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Biologic and geologic characteristics of cold seeps in Monterey Bay, California

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Abstract—Cold seep communities discovered at three previously unknown sites between 600 and 1000 m in Monterey Bay, California, are dominated by chemoautotrophic bacteria (*Beggiatoa* sp.) and vesicomyid clams (5 sp.). Other seep-associated fauna included galatheid crabs (*Munidopsis* sp.), vestimentiferan worms (*Lamellibrachia barhami*?), solemyid clams (*Solemya* sp.), columbellid snails (*Mitrella permodesta, Amphissa* sp.), and pyropeltid limpets (*Pyropelta* sp.). More than 50 species of regional (i.e. non-seep) benthic fauna were also observed at seeps. Ratios of stable carbon isotopes ($\delta^{13}C$) in clam tissues near −36‰ indicate sulfur-oxidizing chemosynthetic production, rather than non-seep food sources, as their principal trophic pathway. The "Mt Crushmore" cold seep site is located in a vertically faulted and fractured region of the Pliocene Purisima Formation along the walls of Monterey Canyon (~635 m), where seepage appears to derive from sulfide-rich fluids within the Purisima Formation. The "Clam Field" cold seep site, also in Monterey Canyon (~900 m) is located near outcrops in the hydrocarbon-bearing Monterey Formation. Chemosynthetic communities were also found at an accretionary-like prism on the continental slope near 1000 m depth (Clam Flat site). Fluid flow at the "Clam Flat" site is thought to represent dewatering of accretionary sediments by tectonic compression, or hydrocarbon formation at depth, or both. Sulfide levels in pore waters were low at Mt Crushmore (*ca* 0.2 mM), and high at the two deeper sites (*ca* 7.0-11.0 mM). Methane was not detected at the Mt Crushmore site, but ranged from 0.06 to 2.0 mM at the other sites. Copyright © 1996 Elsevier Science Ltd

INTRODUCTION

Since their discovery in the 1980s (Paull *et al.*, 1984; Kennicutt *et al.*, 1985) chemoautotrophic or methanotrophic-based communities associated with sea floor seepage have been found in various settings and appear to be common along continental margins. Chemosynthetic communities dominated by vesicomyid clams, mytilid mussels, vestimentiferan or pogonophoran worms, or free-living bacteria, have been reported from hydrocarbon seeps (Kennicutt *et al.*, 1985, 1988, 1989), groundwater seeps (Paull *et al.*, 1984; Hecker, 1985), methane seeps (Kennicutt *et al.*, 1985; Dando *et al.*, 1991), accretionary prisms associated with subduction zones, other sites of tectonically-compressed sediment (Suess *et al.*, 1985; Laubier *et al.*, 1986; Boulègue *et al.*, 1987; Cadet *et al.*, 1987; Le Pichon *et*

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al., 1987; Ohta and Laubier, 1987; Hashimoto *et al.*, 1987, 1989; Jollivet *et al.*, 1990), and relict organic material buried in debris flow deposits (Embley *et al.*, 1990). Fossil cold seeps and associated faunal assemblages have also been reported from several sites (Beauchamp *et al.*, 1989; von Bitter *et al.*, 1990, 1992; Campbell and Bottjer, 1993; Aharon, 1994; Clari *et al.*, 1994).

Biota inhabiting cold seeps include "obligate" species, restricted to sites in direct proximity to fluids rich in sulfide, methane, or perhaps other reducing inorganic compounds (e.g. ammonia; Fisher, 1990), and "regional" species which occupy seeps and neighboring non-seep habitats. Obligate species may be chemoautotrophic (e.g. *Beggiatoa*), or have thiotrophic or methanotrophic symbionts (e.g. vesicomyid clams, mytilid mussels, and vestimentiferan worms), but also may be heterotrophic and rely almost exclusively on chemosynthetic fauna (e.g. galatheid crabs [*Munidopsis* sp.], gastropods [*Mitrella* sp.], limpets [*Pyropelta* sp.]). Regional fauna may forage on chemosynthetic biota (e.g. *Neptunea amianta*, lithodid crabs), but typically are not dependent on chemosynthetic production.

Along central California, chemosynthetic communities were first found in the axial valley of the Monterey Fan Valley System (Embley *et al.*, 1990; McHugh *et al.*, 1992), where vesicomyid clams and pogonophoran worms were patchy, but common, between 3000 and 3600 m depth. Ratios of stable carbon isotopes in tissues of vesicomyid clams from the axial valley site suggested chemosynthetic production by sulfur-oxidizing bacteria as the primary food source (Rau *et al.*, 1990).

Sea floor seepage at other sites in Monterey Bay was suggested by dredged shells of vesicomyid clams (J. Nybakken, personal observation), and side-scan sonar data (Reed *et al.*, 1992). Methane plumes, hydrocarbon seeps and large hydrocarbon deposits along the California coast also increase the likelihood that chemosynthetic fauna are common, though highly localized, in this region. Here, we describe the biological and geological characteristics of three cold seep sites discovered recently in the Monterey Bay region.

REGIONAL GEOLOGY OF MONTEREY BAY AND MONTEREY CANYON

Monterey Bay lies within the Salinian block, an allochthonous Cretaceous basement block that has been tectonically slivered into its present position (Page, 1970) as it was carried northward along the San Andreas fault during the past 21 million years. Near Monterey Bay, the San Andreas fault system, including the Hayward–Calaveras, Palo Colorado–San Gregorio, and San Andreas fault zones, forms the boundary between the North American and Pacific plates. The Palo Colorado–San Gregorio fault zone is a major right-lateral strike-slip fault zone oriented generally north–south, comprising two or more parallel and fairly continuous fault segments extending about 125 km south from Año Nuevo Point to Garrapata Beach (Greene *et al.*, 1973; McCulloch and Greene, 1990). The Monterey Bay fault zone (Fig. 1) is a wide (~10 km) en echelon zone composed of many short (5 km or less) and several longer (up to 15 km) segments and either truncates or merges with the San Gregorio fault segment (Greene *et al.*, 1973; Greene, 1977, 1990).

Monterey Canyon (Fig. 1) crosses the generally northwest–southeast trending offshore faults, and has eroded deeply into the Cretaceous granitic basement of the Salinian block and the overlying Neogene sedimentary rocks of the Miocene Monterey Formation and the Pliocene Purisima Formation (Greene, 1990; Greene *et al.*, 1991). The origin and modification of the canyon resulted from regional tectonic motion since subduction of the Pacific Plate ceased and transform motion began (~21 Ma). Earthquakes in the region

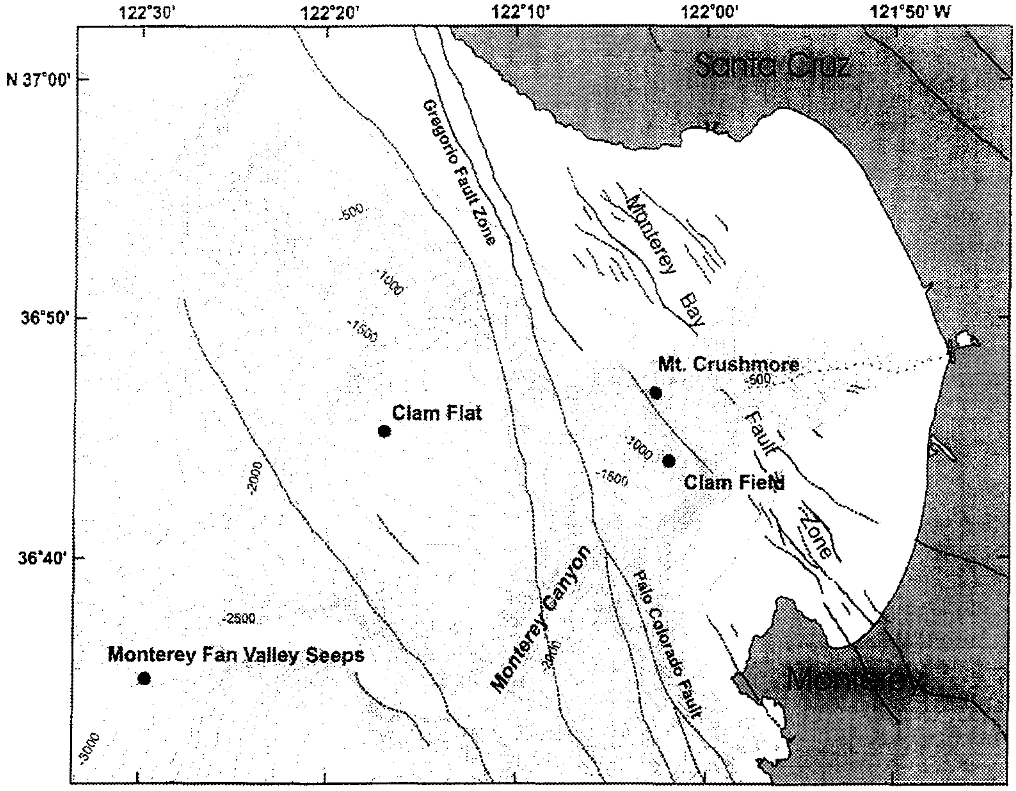

Fig. 1. Bathymetry and geological features of Monterey Bay, including major fault zones, and locations of cold seeps sites (modified from Greene, 1990). Location of Fan Valley Cold Seep site after Embley *et al.* (1990).

result in mass wasting along the walls of the canyon that produces turbidity currents, thereby eroding the canyon.

