracods absent at seep Dominant nematodes were <i>Daptonema</i> (2 spp – 20%, 13%) and <i>Chromadorita</i> (12%); control – <i>Microlaimus</i> (25%); dominance higher in the control sediments (silt) than seep (coarse) but lower H' at seeps. Deeper vertical distribution of seep species; this paper suggests lack of adaptation relative to megafauna; seep assemblages more similar to control than to distant reducing systems (vents and Gulf of Mexico seeps); local adaptation of oxybiotic species suggested	Shirayama & Ohta 1990
				6.8 control		

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Gas hydrates, 790 m	DNA inventories 3.5–3.9 times higher in clam and bacterial mat than in control sites. Total adenylates (biomass estimate) exceeded control by 3.5 and 5.9 times in clam and bacterial mat. Different vertical distribution, biomass concentrated in upper 8 cm in bacterial mat and focused deeper (to 20 cm) in clam bed. Surface focus in control samples. Not compared with control			Lower chlorophyll a inventories in seep sediments suggest higher degradation; aerobic methane oxidation accounts for little of the carbon remineralization	Sommer et al. 2002
<i>Arcobacter</i> mat, mussel bed, 2150 m, 63 μ*, 0–1 cm		53% thin <i>Arcobacter</i> mat, 36% thick <i>Arcobacter</i> mat, 56% mussel beds	34.1% in thin <i>Arcobacter</i> mats, 50% in thick mats, 37.7% in mussel bed (includes copepodites)	Other taxa present include ostracods polychaetes, bivalves, gastropods, isopods	Robinson et al. 2004
<i>Beggiatoa</i> mat, 2215–2238 m	Total meiofauna: 381 in mat vs. 68.45 in control (5.5 times higher), nematodes: 286 in mat vs. 51.5 in control (10 cm ⁻³) (5.5 times higher)	75% at seep vs. 75% in control	22% in <i>Beggiatoa</i> mat, 21% in non seep	Kinorhynchs present in mat, also cumaceans, polychaetes	
Mud volcanoes, surficial sediments, 5000 m	116–6541 (ind 10 cm ⁻²)	93.5–100%	0–2.4%	Polychaetes and copepods were present at similar densities; kinorhynchs present at one site	Olu et al. 1997
Bubbling reef (methane), 42–500 μm*	650 × 10 ³ ind m ⁻²			Nematodes, oligochaetes, polychaetes, <i>Leptonemella aphanothecae</i> with external symbiotic bacteria, penetrates to 22 cm	Jensen et al. 1992

*Mesh size used to separate nematodes from sediments.

seeps (16 m, Montagna et al. 1987), eastern Pacific methane seeps in Monterey Bay (906 m, mainly nematodes and ciliates, Buck & Barry 1998), at the Barbados Accretionary Prism (Olu et al. 1997) and in microbial mats in the Gulf of Mexico (2,230 m) and on Blake Ridge (2,150 m, Robinson et al. 2004). Most of these density enhancements are modest compared with the order-of-magnitude enhancement seen for megafauna relative to ambient sediments. However, Olu et al. (1997) documented one to two orders of magnitude greater meiofauna densities on mud volcanoes at 5000 m than expected for non-seep sediments at these depths. In contrast, little or no density difference from control sites was observed for meiofauna from hydrocarbon seeps off Santa Barbara, California (15 m water depth, Montagna & Spies 1985), the Hatsushima seep off Japan (1170 m, Shirayama & Ohta 1990) or brine seeps in the Gulf of Mexico (70 m, Powell & Bright 1981, Powell et al. 1983). Reduced meiofaunal densities occurred at shallow methane seeps in the North Sea (150 m, Dando et al. 1991) and off Denmark (10 m, Jensen et al. 1992). Often the density patterns are driven by nematodes. Variability of meiofaunal densities appears to be higher within than outside seep sediments due to increased habitat heterogeneity (Montagna & Spies 1985).

While counts or biovolume are the most common means of assessing meiofaunal abundance, Sommer et al. (2002) used DNA and ATP estimates of small-sized benthic biomass. At gas hydrate-fuelled seeps on the Oregon margin (790 m) they found DNA inventories 3.5–3.9 times higher in clam-bed and bacterial mat sediments than in background sediments. Total adenylates from seeps exceeded those from non-seep settings by 3.5 and 5.9 times in clam-bed and bacterial mat sediments, respectively.

Most seep studies record nematodes as the dominant taxon (Table 2), but this is typically true of ambient deep-sea sediments as well. Nematode:copepod ratios range from 4 to 10 at shallow seeps but can exceed 1000 in deep-seep sediments (Table 2). Nematodes exceed foraminiferans as the dominant biomass contributor in Monterey Bay seeps (Buck & Barry 1998) and in density at Hatsushima Cold Seep (Shirayama & Ohta 1990). At the Hatsushima seep, the fraction of nematodes dropped from 94% in the centre of a *Calypptogena soyae* bed to 55% near the edges and 64% in non-seep sediments; nematode:harpacticoid copepod ratios were 188, 4.2 and 6.8, respectively (Shirayama & Ohta 1990). Nematodes formed a higher percentage (88%) of the fauna at an active hydrocarbon seep off Santa Barbara than in low seepage conditions (76%) or non-seep sediments (78%) and the ratio of nematodes:harpacticoid copepods dropped from 40.1 to 9.7 with decreasing seepage (Montagna et al. 1987). Only four copepod species were present inside *Beggiatoa* mats at Santa Barbara seeps, compared with 34 species outside (Montagna & Spies 1985). In *Beggiatoa* mats in Alaminos Canyon, Gulf of Mexico, nematode representation (percentage of total) was equivalent to that in non-seep sediments (75%) (Robinson et al. 2004).

Nematodes are not always the dominant meiofaunal taxon at seeps. At a shallow brine seep in the Gulf of Mexico (72 m, East Flower Garden Bank) the meiofauna was dominated by gnathostomulids, with platyhelminths, aschelminths, nematodes and amphipods present (Powell & Bright 1981, Powell et al. 1983). The Flower Garden fauna is described as a thionebiosis that is dependent on continuous presence of hydrogen sulphide and has well-developed detoxification mechanisms. On the Blake Ridge, nematodes from *Arcobacter* mats and mussel beds formed only 36–56% of the metazoan meiofauna and harpacticoid copepods were surprisingly well represented (34–50%) in these settings (Table 2) (Robinson et al. 2004). Shirayama & Ohta (1990) noted the absence of kinorhynchans and ostracods at Japanese methane seeps, but Olu et al. (1997) reported kinorhynchans from Barbados mud volcanoes. Both groups are present in Alaminos Canyon in the Gulf of Mexico (Robinson et al. 2004). Because many of these studies are based on only two or three cores at each site, definitive statements about seep avoidance by specific taxa cannot be made.

Sulphidic seep sediments might be expected to reduce diversity and elevate dominance, as has been found in hydrothermal vent meiofauna (Vanreusel et al. 1997). Shirayama and Ohta (1990) noted reduced H' among meiofauna at seeps but recorded higher dominance in non-seep sediments.

In a North Sea pockmark, the edges exhibited greater nematode species richness per core (69 and 75 species) than the more active base (29 and 37 species) (Dando et al. 1991).

A detailed comparison of dominant nematode families and genera at the Hatsushima seep, the East Flower Garden Cold Seep, and East Pacific Rise by Shirayama & Ohta (1990) reveals some overlap in families (Xyalidae, Linhomoeidae, Chromadoridae, Cyatholaimidae were at two or three of these), but remarkably little overlap at the genus level. In contrast, nearby control and seep meiofauna had more genera in common. This difference led the authors to suggest that meiofauna may evolve adaptations to seep conditions locally. The species list of nematodes at North Sea pockmarks provided by Dando et al. (1991) also indicates that Linhomoeidae and Chromadoridae are abundant seep families, with large numbers of Comesomatidae, Leptolaimidae and Siphonolaimidae also present in pockmarks.

Relation to sediment conditions

Strong gradients in sulphide and oxygen could be expected to regulate the biology and distribution patterns of metazoan meiofauna. Measurements of porewater solute concentrations made on the same scale as the meiofauna body size (mm) (*sensu* Meyers et al. 1988) could reveal much about the tolerances and preferences of taxa but such measurements have not been made for seep meiofauna. However, there are instances of careful documentation of vertical distribution patterns, symbioses and body morphology in relation to seep conditions that provide insight about how meiofauna interact with their sedimentary environment.

A deeper vertical distribution of seep meiofauna (compared with non-seep assemblages) has been observed for deep-water Japan cold seeps (Shirayama & Ohta 1990). In contrast, at an active shallow hydrocarbon seep the nematodes were concentrated in the upper 2 cm, with reduced density at 6–8 cm relative to control sediments (Montagna et al. 1989). Most other meiofaunal taxa were largely restricted to surface sediments in Montagna's study and thus showed no distinct vertical pattern. Powell et al. (1983) and Jensen (1986) propose that hydrogen sulphide is the primary control on gnathostomulid, nematode and other meiofaunal distributions and diversity in Gollum's Canyon, East Flower Garden in the Gulf of Mexico. None of these taxa, however, had symbionts. At methane-seep pockmarks in the North Sea, the symbiont-bearing nematode *Astomonema* sp. exhibited a density maximum at 5–8 cm, corresponding to the peak of elemental sulphur content (presumably a product of sulphide oxidation) occurring just above the zone of maximum sulphate reduction and sulphide concentration (Dando et al. 1991). The tight link between these properties suggests control of nematode vertical distribution by sediment geochemistry.

Jensen (1986) reported body elongation in thiobiotic nematodes from the Flower Garden brine seeps (Gulf of Mexico). In Monterey Bay (906 m) nematodes with the largest body diameter were from methane seeps (compared with control sediments) but these exhibited no difference in length:diameter relationships (Buck & Barry 1998).

A high incidence of bacterial symbioses has been reported for euglenoid and ciliate meiofauna from Monterey Bay seeps (Buck et al. 2000), which is similar to that observed for meiofauna in the low-oxygen Santa Barbara Basin (Bernhard et al. 2001). Symbiont-bearing nematodes have been reported from several shallow seeps. *Leptonemella aphanothecae* occurs in sandy seep sediments of the Kattegat, Denmark, to depths of 22 cm (Jensen et al. 1992) and *Astomonema* sp. was dominant in pockmark sediments from the North Sea (Dando et al. 1991). It is unknown whether the symbionts in these two species contribute to sulphide detoxification, nutrition or other functions.

Additional remaining questions include (a) the extent to which seep meiofauna show specialized adaptations to distinct microhabitats (e.g., clam beds, mussel beds, bacterial mats), (b) the modes of nutrition and importance of chemosynthetically fixed carbon sources, (c) successional sequences

or relation to seepage intensity and (d) the evolution of specific groups in reducing conditions associated with vents and seeps.

Macrofauna

Abundance, biomass, composition and endemism

Density Despite highly sulphidic conditions present in seep sediments, these environments often support surprisingly high densities of macrofauna. Estimates of density vary with the mesh size employed but values of >10,000 ind m⁻² are common and local patches of >40,000 ind m⁻² can occur (Table 3).

Comparisons of macrofauna from seep and non-seep sediments reveal that the total macrofaunal densities at seeps may be impoverished (North Sea, Dando et al. 1991), enhanced (Santa Barbara, Davis & Spies 1980, Oregon, Sahling et al. 2002, Gulf of Mexico, Levin et al. unpublished data), or identical (Levin et al. 2003) to those in nearby non-seep sediments. Seep macrofauna appear more likely to exhibit higher densities relative to ambient (background) fauna at greater water depths (e.g., >3000 m) (Table 3), perhaps because food is more limiting and methane provides a valuable additional carbon source (Levin & Michener 2002). Variability in the relationship between seep and non-seep macrofaunal densities appears not to be directly related to the geochemistry of seep sediments. Sediments with concentrations of H₂S up to 20 mM appear to support high densities (albeit low diversity) of infauna (Sahling et al. 2002, Levin et al. 2003).

Biomass Biomass is generally dominated by tubeworms and bivalves, with single site values of 1000–3000 kg m⁻² (wet wt) common (Sibuet & Olu-LeRoy 2002). There is a strong positive relationship between bivalve biomass and fluid flow that transcends seep types (e.g., mud volcano sides, slide scarps) (Sibuet & Olu-LeRoy 2002). Among the smaller macrofauna, biomass is highly variable, ranging from 2–170 g m⁻² (Table 3). Macro-infauna of *Calypptogena* beds at Hydrate Ridge exhibited an order of magnitude higher biomass (162 g m⁻²) than those in background sites (10 g m⁻²) but microbial mat and *Acharax* communities did not (Sahling et al. 2002). So few measurements have been made of infaunal biomass, however, that these values are unlikely to represent the full range present at seeps.