The continental slope sediments west of the Palo Colorado–San Gregorio fault zone are subjected to transpressional forces associated with the oblique convergence of the Pacific Plate against the North American Plate (Greene, 1990). Here an apparently elevated ridge (Smooth Ridge) is being uplifted by the oblique fault motion associated with the Palo Colorado–San Gregorio fault zone. This compression may also enhance migration of fluid up through the sediment and seepage along faults exposed on the sea floor (Orange *et al.*, 1993).

METHODS

Survey methods

Sea floor surveys were performed in Monterey Bay from 1992 to 1994 using the remotely operated vehicle (ROV) *Ventana*, operated by the Monterey Bay Aquarium Research Institute (MBARI). Dives were made at several locations in Monterey Canyon, particularly sites where biological evidence (e.g. dredged shells of vesicomyid clams) or geological features (e.g. highly faulted areas or evidence of diatreme extrusion) suggested the presence of cold seeps. Observations of seeps and other benthic habitats were made using a high resolution SONY DXC-3000 video camera recorded to Betacam format tape, and a Photosea 1000 35 mm still camera. Details of *Ventana's* features are discussed in Etchemendy and Davis (1991).

Faunal surveys generally extended to 1000 m depth and were performed along transects from 100 to 3000 m in length, oriented either along depth contours, or from deeper to shallower depths. Transect tracks were altered occasionally to investigate outcrops or other seep-associated features (e.g. pockmarks or areas of high reflectance) identified by sonar. Dive tracks, including the location (latitude, longitude) and depth of cold seeps were recorded by the *Pt Lobos*/*Ventana* navigation system (differential GPS [R.V. *Pt Lobos*], ± 5 m accuracy; ultrashort baseline acoustic navigation system [ROV *Ventana*], ±50 m accuracy). Sites of active or relict seeps were indicated by bacterial mats, vesicomyid clams and other chemosynthetic fauna, or authigenic precipitates and carbonate deposits associated with methane venting.

Geological studies

Geologic features of cold seeps (lithology, faults and fault-scarps, and bedding) were characterized from observations and sample collections during ROV surveys. Rock samples were collected using the robotic arm and stored in the ROV sample drawer for petrological, paleontological, and chemical analyses. Transects near cold seep sites enabled identification and mapping of the local extent of each cold seep and the association of diagnostic geologic features with seep locations to be carried out. Horizontal transects were used to delineate and map faults exposed in the canyon walls. Vertical transects were performed to determine the continuity of faults, map locations of lithologic contacts, and define bedding in the Tertiary sedimentary rocks.

Chemical analyses

Concentrations of dissolved gases in pore waters at cold seeps were characterized from sediment cores collected at each site. Cores ($n = 4$ or 5) were collected using 7.6 cm (ID) by 35 cm long PVC push-cores inserted 10–25 cm into the sediments within aggregations of vesicomyid clams or bacterial mats. Upon recovery at the surface, push-cores were placed immediately in a nitrogen-filled chamber (glove-bag), where subsamples (subcores) were taken with an open-ended 10 cc syringe. Subcores were centrifuged in a nitrogen-flushed chamber at 3000 × G for 20 min to separate pore water from sediment. Pore waters were extracted (500 μl glass syringe) from subcores and immersed in liquid nitrogen to inhibit oxidation of sulfide. Samples were thawed and analyzed within 24 h using a Hewlett Packard Model 5890A Series II Gas Chromatograph, modified for analysis of carbon dioxide, sulfide, oxygen, nitrogen, and methane dissolved in fluid samples.

Biological investigations

Megafauna at cold seeps were identified from video and photographic images, or reference specimens collected by the ROV. Specimens were collected from several small seeps, bacterial mats, and clam patches at each cold seep site using the robotic arm of the ROV. Samples were sorted and identified after each dive.

Stable isotopic analyses

Ratios of stable carbon isotopes ($\delta^{13}C$) of soft tissues from vesicomyid clams at one cold seep site, and several species of regional benthic megafauna at non-seep sites, were used as an index of chemotrophic or heterotrophic production (e.g. Rau *et al.*, (1990) and Fisher *et al.*, (1994)). Five individuals of *Calyptogena kilmeri* were collected from the Clam Field cold seep site, dissected, dried (60°C), powdered, and analyzed by mass spectrometry to determine ratios of stable carbon isotopes ($\delta^{13}C$), expressed here as per mil (‰) values relative to Peedee belemnite.

RESULTS OF BIOLOGICAL AND GEOLOGICAL OBSERVATIONS OF COLD SEEPS

"Mt Crushmore" cold seep

Observations and sample collections during more than 20 ROV dives were used to determine the distribution of cold seeps and regional geology near the Mt Crushmore site (Fig. 2). Surveys extended from 150 to 1000 m depth across the western wall of the Monterey and Soquel canyons. The "Mt Crushmore" site, in Monterey Canyon near the mouth of Soquel Canyon, included small (0.25–3 m diameter) patches of cold seep fauna along a swath ~1 km wide between 580 and 700 m depth (Table 1). The Purisima Formation at Mt Crushmore has been elevated into a shatter ridge from fault movement, tilting sandstone and mudstone beds into vertical dips (Fig. 3a). Although fluid flow was not visually obvious, expression of sulfide-rich fluids was evident from authigenic precipitates (grayish white deposits), bacterial mats, clams, and other seep-associated fauna. Whitish-gray bacterial mats covered bedrock, sediments or megafauna, and the edges of vertical bedding and faults (Fig. 3a,b), and appeared to delineate boundaries of high sulfide concentrations. Sediment-covered rubble at the base of exposed vertical fractures often was occupied by small groups (*ca* 5–250 individuals) of vesicomyid clams (Fig. 3c). Gray bacterial crusts or authigenic precipitates were common to all seep patches, and were the only indication of fluid flow at the smallest seeps (i.e. <0.1 m diameter), where no other obligate fauna were observed. Sulfide concentrations of pore waters in the top 0.1 m of sediment within clam aggregations (Fig. 3f) were low (0.09 mM H_2S; Table 1), but considerably higher than in nearby non-seep sediments, where sulfide was undetectable. Methane was not detected at Mt Crushmore seeps.

The vesicomyid clam *Calyptogena pacifica* (Fig. 3c,e), and bacterial mats (*Beggiatoa* sp; D. Nelson, personal communication, 1996; Fig. 3a,b,d) were the most conspicuous fauna at the Mt Crushmore site (Table 2), and *C. pacifica* accounted for the greatest biomass of any seep species. *Calyptogena kilmeri* and *Calyptogena packardana* sp. nov. (Barry *et al.*, in press, b), were second and third in abundance (and probably biomass) among vesicomyid clams (Fig. 3e). Two additional vesicomyids (*Vesicomya stearnsii, V. gigas*) were rare. The life position of vesicomyid clams varied, though they were usually about 1/2 buried. Shells of dead clams were scattered sparsely in areas downslope from active seeps. Ratios of stable carbon isotopes for foot tissues of *Calyptogena kilmeri* averaged −36.3‰ (s.d. = 0.94, $n = 5$), suggesting that thiotrophic bacterial chemosynthesis is the principal carbon pathway for their metabolism (Fisher, 1990).