Endemism The extent to which macrofauna inhabiting seeps form a distinct assemblage different from non-seep habitats appears to be partially a function of depth. Methane seeps on the shelves off California, Oregon and in the North Sea had dense macrofaunal populations but few endemics (Dando et al. 1991, Levin et al. 2000). Species showing a strong preference for sulphidic seeps on the northern California shelf (35–55 m) were the amphipod *Cheiremedeia zotea*, the isopod *Synidotea angulata*, the cumacean *Diastylopsis dawsoni* and the polychaete *Capitella* sp. (Levin et al. 2000). North Sea pockmarks had high densities of *Siboglinum* and *Thyasira*. From sampling cold seep sites on the outer shelf (160–250 m), upper slope (250–450 m), intermediate slope (450–800 m) and deeper bathyal zones (1450–1600 m) in the Sea of Okhotsk, Sahling et al. (2003) concluded that seep endemic faunas were confined to depths below 370 m. They suggested that higher predation pressure at shallower depths was partly responsible for the absence of seep specialists in shallow water. In studies of seep and non-seep macrofauna on Hydrate Ridge, Sahling et al. (2002) found 25% of the 36 families identified to be present exclusively at seeps. These included Vesicomidae, Solemyidae, Nuculanidae, Provannidae, Pyropeltidae, Hyalogyrinidae, Dorvilleidae and Polynoidae. Ampharetid polychaetes were also very abundant, although not limited to seeps. In this study the proportion of endemic, heterotrophic seep fauna was greatest in the most sulphidic sediments (*Beggiatoa* covered) and least in the *Acharax* community, whereas the proportion of heterotrophic colonists (non-seep fauna) exhibited the reverse pattern.

ECOLOGY OF COLD SEEP SEDIMENTS

Table 3 Characteristics of seep macrofaunal communities

Location	Depth (m)	Habitat type	Methods (mesh size)	Density (no. ind. m ⁻²)	Biomass (g m ⁻²)	Dominant taxa	Diversity	Comparison with non-seep	Remarks	References
Gulf of Alaska, Kodiak Seep	4,445	Pogonophoran field	Submersible box and tube corers (0.3 mm)	6625 ± 1283	13.9 ± 2.6	Pogonophorans, amphipods, bivalves		Densities higher than non-seep		Levin, unpublished data
Gulf of Alaska, Kodiak Seep	4,445	<i>Calyptogenia phaseoliformis</i> bed	Submersible box and tube corers (0.3 mm)	3263 ± 1051	23.5 ± 10.0	Ampharetidae, bivalves, gastropods		Densities similar to non-seep		Levin, unpublished data
Oregon, Hydrate Ridge	590	<i>Calyptogenia</i> bed	Submersible box and tube corers (0.3 mm)	27,013 ± 4296		Oligochaetes, Dorvilleidae, gastropods		Enhanced densities relative to non-seep		Levin, unpublished data
Oregon, Hydrate Ridge	590	Microbial mat	Submersible box and tube corers (0.3 mm)	12,606 ± 6502		Dorvilleidae, Gastropoda (<i>Astyris permodesta</i> , <i>Provanna</i> sp.)				Levin, unpublished data
Oregon, Hydrate Ridge	770	<i>Acharax</i> bed	TV Multicore (MUC) (0.5 mm)	1310	142.8	<i>Acharax</i> sp., Orbiniidae	Rarefaction value, $ES_{(100)} = 29$ (extrapolated)	Similar diversity to reference sites	Oxygen 0.4–0.5 ml l ⁻¹	Sahling et al. 2002
Oregon, Hydrate Ridge	770	<i>Calyptogenia</i> bed (<i>C. kilmeri</i> & <i>C. pacifica</i>)	TV MUC (0.5 mm)	4968	148.8	Ampharetidae, Gastropoda (<i>Hyalogyrina</i> sp.), <i>Calyptogenia pacifica</i> , <i>Vesicomya sternsii</i>	$ES_{(100)} = 14$	Intermediate diversity	Oxygen 0.4–0.5 ml l ⁻¹	Sahling et al. 2002
Oregon, Hydrate Ridge	770	<i>Beggiatoa</i> mat	TV MUC (0.5 mm)	8869	46.9	Ampharetidae, Gastropoda (<i>Hyalogyrina</i> sp., <i>Provanna laevis</i>)	$ES_{(100)} = 8$	Lower diversity than non-seep sites	Oxygen 0.4–0.5 ml l ⁻¹	Sahling et al. 2002

Table 3 (continued) Characteristics of seep macrofaunal communities

Location	Depth (m)	Habitat type	Methods (mesh size)	Density (no. ind. m ⁻²)	Biomass (g m ⁻²)	Dominant taxa	Diversity	Comparison with non-seep	Remarks	References
Northern California (Eel River)	500	<i>Calyptrigena pacifica</i> bed	Remotely Operated Vehicle (ROV)/ Eckman corer (0.3 mm)	16,900 ± 2280	23.8 ± 11.2	Tubificid, capitellid, paraonid polychaetes, nemerteans	Shannon-Wiener information Index, H' (base 2) = 4.99, Es ₍₁₀₀₎ = 36	Similar macrofaunal composition, fewer tanaids		Levin et al. 2003
Northern California (Eel River)	500	Microbial mat	ROV/Eckman corer (0.3 mm)	13,500 ± 4770	1.7 ± 0.4	Dorvilleidae	H' (base 2) = 2.50, Es ₍₁₀₀₎ = 18	More annelid representation, especially dorvilleids	Very high dominance	Levin et al. 2003
Florida Escarpment, Gulf of Mexico	3290	Microbial mat/sulphidic sediments	ALVIN tube cores (0.3 mm)			Hesionidae			High dominance	Levin, Cheung, Mendoza, unpublished data
Green Canyon/ Gulf of Mexico	700	Microbial mat	ALVIN tube cores			Dorvilleidae			High dominance	Robinson et al. 2004
Gulf of Cadiz, Moroccan Atlantic Slope	200–1200	Mud volcanoes	TV grab			Sponges, Hydrozoa, Isopoda, Ostracoda, Copepoda, Amphipoda, Siboginidae				Pannemans et al. in revision

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Skagerrak, Denmark	Methane seep, sediment slump	17,600 (<i>Siboglinum</i> only)	125.1	<i>Siboglinum poseidoni</i> , <i>Paramphionome jeffreysii</i> , <i>Thyasira</i> spp., <i>Thyasira sarsi</i> , <i>Astomonema</i> sp. (nematode)	Dando et al. 1994
North Sea	Pockmark	708-1550	0.3-3.9 dry wt.		Dando et al. 1991
Escanaba Trough	3200-3270 Hydrothermal mounds, <i>C. phaseoliformis</i> area			<i>Amphisamytha galapagensis</i> , <i>Leitoscoloplos</i> n. sp., <i>Priotonospio (Minuspio)</i> n.sp.	Petrecca & Grassle 1987, Grassle & Petrecca 1994
Barbados Accretionary Prism	5000 Mud volcanoes			Maldanid and chaetopterid polychaete fields (>10-cm long tubes), ampharetid polychaetes also present	Olu et al. 1997
				Same density at vent and ambient sediment	
				Dense assemblages covering 53% of a 7000 m ² clam patch, not present away from the seep	

Distinct assemblages of characteristic seep megafauna are in some cases associated with distinct infaunal assemblages. On Hydrate Ridge, the *Beggiatoa*, *Calyptogena* and *Acharax* macrofaunal communities were demonstrated through multivariate analyses to be distinct from one another with respect to density and composition (Sahling et al. 2002). *Beggiatoa* mats exhibited higher densities of *Nuculana*, *Pyropelta*, *Provanna*, *Hyalogyrina* and Ampharetidae (Sahling et al. 2002).

Comparison of *Calyptogena pacifica* bed sediments with non-seep sediments on the northern California margin yielded many of the same macrofauna but higher densities of dorvilleid polychaetes, the capitellid *Mediomastis* spp., the oligochaete *Tectidrilus diversus*, nemerteans and the gastropod *Odostomia* (Levin et al. 2000, 2003). Microbial-mat covered sediments in this setting were mainly inhabited by several species of dorvilleid polychaetes (Levin et al. 2003). Dorvilleid polychaetes were also exceptionally abundant in microbial mat sediments at Hydrate Ridge on the Oregon margin (Sahling et al., 2002, Levin, unpublished observation) and at Bush Hill in the Gulf of Mexico (Robinson et al. 2004), in whale fall sediments of the eastern Pacific (Smith & Baco 2003, G. Mendoza personal communication), in hydrothermal sediments of Guaymas Basin (Grassle et al. 1985), and in oxygen minimum zone sediments off northern Chile (Levin 2003). Levin et al. (unpublished data), with help of dorvilleid specialist B. Hilbig, documented up to 17 species of dorvilleid polychaetes in seep sediments from northern California and Oregon, with 10 species belonging to the genus *Ophryotrocha*. Other macrofaunal taxa frequently encountered in seep sediments include ampharetid and hesionid polychaetes, tubificid oligochaetes, gastropods and gammarid amphipods (Table 3).

Seep mussel beds on the Blake Ridge support a diverse group of smaller macrofauna that include chaetopterid, maldanid, capitellid and nautiliniellid (mussel symbiont) polychaetes, sipunculans, and chirodotid holothurians (Van Dover et al. 2003). There are not yet comparisons of these with fauna in the surrounding habitats, so it is unclear whether these are specialists. Hydrate ice is one substratum that appears to support high densities (up to 3000 ind m⁻²) of a seep specialist, *Hesiocaeca methanicola* (Desbruyères & Toulmond 1998, Fisher et al. 2000). This worm occurs in monospecific aggregations on exposed hydrate surfaces at 540 m in the Gulf of Mexico and, based on isotopic and microscopic examination, appears to feed heterotrophically on bacteria associated with the hydrate. Hypogenic caves with methane seepage that are isolated from the ocean support an entirely different macrofauna, one dominated by crustaceans, arachnids, insects, nematodes and oligochaetes (Forti et al. 2002).

Species diversity It is unlikely that there is a complete accounting of macrofaunal diversity within any single seep ecosystem but there is evidence that diversity is high relative to hydrothermal vent habitats. Limited sampling of clam-bed and microbial mat habitats on the northern California slope yielded 83 species (Levin et al. 2003). A comparable number (86) are reported for the San Clemente cold seep (Poehls et al. unpublished data in Baco & Smith 2003); it is unclear whether these include vestimentiferan associates only or sediment fauna as well. Bergquist et al. (2003) recorded 66 species associated with vestimentiferan aggregations in the Gulf of Mexico. Baco and Smith (2003) suggested that seep diversity is lower than that of whale fall communities in the Pacific, due mainly to a greater suite of niches associated with whale skeletons. In a comparison of mussel bed invertebrates at seeps and hydrothermal vents, Turnipseed et al. (2003) found higher diversity at two seeps than at most of the six vent sites examined. Once the full range of byssus threads, tube and shell surfaces, carbonates, internal body cavities and sediments are explored, scientists are likely to find faunal diversity at seeps equivalent to or higher than that in other reducing ecosystems.

The macrofaunal assemblages in highly sulphidic seep sediments often exhibit low diversity, particularly in sediments covered by mats of sulphur bacteria (Sahling et al. 2002, Levin et al. 2003). High-density patches of macrofauna often consist of aggregations of one or a few species, sometimes siboglinid pogonophorans (polychaetes) or bivalves (Dando et al. 1994). In microbial-mat covered sediments these may be dorvilleid polychaetes at depths of 500–800 m in the Pacific and

Gulf of Mexico (Levin unpublished data) or hesionid polychaetes in deeper waters (Gulf of Mexico, Levin unpublished data, Table 3). While reduced diversity at seeps has been noted frequently (Grassle et al. 1985, Sahling et al. 2002, Levin et al. unpublished data), low levels of sulphide may enhance diversity (relative to background conditions) by promoting the survival of both sulphophilic and ambient species. Macrofaunal species richness was higher in *Calyptogenia* bed sediments on the northern California slope (maximum sulphide concentration 2 mM) than in background or highly sulphidic microbial mat sediments (Levin et al. 2003). Diversity was similar to that in non-seep sediments for macrofauna of hydrocarbon seeps off Santa Barbara (16 m, Montagna et al. 1989) and in *Acharax* beds at Hydrate Ridge (Sahling et al. 2002).

Microhabitats and the role of sediment geochemistry Composition of seep macrofauna varies greatly among different ecological habitats within the same geographic region or geological feature. While seep habitats are often characterized by the dominant megafaunal feature (clam beds, pogonophoran fields, microbial mats, mussel beds), it is often the geochemical characteristics of the sediments that are responsible for distinct epifaunal and infaunal assemblages (Sahling et al. 2002, Levin et al. 2003). Sampling at a high spatial resolution has demonstrated that infaunal composition will change on scales of centimetres in accordance with seepage rates, sulphide concentration, and biological activities (i.e., clam pumping) (Sahling et al. 2002). Distinct infaunal assemblages occur in *Beggiatoa*, *Calyptogenia*, *Acharax* and non-seep habitats on Hydrate Ridge; these exhibit one to two order of magnitude variation in sulphide flux and sulphide concentration (Sahling et al. 2002). In *Beggiatoa* mats, where sulphide concentrations exceeded 25 mM and fluxes were 23–13 mol m⁻² yr⁻¹, there was a low macrofaunal abundance:biomass ratio and low diversity characteristic of severe disturbance (Sahling et al. 2002). Similar observations were made in microbial mats on the northern California slope (Levin et al. 2003).