Other obligate seep species found only in close association with sulfide rich fluids were solemyid clams (*Solemya* sp.), columbellid gastropods (*Mitrella permodesta, Amphissa* sp.),

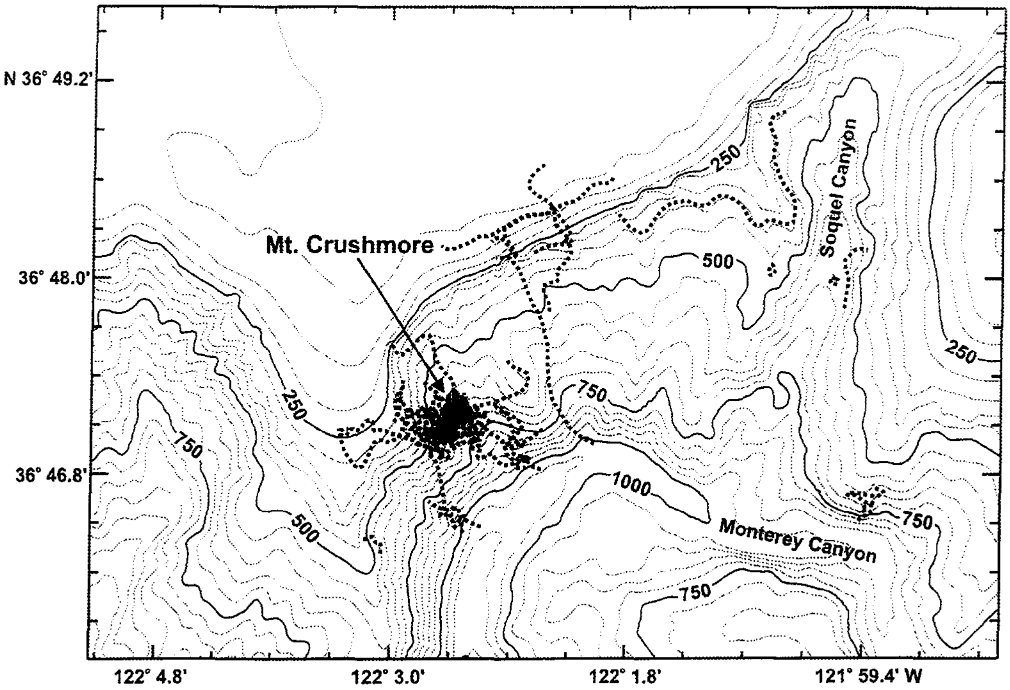

Fig. 2. Map of Mt Crushmore Cold Seep site. Bathymetry shown in 50 m intervals (gray contours). ROV survey tracks indicated in black dashed lines. Cold seep location shown in dark gray.

Table 1. Characteristics of cold seep sites in Monterey Bay. Pore chemistry values represent means [SD] of 4 or 5 cores

	Mt Crushmore	Clam Field	Clam Flat
General Location	Monterey Canyon	Monterey Canyon	Smooth Ridge
Latitude	36° 47.1′ N	36° 44.0′ N	36° 44.7′ N
Longitude	122° 2.6′ W	122° 2.0′ W	122° 16.6′ W
Depth Range (Major)	580–700 (635)	875–920 (900)	980–1010(1004)
Slope of Region	30–40°	~15–20°	~1°
Geologic Formation	Purisima	Monterey	Hemipelagic Sediment
Fault Relationship	Monterey Fault Zone	Monterey Fault Zone	Mud Volcano
Local Geologic Structure	Faulted Outcrop	Faulted Outcrop/Sediment	Sediment, Carbonates,
Source of Fluid Flow	Artesian?	?	Tectonic Compression, Sediment Compaction Pock Marks
Seep Characteristics	Small Seeps (~0.5 m)	Extensive Seep Area (150 m)	Large Seeps (~2.0 m)
Dominant Species	*Calyptogena pacifica*	*Calyptogena kilmeri*	*Calyptogena kilmeri*
Fluid Chemistry			
Sulfide Concentration	Low (0.09 mM [1.2])	High (10.9 mM [2.6])	High (11.3 mM [4.3])
Methane Concentration	Absent	Low (10.6 μM [7.4])	High (310.6 μM [75.0])
Number of ROV dives	20	25	15

Table 2. List of obligate and non-obligate megafauna associated with cold seeps in Monterey Bay. Obligate species occur only in direct contact with seeps. Non-obligate species occur at seeps and other benthic habitats. A-abundant, C-common, O-occasional, R-rare, X-present. Bold upper case lettering at collection site columns indicates species collected during this study

Organism	Obligate?	Mt Crushmore	Clam Field	Clam Flats	Fan Valley
MONERA					
Beggiatoa sp.	Y	**A**	**A**	**A**	X
CNIDARIA					
Anthozoa					
Alcyonacea					
Alcyoniidae					
Anthomastus ritteri	N	**R**	**R**		
Pennatulacea					
Umbellulidae					
Umbellula lindahli?	N	**R**	**R**		X
Actinaria					
Actinostolidae					
Stomphia sp.	N	**C**	**C**	**O**	
Paractinostola sp.	N	**C**	**C**	**O**	
Unknown sp.	N	**O**	**O**	**O**	X
MOLLUSCA					
Polyplacophora					
Leptochiton sp.	?	**R**			
Gastropoda					
Patellogastropoda					
Unknown sp.	?	**R**			
Pyropeltidae					
Pyropelta sp.	?	**O**?	**O**?	**O**?	
Neogastropoda					
Buccinidae					
Neptunea amianta	N	**C**	**C**	**C**	
Columbellidae					
Amphissa bicolor	N	**O**?	**O**?	**O**?	
Mitrella permodesta	Y	**A**	**A**	**C**	
Bivalvia					
Solemyoida					
Solemyidae					
Solemya sp.	Y		**R**	**R**	X
Nuculoida					
Nuculanidae					
Nuculana sp.	N	**R**	**R**	**R**	
Yoldiidae	N	**R**	**R**	**R**	
Yoldia sp.	N	**C**	**C**	**C**	
Veneroida					
Vesicomyidae					
Calyptogena kilmeri	Y	**R**	**A**	**A**	
Calyptogena pacifica	Y	**A**	**O**	**O**	
Calyptogena packardana sp. nov.	Y	**A**	**R**	**R**	
Calyptogena c.f. phaseoliformis	Y				X

(*continued*)

Table 2. (Continued)

Organism	Obligate?	Mt Crushmore	Clam Field	Clam Flats	Fan Valley
MOLLUSCA (*continued*)					
Vesicomya gigas	Y		R	R	
Vesicomya stearnsii	Y	R	O	O	
Unknown sp. (Fan Valley)	Y				X
ANNELIDA					
Polychaeta					
Ampharetidae					
Eclysippe sp.	N		A		
Ampharetidae genus 1	N			R	
Amphinomidae					
Chloeia sp.	N	R			
Capitellidae					
Capitella capitata	N	R			
Flabelligeridae					
Brada sp.	N	A	R	C	
Pherusa sp.	N	C			
Nereididae					
Nereis sp. 1	N		A	R	
Nereis sp. 2	N	R		R	
Polynoidae					
Lepidonotus sp.	N	R		R	
Terebellidae					
Amphitritnae sp.	N	R		R	
Trichobranchidae					
Terebellides sp.	N	R			
POGONOPHORA					
Thecanephria					
Polybrachiidae					
Polybrachia sp.	Y				X
VESTIMENTIFERA					
Basibranchia					
Lamellibrachiida					
Lamellibrachiidae					
Lamellibrachia barhami?	Y		R		
ARTHROPODA					
Crustacea-Malacostraca					
Decapoda					
Paguridae-unknown sp.	N	C	C	C	
Lithodidae					
Lithodes aequispina?	N	O	O	O	
Lithodes couesi?	N	O	O	O	
Majidae					
Chorilia longipes	N	C	C	C	
Chionoecetes bairdi	N		O		

(*continued*)

Table 2. (Continued)