The vertical distribution of macrofauna within the sediment column appears to be regulated in part by oxygen and sulphide concentrations. As sulphide concentrations become higher and sulphide is present closer to the sediment surface, most macrofauna will become concentrated in the uppermost part of the sediment column. For example, 91% of the macrofauna occur in the top 2 cm in microbial mat sediments, compared with 71% in clam-bed sediments and 62% in non-seep sediments on the northern California slope (Eel River). Vertical distributions of annelid taxa collected at this site (Paraonidae, Cossuridae, Cirratulidae, Tubificidae) appeared compressed upwards in seep sediments relative to non-seep sediments (Levin et al. 2003). Vertical partitioning of seep sediments was investigated for dorvilleid species in the Eel River Basin. Whereas no partitioning was evident for five dorvilleid species in microbial mat sediments, two species inhabiting clam-bed sediments appear to partition the environment vertically. *Parougia* sp. inhabited the upper 2 cm where sulphide concentrations were <1 mM, and *Exallopus* sp. primarily occupied 5–10-cm deep sediments, where sulphide concentrations were higher (up to 2 mM) (Levin et al. 2003).

High resolution (mm-cm scale) studies of sulphide concentration in relation to macrofaunal abundance in seep sediments reveal that few taxa tolerate sulphide at concentrations of 1 mM or higher. Typical L-shaped relationships (high densities at sulphide concentrations <1 mM and densities near 0 at sulphide concentrations of 1–20 mM) are observed for most annelid families, gastropods, amphipods, tanaids and nemerteans in northern California seep sediments (Levin et al. 2003). Exceptions are dorvilleid polychaetes and vesicomid bivalves (mainly *Calyptogenia* spp.), which occur at their highest densities at sulphide concentrations of 1–6 mM (Figure 9). These taxa exhibit reduced densities from 6–14 mM and are absent when concentration exceeds 14 mM. Filamentous sulphur bacteria show similar sulphide preferences (Levin et al. 2003).

Gas hydrate may have a direct influence on infauna by affecting the physical properties of sediments. Sahling et al. (2002) suggest that mm-thin layers of hydrate present below bacterial mats may exclude macrofauna typical of deeper sediments. Floating hydrates and gas bubbles may

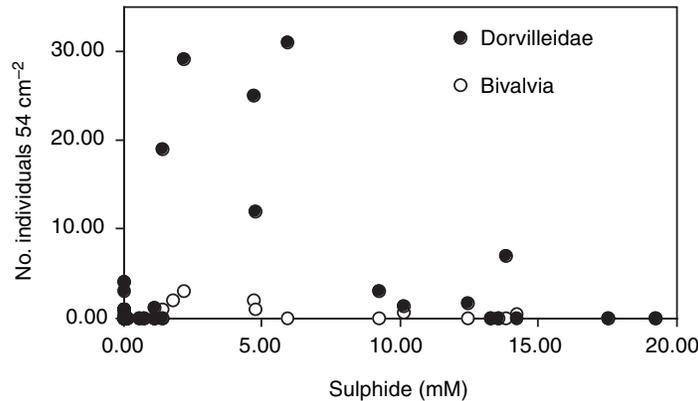


Figure 9 Scatter plots of dorvilleid polychaete and bivalve (mainly *Vesicomya*) density as a function of pore-water sulphide concentration (measured by microelectrode), determined for 1-cm thick core fractions from non-seep, microbial mat and clam-bed sediments on the northern California (Eel River) slope, 500 m.

also induce sediment disturbance. Precipitation of carbonate concretions within sediment (e.g., Figures 2, 3, 7A) is also likely to modify the substratum and geochemistry in ways that affect infauna. To date there have been no direct studies of organism-substratum-disturbance interactions at seeps.

Nutrition of fauna in seep sediments

The most detailed understanding of nutrition at seeps has been developed for the large fauna that host endosymbiotic chemoautotrophic bacteria. Much of this information is derived from combined use of stable isotopic signatures, autotrophic enzyme analyses, electron microscopic studies and molecular sequencing of symbionts. Both methane-based and sulphur-based symbioses fuel much of the consumer biomass at seeps via tubeworms, mussels and clams. Vesicomimid clams have exclusively thiotrophic nutrition, with symbionts transmitted through eggs (Peek et al. 1998). Vestimentiferan tubeworms and bathymodiolid mussels may derive their nutrition from thiotrophic, methanotrophic or both types of symbionts (Fisher 1990, Fisher et al. 1997). Among perviate Pogonophora, there is one shallow water methanotroph (Schmaljohann & Flugel 1987) and the rest appear thiotrophic (Tunnicliffe et al. 2003). Cladorhizid sponges have only methanotrophic symbionts (Vacelet et al. 1995). Among the non-vesicomimid taxa, lucinid, solemyid and thyasirid bivalve symbionts all appear to be thiotrophic. The mussels and some clams (e.g., thyasirids) may also be mixotrophic, feeding on particulate organic matter to supplement symbiont-derived nutrition (Page et al. 1990, Dufour & Felbeck 2003).

Very low $\delta^{15}\text{N}$ signatures in invertebrates inhabiting reducing ecosystems have led scientists to investigate inorganic nitrogen assimilation. Symbiont assimilation of ammonium and some nitrate (but not N_2) has been documented for vent tubeworms, clams and a methanotrophic seep mussel (Lee & Childress 1994, 1996, Lee et al. 1999b). A shallow water clam, *Solemya* was shown to assimilate ammonium without the involvement of its symbionts (Lee et al. 1999b), but virtually nothing is known about inorganic nitrogen assimilation for the majority of seep species.

Less information is available about the nutrition of smaller invertebrates that live within seep sediments, although this is changing. Sources of nutrition for these organisms include organic matter derived chemosynthetically from endosymbioses or ectosymbioses, heterotrophic consumption of free-living chemolithotrophic bacteria and archaea, or consumption of photosynthetically

derived material originating in the plankton, on land or in the littoral zone. Most existing knowledge about infaunal nutrition at seeps is derived from analyses of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and sometimes $\delta^{34}\text{S}$ signatures of animal tissues, which reflect both diet and trophic level (Conway et al. 1994). Scientists have assessed the relative importance of chemosynthetic vs. photosynthetic food sources, and in some cases evaluated the significance of methanotrophy vs. thiotrophy or the relative contribution of methane-derived carbon using stable isotopic analyses.

A range of microbial metabolic processes involving a diversity of electron donors and electron acceptors may generate chemosynthetic food sources. Under aerobic conditions these may include H oxidation, S oxidation, Fe oxidation and methane oxidation. Anaerobic processes include methanogenesis, S and sulphate reduction, H oxidation, denitrification and methane oxidation (Tunnicliffe et al. 2003). The relative importance of these in overall seep ecosystem metabolism has not been established. Growing use of lipid biomarkers, particularly fatty acids (Fullarton et al. 1995, Pond et al. 1997, 1998) offers promise for higher resolution of dietary components but these techniques are just starting to be applied to seeps.