Organism	Obligate?	Mt Crushmore	Clam Field	Clam Flats	Fan Valley
ARTHROPODA (*continued*)					
Galatheidae					
Munidopsis sp.	Y?	c			
Munida quadrispina	N	**C**	**C**	**O**	X
BRACHIOPODA					
Articulata					
Terebratulida					
Terebratulidae					
Terebratulina sp.	N	**O**			
Laqueidae					
Laqueus californianus californica	N	**C**			
L.c. vancouveriensis	N	**C**			
Inarticulata					
Glottidia albida?	N			**R**	
ECHINODERMATA					
Crinoidea					
Comatulida					
Antidonidae					
Florometra? sp.	N	**R**			X
Asteroidea					
Paxillosida					
Astropectinidae					
Thrissacanthias penicillatus	N	**X**	**X**		
Notomyotida					
Goniasteridae					
Hippasteria californica	N	**X**	**X**	**X**	
Spinulosida					
Solasteridae					
Solaster borealis	N	**X**	**X**	**X**	
Pterasteridae					
Pteraster jordani?	N	**X**	**X**	**X**	
Forcipulatida					
Zorasteridae					
Zoraster sp.	N	**O**	**O**		
Asteriidae					
Rathbunaster californicus	N	**R**			
Brisingida					
Brisingidae					
Brisingella? Sp.	N	X	X		
Unknown sp.	N	O	O	O	
Ophiuroidea					
Unknown sp.	N	O	**R**	**R**	
Phrynophiurida					
Asteronychidae					
Asteronyx loveni	N	**O**	**O**		

(*continued*)

Table 2. (*Continued*)

Organism	Obligate?	Mt Crushmore	Clam Field	Clam Flats	Fan Valley
ECHINODERMATA (*continued*)					
Echinoidea					
Echinoida					
Strongylocentrotidae					
Allocentrotus fragilus	N	R			
Spatangoida					
Schizasteridae					
Brisaster latifrons	N	O	O		
Holothuroidea					
Dendrochirotida					
Psolidae					
Psolus sp.	N	C	O		
Elasipodida					
Laetmogonidae					
Pannychia moseleyi	N	R			
CHORDATA					
Agnatha					
Myxinidae					
Eptatretus sp.	N	C	C	O	
Chondrichthys					
Squaliformes					
Scyliorhinidae					
Apristurus brunneus	N	R	R		
Osteichthyes					
Gadiformes					
Macrouridae					
Coryphaenoides acrolepis	N	O	O	O	
Nezumia stegidolepis?	N	R	R	R	
Zoarcidae					
Aprodon cortezianus	N	O	O	O	
Perciformes					
Scorpaenidae					
Sebastolobus alaskanus	N	C	C	C	
Sebastolobus altivelis	N	C	C	C	
Pleuronectiformes					
Pleuronectidae					
Embassichthys bathybius	N	O	O	O	
Microstomus pacificus	N	C	C	C	

patellacean limpets (*Pyropelta* sp.), chitons (*Leptochiton* sp.), galatheid crabs (*Munidopsis* sp.), and polychaete worms (Table 2). *Solemya* sp. clams were rare, and perhaps under-represented owing to their deeper position in the sediment (Reid, 1980; Fisher, 1990). Columbellid gastropods were patchy in abundance, but common on exposed clam shells and smooth rock surfaces covered with grayish white deposits (Figs 3c and 4d). Pyropeltid limpets occurred occasionally on shells of columbellid gastropods. *Leptochiton* sp. chitons were rare, and generally occurred on bacteria covered rocks. Several species of polychaete worms were collected from core samples of cold seep sediment. An unknown species of galatheid crab (*Munidopsis* sp.) was found only in association with mats of *Beggiatoa*, upon which they appeared to graze, and often were covered with bacterial filaments (Fig. 3d).

Numerous regional species inhabited Mt Crushmore seeps (Table 2). Gastropod molluscs, especially *Neptunea amianta*, scavenge and perhaps prey on vesicomyid clams, but were also common in nearby non-seep habitats. Fishes, especially dover sole (*Microstomus pacificus*), hagfish (*Eptatretus* sp.), thornyheads (*Sebastolobus alaskanus*), and deep-sea sole (*Embassichthys bathybius*) were commonly at seeps, but were not observed to prey on seep-associated organisms. Lithodid crabs (*Lithodes aequispina*) and tanner crabs (*Chionoecetes bairdi*) were observed occasionally at seeps, and can prey on vesicomyid clams. Small majid crabs (*Chorilia longipes*) frequently "tend" vesicomyid clams, and may graze on bacterial filaments or clam siphons.

Fluid seepage at Mt Crushmore may result from artesian-flow in the Purisima Formation. The Purisima Formation is inclined seaward in northern Monterey Bay and outcrops along the northern walls of Monterey Canyon (Greene, 1977). Greene *et al.* (1991) proposed that sulfide-rich fluids seeping from the canyon walls derive from fresh water percolating into the Purisima Formation in the Santa Cruz Mountains. Owing to down-dip towards the southwest, fluids may percolate through permeable Purisima Formation strata and exit at Mt Crushmore, some 1000 m lower in elevation. Vertical fracturing and faulting near seep locations appears to intercept and consolidate fluid flow to the canyon wall.

Clam Field cold seep site

The Clam Field site is located ~6 km south of Mt Crushmore in the Monterey Formation (Table 1; Fig. 1). Shells of *Calyptogena kilmeri* dredged nearby in the 1980s (J. Nybakken, unpublished) suggested the presence of cold seeps, and prompted exploration of this area (Fig. 5). The Clam Field site is restricted to the western wall (inclined from west to east about 15°+) of the Monterey Canyon along a swath approximately 500–1000 m wide, between 875 and 920 m depth. The Monterey Formation, a highly fractured, hydrocarbon-bearing shale that underlies the Purisima Formation in Monterey Bay (Greene, 1977), is exposed locally from ~760 m to greater than 1000 m. The central Clam Field site is a long, narrow (*ca* 2 m wide by 150 m long) band of small seeps located at the base and slightly downslope (~1–3 m) of a small (~1 m high) cliff, parallel to exposed bedding in the area. Debris-apron sediment near Clam Field seeps is principally fine black mud, mixed with gravel and scree from the cliff upslope.

Dense aggregations of vesicomyid clams (primarily *Calyptogena kilmeri*) in patches approximately 0.1–3 m across were found throughout this band, and abundant shell debris littered the sea floor to about 30 m below the main seep area (Fig. 4a,b). Scattered small seeps were also located along the strike of sedimentary bedding north of the Clam Field site, within the same depth range. Surficial sediment at the center of large seep patches was locally dark gray to black in color, suggesting very low oxygen and high sulfide levels.

Like the Mt Crushmore seeps, vesicomyid clams and bacterial mats were the dominant fauna at the Clam Field site (Table 2). Bacterial mats (*Beggiatoa* sp.) were common on clam shells and the sediment surface near aggregations of vesicomyid clams, but did not form the shroud-like cover characteristic of Mt Crushmore seeps. *Calyptogena kilmeri*, rather than *C. pacifica*, was the dominant vesicomyid clam at the Clam Field site. Solemyid clams (*Solemya* sp.) were observed occasionally, and may have been present in greater numbers below the sediment surface. A few individuals of vestimentiferan worms (*Lamellibrachia barhami*?; Fig. 4c) were also present at the Clam Field site. Columbellid gastropods were abundant on

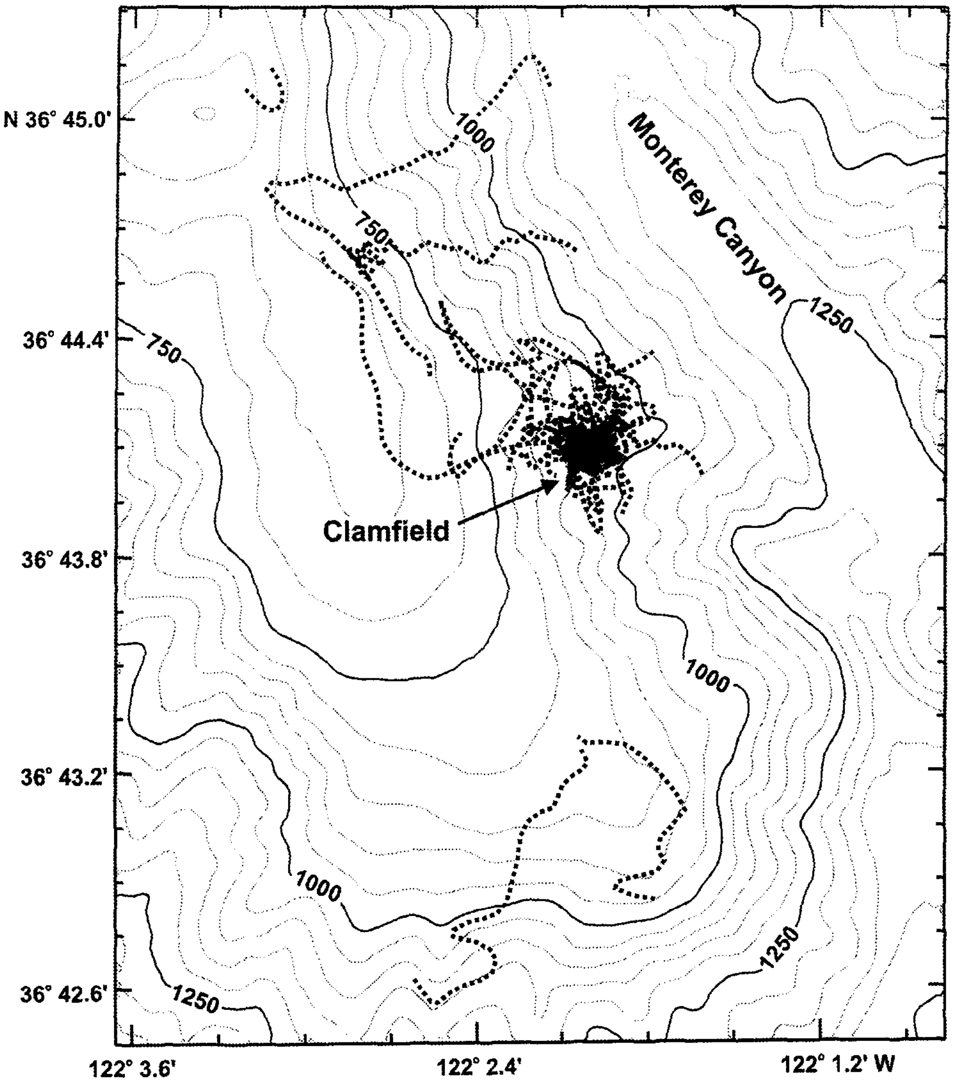

Fig. 5. Map of Clam Field Cold Seep site. Bathymetric contour interval is 50 m (gray). ROV tracks indicated by black dashed lines. Cold seep location shown by dark gray.

shells of *C. kilmeri*, on exposed rocks with bacterial or precipitate mats, and on black surficial sediments (Fig. 4a, c, d).

Sulfide levels were high at the Clam Field site and averaged 10.9 mM H_2S from 0 to 10 cm depth within clam aggregations (Table 1). Methane levels were also high and paralleled sulfide concentrations, with average concentrations within clam aggregations of 10.6 μM CH_4. Even though reduced inorganic compounds were concentrated in pore waters, fluid expression at the surface was not visually evident. The presence of a vestimentiferan worm on a rock ~5 cm above the sediment surface (Fig. 4c) suggests, however, that sulfide levels were sufficiently high to support chemosynthesis above the sediment surface, although sulfide may also flow through the rock.

Stable carbon isotopes ($\delta^{13}C$) from tissues of *Calyptogena kilmeri* from the Clam Field site ranged from −38.9‰ to −35.6‰ ($n=3$), indicative of thiotrophic bacterial production. In contrast, isotopic ratios for non-obligate benthic megafauna (*Anthomastus ritteri, Neptunea amianta, Rathbunaster californicus, Asteronyx loveni, Allocentrotus fragilus, Psolus* sp.) collected at non-seep locations in Monterey Canyon represented photosynthetic sources and varied from −19.1‰ to −12.7‰. The low $\delta^{13}C$ of clam tissues are similar to *C. phaseoliformis* c.f. from 3000 to 3600 m in the Ascension Fan-Valley (Rau *et al.*, 1990). Further studies will evaluate differences in isotopic ratios among seep sites and indicate the relative importance of seep-derived production to non-obligate megafauna at seep sites and near-seep localities.

The source of fluid flow at the Clam Field site is unclear. Like the Purisima Formation, the Monterey Formation outcrops in the Santa Cruz Mountains and is infiltrated by rain water. Greene *et al.* (1993) speculated that ground water flow through the Monterey Formation may accumulate sulfides via hydrocarbon degradation. As in the Purisima Formation, flow in the Monterey Formation is channeled along faults to the wall of Monterey Canyon. High levels of sulfide and methane at Clam Field seeps support the hypothesis that aquifer-driven flow percolates through this organic-rich deposit. Alternatively, fluid flow may be driven from below, via tectonic compression, as suggested by sparse carbonate deposits in this area.

Clam Flat site

Cold seeps communities were observed between 980 and 1010 m depth on the continental slope west of Monterey Bay (Table 1; Figs 1 and 6). High reflectance was first observed in side-scan acoustic imagery from the Smooth Ridge (Reed *et al.*, 1992) near the "Clam Flat" cold seep site. Interpretation of side scan sonographs indicated circular structures on the sea floor (mud volcanoes?) potentially associated with compression-driven seepage of sulfide and methane-rich fluids, as postulated by Greene *et al.* (1993). Tectonic compression in this region may result from oblique convergence of the Pacific and North American plates, leading to "squeezing" of near-surface sediment and outflow of CO_2-saturated interstitial fluid (Greene *et al.*, 1993; Orange *et al.*, 1993). Fluid expulsion in this area promotes surficial carbonate deposition and release of sulfide and methane-rich fluids at the sediment–water interface (Kulm and Suess, 1990).

Although the hydrology of the Clam Flat site differs from both the Mt Crushmore and Clam Field sites, the biota and pore water chemistry of Clam Flat were similar to the Clam Field site. Five to 10 small (0.25–10 m^2) aggregations of clams and other cold seep fauna were found in cold seeps at Clam Flat (Fig. 4e). Aggregations of hundreds to thousands of live clams were located along the lower edges of small (~1 m) scarps, and in small shallow depressions suggestive of methane "blowouts". Shells of dead clams were common near aggregations. Recruitment of juvenile clams was evident from aggregations of hundreds of juvenile *C. kilmeri* at some seep patches. Bacterial mats at the Clam Flat site were common, but less densely developed than at the Mt Crushmore site. Sulfide concentrations from within clam aggregations were similar in magnitude to the Clam Field Site (Table 1). Methane levels were also high ($[CH_4]=310.7$ μM; s.d. $=75.0$) in the center of clam aggregations.

Megafauna at the Clam Flat site were similar to the Clam Field and Mt Crushmore sites, though with slightly fewer species (Table 2). Vesicomyid clams (principally *Calyptogena* *kilmeri*) were the dominant obligate taxa, and accounted for the greatest abundance and biomass. Burrow trails of vesicomyid clams were present, but rare. Regional fauna were similar in abundance and species composition to the Mt Crushmore and Clam Field sites. Gastropods (e.g. *Neptunea amianta*) were abundant, as were the bivalves *Yoldia* and *Nuculana* sp., which may be more abundant than in nearby non-seep habitats.

The high acoustic reflectivity characterizing the Clam Flat region results from the abundant authigenic carbonate and biogenic carbonate (clam shells) at cold seeps. The presence of seep-associated biota and methane-induced pockmarks indicates that fluids move *through* this feature. Moreover, occurrence of seep-associated communities at the base of small scarps suggests a causative link between mud diapirism and fluid flow. The region separating an upthrust section from its surrounding material is usually a locus of shear strain (Brown and Orange, 1993); shear reorients the rock fabric along margins of the upthrust region and provides anisotropic permeability and a preferential conduit for expulsion of over-pressured fluids from depth.