There are few studies of protozoan or metazoan meiofaunal diets at seeps largely because the effort required to obtain sufficient amounts of organic matter for isotopic analyses is prohibitory. Documentation of ectosymbioses in seep nematodes (Dando et al. 1991, Jensen et al. 1992) and in euglenoids and ciliates (Buck & Barry 1998) indicates a possible nutritional role for chemosynthetic bacteria in these taxa. Nematode isotope signatures presented by Van Dover et al. (2003) for Blake Ridge seeps (2,155 m) reveal very light $\delta^{13}\text{C}$ (-45 to -50‰) but relatively heavy $\delta^{15}\text{N}$ (9 – 11‰), suggesting utilization of chemosynthetically derived organic matter, but at a high trophic level, possibly as decomposers. Werne et al. (2002) present molecular isotopic evidence that bacterivorous ciliates are feeding primarily on methane-derived carbon from archaea and bacteria at the Kazam mud volcano in the Mediterranean Sea, based largely on the isotopic signatures of tetrahymenol, a lipid biomarker produced by marine ciliates when they use procaryotes as their sole food source.

Among the macrofauna, stable-isotope based nutritional investigations have now been carried out for a variety of shallow- and deep-water seeps in the Atlantic, Pacific and Gulf of Mexico. The absence of significant chemosynthetic contribution to the nutrition of shallow-water seep infauna appears to be a widespread phenomenon. $\delta^{13}\text{C}$ signatures for seep infauna typically ranged between -16 and -20‰ for methane seeps at 115 m in the North Sea (Dando et al. 1991) and at 35–55 m off northern California (Levin et al. 2000), indicating a largely marine plankton-derived diet. Similarly, at bubbling reefs in the Kattegat (Denmark), the rock invertebrates had signatures of -17 to -34‰ (Jensen et al. 1992). There are some exceptions, notably nematodes, pogonophorans and a thyasirid in the North Sea (Dando et al. 1991, 1994). Similar observations of limited chemosynthetic contributions to diet have been made for epifauna on seep carbonates at 10–12 m in the Kattegat (Jensen et al. 1992), and for fishes and crustaceans at a 132-m seep off Oregon (Juhl & Taghon 1993). High availability of photosynthetically produced food may be partly responsible for these observations.

In contrast to results from shallow water, macrofauna from seeps at bathyal and abyssal depths show a highly variable dependence on chemosynthetic food sources (Figure 10). This dependence has been examined for seeps in the northeast Pacific Ocean off Alaska (4,445 m), Oregon (590 m), California (500 m), in the Gulf of Mexico (2200–3300 m) and the Blake Ridge in the Atlantic Ocean (2155 m). Average infaunal $\delta^{13}\text{C}$ signatures are exceptionally light at methane seeps in the Gulf of Alaska and on the Oregon Margin (-41 to -46‰) (Levin & Michener 2002), in sulphidic/microbial mat sediments of the Florida Escarpment in the Gulf of Mexico (average -51‰) (Levin et al. unpublished data), and on the Blake Ridge (-40 to -50‰) (Van Dover et al. 2003). At these sites the majority of infauna appear to be using local chemosynthetic production from the seep. Estimates of methane contribution to the carbon pool for seep infauna range from 32–51% for Gulf of Alaska pogonophoran fields, 20–44% for Oregon microbial mats (Levin & Michener

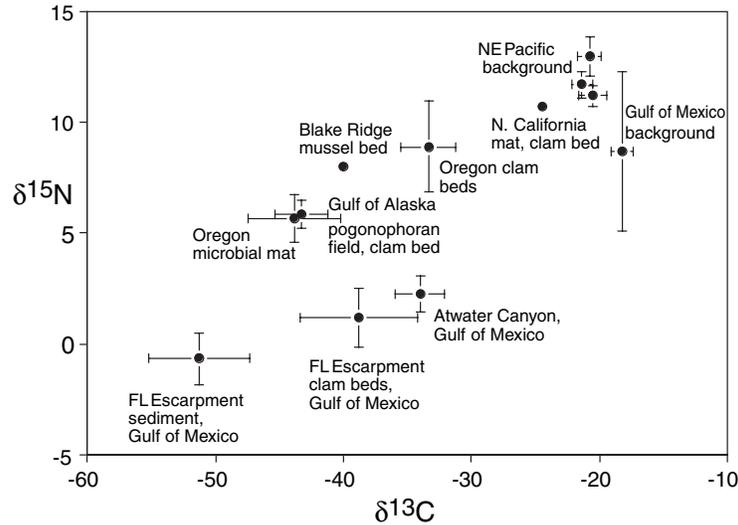


Figure 10 Average stable isotopic signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) ± 1 SD of macroinfauna from seeps and background sediments. Data are from Levin & Michener (2002), Van Dover et al. (2003) and Levin unpublished. Note there is a positive linear relationship between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, but that the Pacific (and one Atlantic) sites fall along a different line than the Gulf of Mexico sites.

2002) and 15–40% for sipunculans from the Blake Ridge (Van Dover et al. 2003). The fraction of this methane that is derived from fossil sources, rather than from recent biogenic generation, is unknown. Paull et al. (1985) showed, by ^{14}C analysis of mussel tissues from the Florida Escarpment seeps, that very little (<25%) of the carbon is of fossil origin, despite exceptionally light $\delta^{13}\text{C}$ signatures.

In other regions seep macrofauna have much heavier $\delta^{13}\text{C}$ signatures. This is observed in clam beds off Oregon and California, and microbial mat sediments on the Eel River margin or in Atwater Valley, Gulf of Mexico (Levin & Michener 2002, Levin et al. unpublished data) (Figure 10), reflecting incorporation of largely thiotrophically-derived C or even photosynthetically fixed organic matter.

Possible evidence for the influence of seepage intensity on animal nutrition comes from the observation of distinctive isotope signatures in different local habitat patches. Microbial mat infauna have lighter $\delta^{13}\text{C}$ signatures than those in nearby clam beds on the Oregon margin, but not on the California margin (Levin & Michener 2002). Average infaunal $\delta^{13}\text{C}$ signatures varied by nearly 5‰ ($-24.6 \pm 1.1\text{‰}$ vs. $-19.9 \pm 0.3\text{‰}$, $P < 0.001$) in two nearby *Calyptogena pacifica* patches, suggesting different seepage activities, but fluxes or sulphide concentrations were not measured (Levin et al. 2000). Even greater differences were observed for macrofauna inhabiting nearby black (average $\delta^{13}\text{C} = -67.0\text{‰}$) and white sediment patches (average $\delta^{13}\text{C} = -36.9\text{‰}$) at seeps on the Florida Escarpment in the Gulf of Mexico (Levin et al. unpublished data).