DISCUSSION

Composition and biology of faunal communities

Vesicomyid clams were the principal taxa of all seep sites in Monterey Bay, whereas solemyid clams and vestimentiferan worms were rare, and mytilid mussels were conspicuously absent. This pattern of seep community composition is common throughout the Pacific Basin. Vesicomyids were the most abundant group at seeps found in northern California (Kulm *et al.*, 1986a) and along the axis of the Monterey-Ascension Fan Valley (Embley *et al.*, 1990), where pogonophorans also occurred in lower abundances. Similarly, vesicomyids were the principal taxon at seeps off Japan (Juniper and Sibuet, 1987; Sibuet *et al.*, 1988; Hashimoto *et al.*, 1989) and Peru (Kulm *et al.*, (1986b) and Olu *et al.*, (1994)). Other taxa were common at these seeps, but generally of secondary importance, including mat-forming thiotrophic bacteria (*Beggiatoa* sp.), vestimentiferan worms, galatheid crabs (*Munida* sp., *Munidopsis* sp.), and serpulid polychaetes (non-chemosynthetic serpulids were abundant at Peruvian seeps; Fiala-Médioni, personal communication, 1994). Given the relatively close proximity of hydrothermal vents, warm seeps, and cold seeps near Japan, which may all supply larvae to the region, the fairly restricted taxonomic composition of Japanese cold seeps is somewhat surprizing, and supports the hypothesis of strict geochemical control over vent and seep community structure.

Chemosynthetic production by seep and vent fauna throughout the Pacific is based largely on thiotrophic endosymbiotic bacteria, including all vesicomyids and mytilids studied (Fiala-Médioni *et al.*, 1994), solemyids, lucinids, thyasirids, and vestimentiferans (Fisher, 1990). Isotopic carbon ratios of tissue from *Calyptogena kilmeri* from the Clam Field site were near −36‰, within the range reported for thiotrophic species, and suggestive of sulfur-based chemosynthesis for vesicomyids in Monterey Bay. Although vesicomyid clams have been found at seeps where H_2S was not detected, and were once proposed to rely on methanotrophic bacterial symbionts (Kulm *et al.*, 1986a), subsequent studies indicate sulfur-oxidation is the only chemosynthetic trophic pathway utilized by this group (Fisher, 1990; Fiala-Médioni *et al.*, 1994).

Factors responsible for the dominance of cold seeps by vesicomyid clams (e.g. fluid

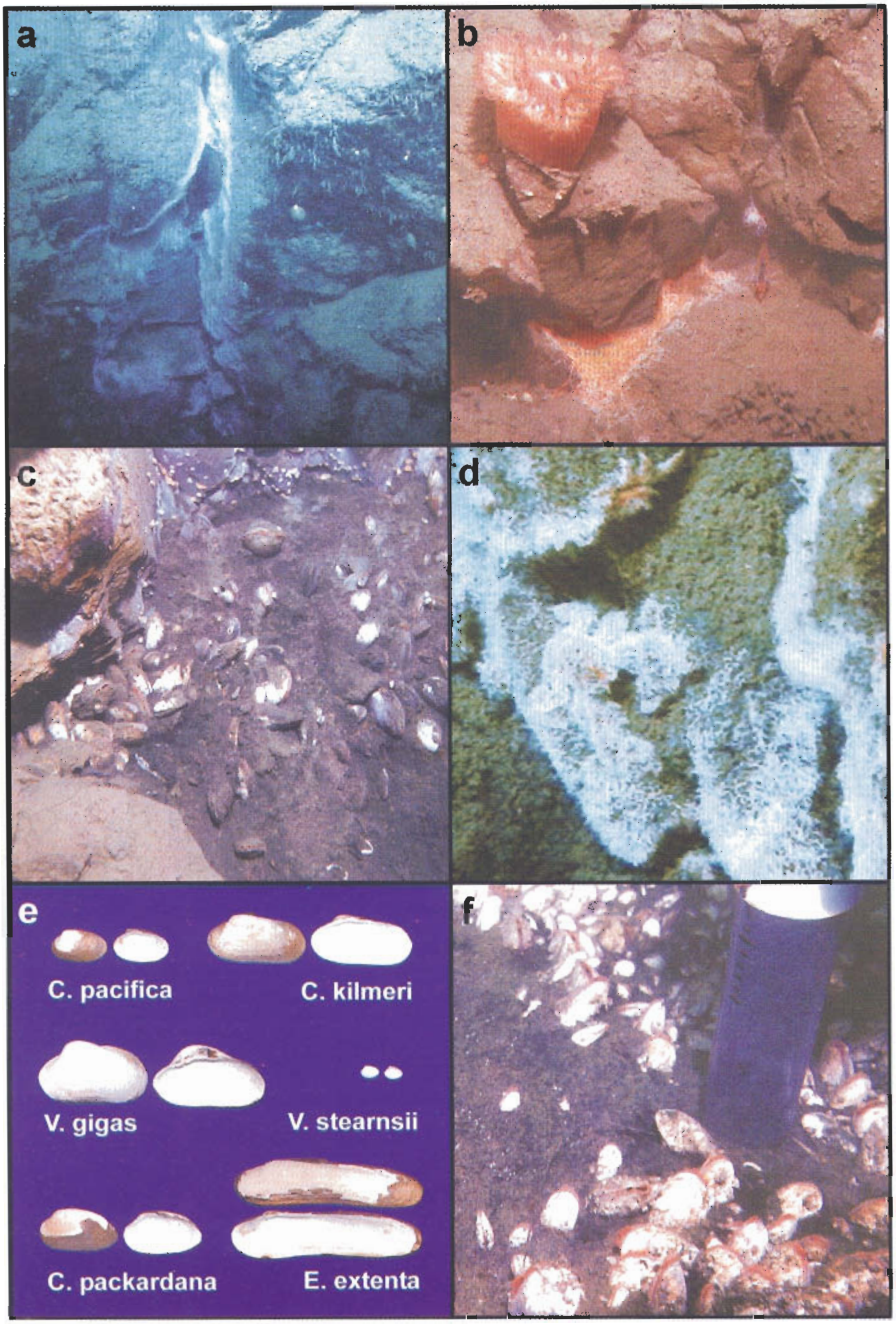

Fig. 3. Digital scanned photographs or video images from the Mt Crushmore Cold Seep. (a) Vertically dipping strata lined with *Beggiatoa* sp. bacterial mats. (b) Orange free-living bacterial mats. (c) Aggregation of vesicomyid clams (principally *Calyptogena pacifica*). (d) Obligate galatheid crab (*Munidopsis* sp.). (e) Vesicomyid clams of Monterey Bay. Scale is identical for all species, total length of *C. phaseoliformis* is 175 mm. (f) Sediment core penetrating margin of clam aggregation. Core tube diameter is 9.0 cm.