It is apparent from the nitrogen isotope signatures of Pacific seep macrofauna, including crustaceans, polychaetes, molluscs, sipunculans, echinoderms and cnidarians, that the majority of individuals derive their nutrition heterotrophically rather than from symbionts. Well-known exceptions are thyasirid, lucinid, solemyid, vesicomid and bathymodiolid bivalves, and all pogonophorans and vestimentiferans. Several other seep polychaetes, including polynoids and ampharetids from Kodiak seeps in the Gulf of Alaska (Levin & Michener 2002) and the dorvilleid *Parougia* sp. from the Eel River margin, northern California (Levin unpublished data), have exceptionally light $\delta^{15}\text{N}$ signatures

(near or below 0) characteristic of taxa known to possess symbionts and should also be examined for possible endosymbioses.

Notably, within a single seep site, $\delta^{13}\text{C}$ signatures may vary among species by 70‰ (Levin & Michener 2002), reflecting a mixture of nutritional sources including carbon from archaeal-derived lipids (which can have $\delta^{13}\text{C}$ values of -69 to -111‰ in seep sediments; Werne et al. 2002, Zhang et al. 2003), methanotrophy, thiotrophy and photosynthesis. Several lines of evidence indicate that closely related infauna can specialize on different food sources in seeps sediments. Three co-occurring dorvilleid polychaete species have highly distinctive isotopic signatures in Eel River seep sediments, suggesting strong diet partitioning (L. Levin unpublished data). Isotopic signatures much lighter than that of methane are usually associated with lipids derived from anaerobic methane oxidation (Hinrichs et al. 2000). The observation of extremely negative $\delta^{13}\text{C}$ values (<-70‰) in some annelids from seeps in the Pacific and Gulf of Mexico (Levin & Michener 2002) indicates that these organisms either selectively ingest archaeal-derived carbon or live in sediment horizons where this is the primary carbon source available.

Stable isotopes provide only indistinct clues about the diets of seep infauna. Terrestrial organic matter with isotope signatures near -25‰ can mask the contributions of chemosynthetically fixed carbon (Levin et al. 2000). A suite of more complex techniques should be employed to examine the relative contributions of food items to animal diets and of different carbon-fixation pathways to the animal carbon pool. These methods might include fatty acid analysis of tissues (including stable isotopic signatures of fatty acids; Pond et al. 1997, 2000), molecular sequencing of gut contents (Duplessis et al. 2004), use of inorganic isotopic tracers such as $^{14}\text{CO}_2$, $^{13}\text{CO}_2$, and $^{35}\text{SO}_4$, as well as more traditional feeding experiments and gut content observations. MacAvoy et al. (2002b) demonstrated that chemosynthetically produced essential and precursor fatty acids isolated from host tissues (mussels and tubeworms) will retain the $\delta^{13}\text{C}$ signature of the bacteria that made them, allowing specific identification of the carbon sources used by symbionts for fatty acid synthesis, and ultimately the tracking of these through the food web.

Transfer of seep organic matter to the surrounding deep-sea ecosystem

The extent to which primary and secondary production in seep sediments is transferred to higher consumers and to the surrounding (non-seep) deep-sea ecosystem has been investigated largely through stable isotopic analyses. A detailed study of mobile consumers at relatively shallow (500–600 m) seeps in the Gulf of Mexico by MacAvoy et al. (2002a) revealed a range of dependence on seep production. Gastropods, sea stars, crabs and selected fishes sampled near seeps exhibited isotopic signatures consistent with 50–100% dependence on seep-derived carbon. In contrast vagrant predators (the isopod *Bathynomus giganteus* and, to a lesser extent, the hagfishes *Eptatretus* and *Rochina crassa*) appeared to rely mainly on photosynthetically derived foods, but were responsible for some export of seep production. These authors conclude that only a limited number of background species are exploiting seep production in the Gulf of Mexico, due either to sufficient food in the ambient deep sea or to biotic defenses by seep prey. However, Kelley et al. (1998) suggested that light C in sediments of the Gulf of Mexico reflect widespread export of organic matter from seeps to background deep-sea bacteria.

Sahling et al. (2003) suggested that export of seep production is related to depth in the Sea of Okhotsk based on stable isotopic analyses. Galatheid crabs at seeps in the Gulf of Alaska (4500 m) (Levin & Michener 2002) and in the Sea of Okhotsk (1450–1600 m) (Sahling et al. 2003) consume prey with tissues derived from chemosynthetically fixed carbon. There is less evidence of this for mobile urchins, crabs, asteroids and cnidarians collected at seeps on the Oregon and California

margin; these taxa seem to have photosynthesis-based diets (Levin & Michener 2002). Quantitative energy budgets that examine the transfers of photo- and chemosynthetically derived carbon into and out of seeps have yet to be constructed.

The possibility that organisms with complex life cycles may actively contribute photosynthetically derived organic matter to seeps should also be considered. Fatty acid analysis by Pond et al. (2000) has shown that the early life stages of hydrothermal vent shrimp feed on phytoplankton, probably in surface waters, before taking up a benthic existence at vents. No comparable ontogenetic patterns are known for seep taxa, although sablefish commonly seen feeding at 500-m seeps on the northern California margin are known to have pelagic life stages that feed near the surface (Adams et al. 1995).

Adaptations and tolerances of seep infauna

The mechanisms that enable animals (and plants) to survive in reducing environments have been a fertile area for discovery of novel physiological and biochemical capabilities. Most have centered around adaptation to sulphides (e.g., Powell & Somero 1986, Arp et al. 1987, 1995, Julian et al. 1999a,b, Lee et al. 1996, 1999a) because seep and vent animals may experience exceptionally high sulphide concentrations within sediments (e.g., Figure 9). Hydrogen sulphide interferes with aerobic metabolism by disrupting the transport of oxygen by haemoglobin and inhibiting ATP production by the electron transport chain through binding to cytochrome c oxidase (CytOx) (Somero et al. 1989). Despite its toxicity, some animals have been found to tolerate relatively high sulphide levels. Adaptation to sulphides include (1) the removal of sulphide at the body wall through a layer of sulphide-oxidizing bacteria, and/or enzymatic sulphide oxidation, (2) sulphide-insensitive haemoglobin, (3) reversible sulphide binding to blood components, (4) mitochondrial sulphide oxidation to less toxic compounds (e.g., thiosulphate) with ATP synthesis and (5) reliance on anaerobic respiration at high sulphide levels (Powell et al. 1979, Grieshaber & Volkel 1998). Symbiotic sulphide oxidation is a widespread adaptation present in siboglinid annelids (formerly pogonophorans McHugh 1997, Rouse & Fauchald 1997, Halanych et al. 1998, 2002) and a host of bivalves and annelids occurring at hydrothermal vents and methane seeps (Fisher 1990, Childress & Fisher 1992). In siboglinids, sulphide tolerance has been hypothesized to be driving the evolution of the clade (Schulze & Halanych 2003). Dorvilleid polychaetes, which exhibit high species richness at methane seeps and whale falls where sediments have porewater sulphide concentrations >10 mM, may also have radiated in sulphidic environments (G. Mendoza et al. personal communication). Differential sulphide tolerances also may drive differentiation in members of the genus *Capitella* (Gamenick et al. 1998). *Capitella* exhibits a preference for seep sediments at shelf depths off California (Levin et al. 2000).

For animals that rely on oxidation of reduced compounds by symbiotic bacteria, acquisition of oxygen and sulphide (or methane) presents a challenge. Adaptations may include separating the acquisition of oxygen and sulphide in space (by extending the body between environments, see Dufour & Felbeck 2003 for an extreme example) or in time (by moving between environments) (Fisher 1996). Seep vestimentiferans obtain oxygen from the plume and sulphide through diffusion into a 'root'-like posterior extension that penetrates deeply into the sediment (Julian et al. 1999a, Freytag et al. 2001). This adaptation allows them to persist in environments where oxygen and sulphide may be separated by 50 cm or more. Vesicomyid clams also acquire oxygen sulphide from different places, albeit over shorter distances (Childress et al. 1991). Smaller taxa (e.g., nematodes and oligochaetes) may migrate vertically between oxygen, sulphide and nitrate sources in sediments, storing one or the other. Large vacuole-bearing sulphur bacteria (e.g., *Thioploca*) are able to do the same, gliding vertically in sheaths. In contrast, some animals may behave in a way that promotes

the production of sulphide. Downward pumping of seawater sulphate by clams (Wallmann et al. 1997) will enhance sulphate reduction, providing symbionts with a continuous source of sulphide.

Investigations of morphological adaptations that enhance fitness in sulphidic sediments have been limited mainly to megafauna. Among meiofauna, body morphology appears to reflect adaptation to limited oxygen and to be correlated with the amount of dissolved sulphide in the environment. Jensen et al. (1992) reported all thiotrophic nematodes from the East Flower Garden Brine seep to exhibit body elongation, a high surface area: volume ratio and a short body radius, relative to oxybiotic nematodes in the area.

Megafaunal activities within seep sediments (root and foot penetrations, burrowing, pumping and sulphide extraction) are certain to have significant consequences for other microbes and infauna. Dattagupta (2004) suggests that release of sulphate by roots of seep vestimentiferans in the Gulf of Mexico enhances sulphate reduction locally and thus the production of sulphide required by their symbionts. 'Second-order' interactions between megafauna and seep infauna have rarely been examined but are particularly likely to affect the distribution of Foraminifera and metazoan meiofauna. Research in shallow-water and bathyal non-seep sediments demonstrates major influence of macrofaunal and megafaunal animal activities on the distribution and nutrition of other infauna (Reise 1985, Levin et al. 1997, Olafsson 2003). Microbial mats may also modify the sediment geochemistry and substratum in ways that affect associated biota (Robinson et al. 2004). Given the limited oxygen and highly sulphidic nature of seep sediments, there should be extensive biotic control over geochemical microenvironments that determines physiological status, food supply, settlement cues and other ecological features for microbes and smaller infaunal invertebrates.

Future directions

Seep environments have now been recognised for two decades. During this period many new seep locations have been discovered and thorough descriptions of seep communities have emerged. However, mechanistic understanding of their function and dynamics is in its infancy, particularly with respect to higher organisms residing within seep sediments. Research has revealed a strong control on faunal evolution, adaptation and distribution by the availability of reduced compounds. Further investigations that integrate the geophysical, geochemical and microbial processes controlling this availability, with animal functional and numerical responses, should yield valuable insight. Many ecological processes, such as animal migrations, reproduction, larval settlement, behaviour, nutrition, biotic interactions, and community succession at seeps all are likely to be tightly linked to aspects of fluid flow and microbial processes. These interactions will be complex, with significant spatial and temporal variation in the players and processes on multiple scales. A melding of geochemistry with genomics and ecology will further elucidate the dynamics of seep environments, as it has begun to do for hydrothermal ecosystems (Reysenbach & Shock 2002). Future investigation of organic inputs from and exports to the non-seep marine system will benefit from advances in fatty acid, isotope and micro technologies. Such studies will clarify the role of seeps in global processes such as biogeochemical cycling and biodiversity maintenance. The difficult problems of larval dispersal and population connectivity among seeps may soon be addressed by novel applications of microchemistry (elemental fingerprinting) and molecular identifications of larvae.

Because there have been only a few detailed investigations of seep macro- and meiofauna, very little is known about the biogeography of these organisms on a global basis. The extent to which species are shared with background communities or with hydrothermal vent, whale fall or other reducing ecosystems has been examined only for bivalves and tubeworms. Typically there are shared genera (*Vesicomya*, *Calyptogenia*, *Bathymodiolus*, *Lamellibrachia*) but not species (Baco & Smith 2003). At least some overlap is expected among infauna, but comparison of seep and whale

fall dorvilleids from the Pacific show few species in common (G. Mendoza et al. personal communication). Sahling et al. (2002) reported four shared species between Hydrate Ridge seeps and Guaymas hydrothermal mounds.

Numerous seep specialist taxa have evolved to tolerate high sulphide concentrations (mainly annelids and bivalves), but the magnitude of tolerances and the underlying mechanisms are unknown for most taxa except for selected vestimentiferan tubeworms, mussels and bivalves. Certain seep assemblages have yet to be studied in detail. These include most infaunal assemblages and the macrofauna associated with carbonate concretions (but see Jensen et al. 1992).

Many new seep sites and settings will be discovered in the coming decades, including some in parts of the world where seeps have yet to be identified. Especially novel environments are likely to be found where seeps interact with other unusual geological or oceanographic constructs (e.g., with oxygen minimum zones, in trenches, or at subducting spreading ridges). From these discoveries will spring an endless fount of interdisciplinary research challenges for biologists, microbiologists and oceanographers.

Acknowledgements

I gratefully acknowledge the support of the NOAA West Coast National Undersea Research Center (via UAF 00:0050, 04-0112), which has made it possible for me to pursue my interests in methane seep ecosystems, and the National Science Foundation (OCE 04 25317) for recent support of seep research. This review has benefited from my collaborations with A. Rathburn, W. Ziebis, J. Gieskes, K. Brown, M. Tryon, C. Mahn, G. Mendoza, J. Bernhard, R. Carney and C. Fisher. I thank W. Ziebis, J. Bernhard, A. Rathburn, M. Tryon and H. Sahling for their critiques and contributions to various parts of the manuscript. K. Campbell generously provided a base map of seep distributions and K. Brown made available the map of Eel River habitats. I thank J. Gonzalez and P. McMillan for technical assistance with manuscript preparation.

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