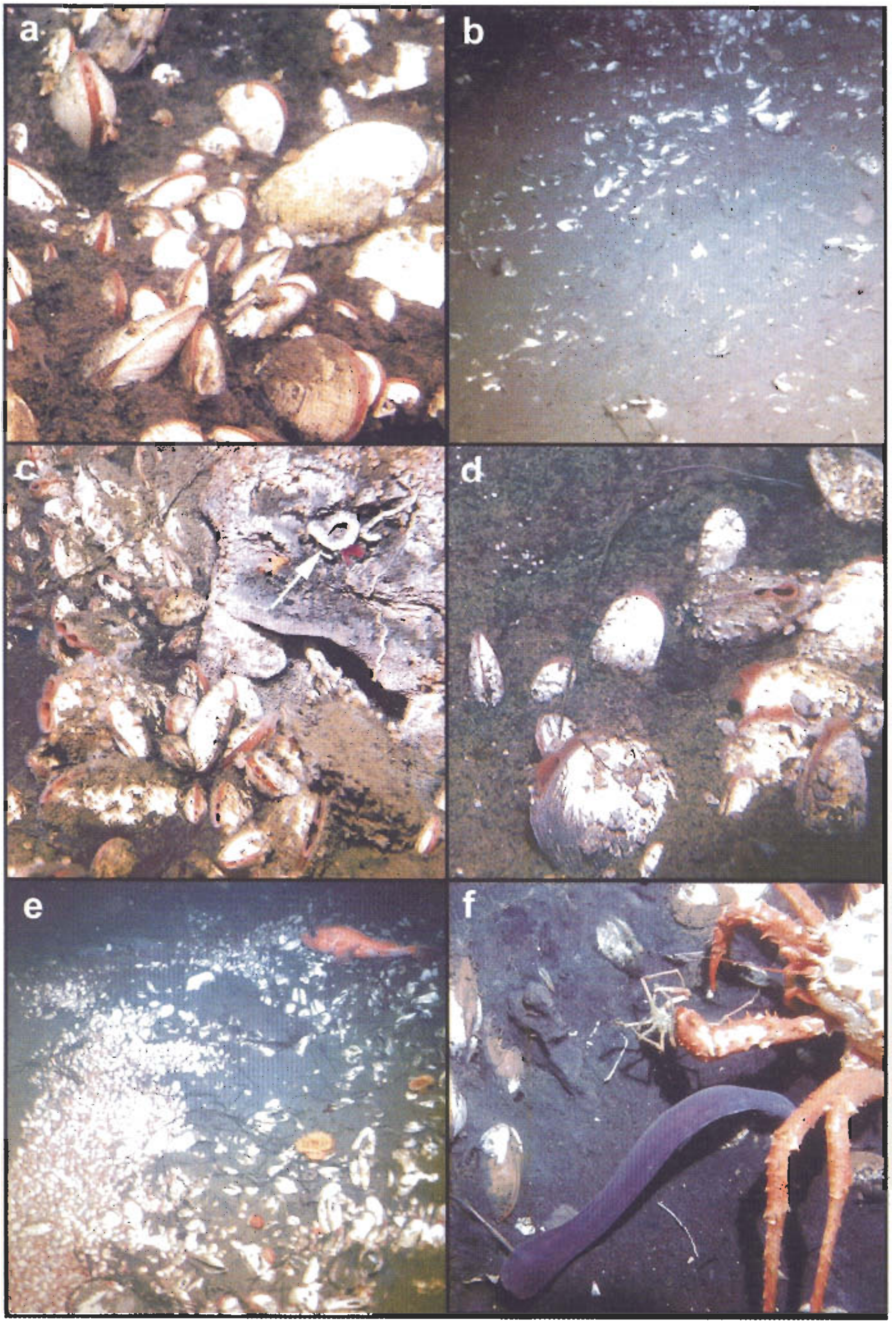

Fig. 4. Digital scanned photographic images of fauna from the Clam Field Cold Seep. (a) Aggregation of vesicomyid clams (mainly *Calyptogena kilmeri*). (b) Shell debris (*C. kilmeri*) slightly downslope of active seep patches. (c) Vestimentiferan worm (*Lamellibrachia barhami*?: indicated by arrow) on rock covered with bacteria or authigenic precipitates, adjacent to aggregation of *C. kilmeri*. (d) Columbellid gastropods (mainly *Mitrella permodesta*) on *C. kilmeri*. (e) Typical small seep at Clam Flat. Note the dense group of juvenile *C. kilmeri* on the left, and abrupt boundary of aggregation at left. Actinostolid anemones visible in middle, and *Sebastolobus* sp. in background. (f) Hagfish (*Eptatretus* sp.) and lithodid crab (*Lithodes aequispina*?) at Clam Field seep. *Paralithodes* is holding smaller crab (*Chorilia*? sp.) in chelipeds.

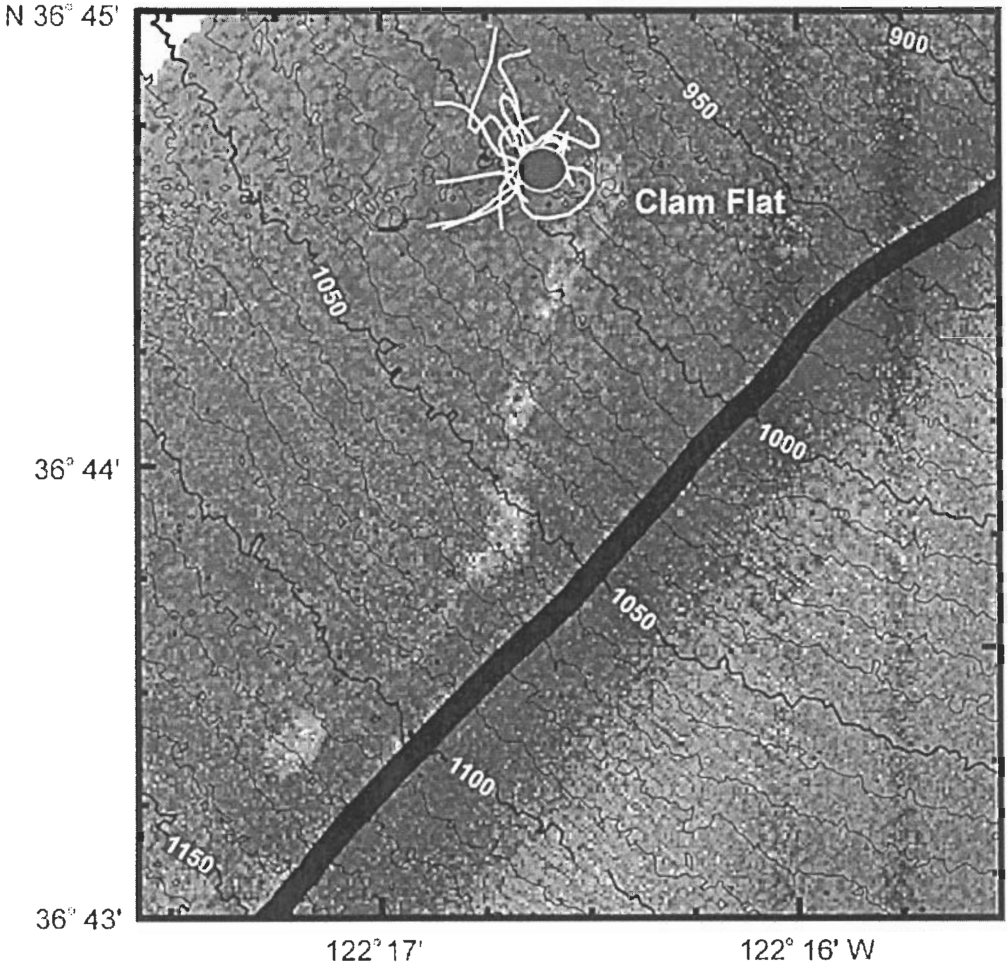

Fig. 6. Bathymetry (black lines) and ROV tracks (white lines) overlaid on side scan imagery of Clam Flat region. Thick black line indicates path of side scan survey track. Note light colored areas representing bottom relief, located near and below Clam Flat site.

chemistry, larval supply, biological interactions) are little known. Vesicomyids may have greater tolerance for seep environments than other seep taxa, owing to spatial segregation of gas exchange (Fisher, 1990), and potentially lower requirements for sulfide (e.g. some vesicomyids live in anaerobic, non-seep habitats; Childress *et al.*, 1993), which would allow these bivalves to exploit low sulfide seeps and peripheral areas of high sulfide seeps. Sulfide values from 0.1 to 11 mM H_2S were typical within aggregations of vesicomyid clams in Monterey Bay, close to values reported from other cold seeps with vesicomyid clams or mytilid mussels (MacDonald *et al.*, 1990a; Masuzawa *et al.*, 1992).

The scant data available suggest that vestimentiferans and thiotrophic mussels require higher sulfide levels than vesicomyids. Although vestimentiferans were rare at Monterey Bay seeps, they are common at seeps off Japan (e.g. Hashimoto *et al.*, 1987, 1989), perhaps related to higher sulfide fluxes, greater larval abundance, or both. Although all gas exchange (including sulfide) is thought to occur at the obturacular plume of vestimentiferans from hydrothermal vents (i.e. *Riftia* sp.), genera from cold seeps (e.g. *Lamellibrachia* and *Escarpia*), may segregate gas exchange partially, by absorbing sulfide through their tubes beneath the sediment surface, and oxygen and carbon dioxide at the obturacular plume (Fisher, 1990). Thus, as postulated for vesicomyids, sulfide uptake is shifted beneath the redox boundary, where stable sulfide levels may persist, regardless of fluctuations in seepage rates. Nevertheless, seeps in Monterey Bay appear to have very low seepage rates (D. Orange *et al.*, unpublished data), and may generally be marginally sufficient or inadequate to support vestimentiferans. The rarity or absence of solemyids, lucinids, and thyasirids at Monterey Bay seeps is surprizing, considering their abundance in anoxic sediments in non-seep habitats where sulfide fluxes may be low. However, these groups may be under-represented owing to their position beneath the sediment surface.

Although the megafauna of cold seeps exhibit high taxonomic similarity at a familial level throughout Monterey Bay and the Pacific Ocean basin, the distribution of individual species (i.e. vesicomyid clams) at seeps in Monterey Bay corresponded closely to patterns of sulfide and methane concentrations. Thiotrophic species are probably distributed with respect to species-specific ranges of sulfide concentrations owing both to energetic dependence on sulfide and sulfide tolerance, yet may also be influenced by methane or other parameters. *Calyptogena kilmeri* was most abundant at seeps with highest sulfide concentrations, and although *C. pacifica* occurred at these sites, it was less abundant and usually in peripheral positions where sulfide levels were lower (Barry *et al.*, in press, a). This pattern also indicates a lower requirement for sulfide by *C. pacifica*, relative to *C. kilmeri*, and is supported by blood serum binding affinities for sulfide by these species (Kochevar and Barry, 1993, 1994). Thus, small scale geochemical variation most likely regulates the distribution of seep species.

In contrast to sites in Monterey Bay with no methanotrophic species, seep communities in the Gulf of Mexico and along the Florida Escarpment are inhabited by methanotrophic mytilid mussels (in addition to phyla found in Monterey Bay), which are distributed in relation to environmental levels of sulfide, methane, ammonia, hydrocarbons, and high salinity brine (Paull *et al.*, 1984; MacDonald *et al.*, 1989, 1990a, 1990b, 1990c). Highest densities of methanotrophic mytilid mussels, which can be methanotrophic, thiotrophic, or both (Fisher, 1993), occurred where methane levels were elevated greatly (regardless of sulfide levels), especially where pore water salinities were hypersaline. Methane mussels were most common where methane gas bubbled from the bottom, around methane-rich saline pools on the sea floor (MacDonald *et al.*, 1990c), and at the base of highly saline seeps along the Florida Escarpment (Paull *et al.*, 1984). The association of methane mussels with high salinity brine is likely related to the stabilizing effect of brine on methane concentrations near the sea floor. High density brine released at the benthic boundary mixes with overlying waters much more slowly than normal salinity seawater, consequently elevating methane levels near mussel populations. Absence of methane mussels or other methanotrophic metazoans from the Pacific basin may be related to fundamental differences between methane and sulfide-based metabolism, and linked also to the absence or rarity of evaporite deposits from the Pacific, which are fundamental to brine production.

The role of biological interactions among seep and non-seep species in structuring cold seep communities is poorly understood. Lithodid and brachyuran crabs observed during ROV dives (Fig. 4f) rarely attacked vesicomyid clams but have been observed to prey on vesicomyids at other seeps (Hashimoto *et al.*, 1989). Tanner crabs (*Chionoecetes bairdi*) prey on vesicomyid clams in laboratory aquaria (J. P. Barry, personal observation), and may influence clam populations. Buccinid snails (*Neptunea amianta*) are abundant throughout the continental slope and scavenge vesicomyid clams at cold seeps in Monterey Bay. Holes drilled in vesicomyid shells provide further evidence of predation. Mortality of juvenile vesicomyids from predation by *Neptunea* is potentially important in regulating rates of recruitment for some clam populations and requires further study. Large *Octopus dolfleini* also occur in the vicinity of seeps, but have not been observed to prey on seep fauna. Columbellid gastropods are a common seep species, but appear to have little influence on their hosts (vesicomyid clams), other than a potential benefit from removal of bacterial films on shells. Several benthic fishes occur at seeps in Monterey Bay, however predation events or other impacts to clam populations or bacterial mats were not observed. Intertidal crabs (*Pachygrapsus crassipes*) and limpets (*Lottia limatula*) have also been reported to graze on chemosynthetic bacteria at intertidal hot springs (Trager and DeNiro, 1990), but clearly do not depend on bacteria.

Regional geology and cold seep distribution

Recent discoveries of cold seeps along continental margins in the eastern and western Pacific Ocean and the Gulf of Mexico support the notion that sulfide and methane-based communities are a common feature of continental borderlands, as predicted by Kulm *et al.* (1986a). Because individual seeps are small and chemosynthetic communities are rare, highly localized, and often found among bedrock exposures or outcrops, it is not surprizing that these communities have eluded discovery until recently. Recent exploration of rugged submarine terrain, which are relatively inaccessible to conventional gear, by submersibles and ROVs has led to the discovery of cold seeps and hydrothermal vents, in part by allowing access to geologically complex environments. Moreover, increased understanding of processes regulating fluid flow from benthic sediments (Moore *et al.*, 1990; Tobin *et al.*, 1993; Orange *et al.*, 1993, 1994) focuses benthic exploration surveys at appropriate sites, further enhancing the likelihood of cold seep discovery.

Within the Monterey Bay region, at least four lithologically distinct geologic settings provide conditions suitable for the establishment and persistence of chemosynthetic communities. Aquifer-related flow at heavily-faulted exposures in Monterey Canyon may be responsible for seep communities at the Mt Crushmore site in the porous Purisima Formation, and the Clam Field site in the hydrocarbon-laden Monterey Formation. Tectonic compression of hemipelagic sediments appears to account for methane and sulfide release at the Clam Flat site, and outgassing of relict organic debris deposits is hypothesized to support chemosynthetic communities in the canyon axis at the Monterey-Ascension Fan site (Embley *et al.*, 1990). In all cases, geologic conduits (i.e. faults) probably funnel fluids from depth to localized zones of expulsion at the surface. Highly permeable stratigraphic horizons (Purisima Formation; Mt Crushmore), mud extrusions or diatremes (Clam Flat), and fault zones with associated fracture permeability (Clam Field, Mt Crushmore), are all examples of such conduits.

The geologic complexity and tectonically dynamic nature of continental margins surrounding the Pacific Ocean basin favor cold seep formation in a variety of geologic settings including subduction zones, accretionary complexes, and transform faulted boundaries that produce mud volcanoes or diatremes, fault zones, channels and canyons, and submarine artesian springs. Along active tectonic boundaries, faults can intercept and focus fluid migration, enhancing the development and persistence of chemosynthetic communities. The often narrow continental shelves, steep slopes, and common occurrence of submarine canyons, faulted porous strata, or unconsolidated sediment promote localized upward or outward flow of sulfide and methane-rich pore waters, thereby supporting chemosynthetic communities.

Cold seeps are known from several Pacific sites with lithologies similar to seep sites in Monterey Bay. These include fluid flow in canyons or other erosional features of tectonically active regions, such as the Japan subduction zone (Sibuet *et al.*, 1988), and the Oregon accretionary complex (Moore *et al.*, 1990; McAdoo *et al.*, 1994; Orange *et al.*, 1994). Upward fluid migration owing to over-pressure of continental slope sediments via tectonic compression is associated with cold seeps along the Oregon subduction zone (Kulm *et al.*, 1986a; Moore *et al.*, 1990; Tobin *et al.*, 1993; Orange *et al.*, 1994), northern California (Kennicutt *et al.*, 1989), Japan subduction zone (Sibuet *et al.*, 1988; Juniper and Sibuet, 1987), Peru subduction zone (Olu *et al.*, 1994), and the Barbados accretionary prism (Le Pichon *et al.*, 1990). Fluid release from submarine exposures of freshwater aquifers, as suggested for the Mt Crushmore site, has been observed at several sites (Hovland and Judd, 1988), and may be common along active or passive continental margins.

In contrast, the physiography and relative stability of passive continental margins of the Atlantic Basin provides very different geochemical settings for cold seep communities. Highly saline and methane-rich brines may be a more common feature of seeps along passive or trailing plate continental borderlands, where evaporitic deposits commonly occur, than along active margins, particularly convergent subducting margins. Indeed, the tectonic configuration and history of ocean basins appear to have a fundamental and pervasive influence on the composition of seep communities, evident in comparisons among seep communities of the Pacific and the Gulf of Mexico. Evaporite deposits common along Atlantic continental margins are rare in the Pacific, and influence greatly the fluid chemistry of pore waters at cold seeps. If the high density of brine-based seeps plays an important role in enhancing habitat quality for methanotrophic seep species by inhibiting mixing of methane-rich brine with bottom waters, we expect few discoveries of methanotrophic metazoan communities in the Pacific Basin, where evaporites are rare. Although such differences may explain partially the divergent pattern of community structure between seeps in the Pacific and Atlantic Ocean basins, further research is necessary to quantify the influence of geochemical and geophysical controls, and biological interactions, on the organization of cold seeps communities.

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