



Biogeography, biodiversity and fluid dependence of deep-sea cold-seep communities at active and passive margins

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Abstract

To date, several cold-seep areas which fuel chemosynthesis-based benthic communities have been explored, mainly by deployment of manned submersibles. They are located in the Atlantic and in the Eastern and Western Pacific oceans and in the Mediterranean Sea, in depths ranging between 400 and 6000 m in different geological contexts in passive and active margins. Our study is based on a review of the existent literature on 24 deep cold seeps. The geographic distribution of seeps, the variations of origin and composition of fluids, and rates of fluid flow are presented as they are important factors which explain the spatial heterogeneity and the biomass of biological communities. Methane-rich fluid of thermogenic and/or biogenic origin is the principal source of energy for high-productive communities; however, production of sulphide by sulphate reduction in the sediment also has a major role. The dominant seep species are large bivalves belonging to the families Vesicomyidae or Mytilidae. Other symbiont-containing species occur belonging to Solemyidae, Thyasiridae, Lucinidae bivalves, Pogonophora worms, Cladorhizidae and Hymedesmiidae sponges. Most of the symbiont-containing cold-seep species are new to science. Different symbiont-containing species rely on sulphide or methane oxidation, or both, via chemoautotrophic endosymbiotic bacteria. A total of 211 species, from which 64 are symbiont-containing species, have been inventoried. Patterns in biodiversity and biogeography are proposed. A large majority of the species are endemic to a seep area and the symbiont-containing species are mainly endemic to the cold-seep ecosystem. A comparison of species found in other deep chemosynthesis-based ecosystems, hydrothermal vents, whale carcass and shipwreck reduced habitats, reveals from the existing data, that only 13 species, of which five are symbiont-containing species occur, at both seeps and hydrothermal vents. The species richness of cold-seep communities decreases with depth. High diversity compared to that on hydrothermal vent sites is found at several seeps. This may be explained by the duration of fluid flow, the sediment substrate which may favour long-term conditions with accumulation of sulphide and the evolution of cold seeps. © 1998 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Whereas the deep sea is generally characterised by low population densities, low biomass and high species diversity (Hessler and Sanders, 1967; Grassle and Maciolek, 1992), the luxuriant clusters of chemosynthetic organisms first discovered at the Galapagos Rift hydrothermal vents (Lonsdale, 1977) are in contrast, very high in biomass and relatively low in diversity with highly adapted, mainly novel megafaunal species (Hessler and Smithey, 1983; Tunnicliffe, 1991). Hydrothermal vents are supported by high levels of *in situ* chemosynthesis and considered as oases (Laubier, 1989) separated from the surrounding environment often (but wrongly) considered to be a desert. The last decade has led to the investigation of productive ecosystems at cold seeps, which host highly diverse and abundant chemosymbiotic biota (Carney, 1994).

Since the discoveries of cold-seep organisms on a passive margin (Paull et al., 1984), several other cold seeps localised on passive and active margins in the Pacific and Atlantic oceans have been visited by deployment of the manned submersibles *Alvin*, *Nautil*, *Shinkai* and *Johnson–Sea–Link*. Exploration of different geological settings reveals several forms of seafloor seepage of reduced chemical substances that fuel chemosynthesis-based benthic communities. On passive margins, whereas the dense populations of large epifaunal organisms at the base of the Florida escarpment in the Gulf of Mexico are associated with hypersaline, cold sulphide seeps (Paull et al., 1984), the chemosynthetic mussels discovered one year later on the Louisiana slope in the Gulf of Mexico are associated with hydrocarbon seeps (Kennicutt et al., 1985). On active margins, following the discovery of bivalves and tube worms on the sedimentary accretionary complex at the Oregon continental margin (Suess et al., 1985), the exploration of other subduction zones, in the Japan Trench region (Laubier et al., 1986; Juniper and Sibuet, 1987; Sibuet et al., 1988; Ohta, 1990), on the Barbados prism at 1000–2000 m (Faugères et al., 1987; Jollivet et al., 1990; Olu et al., 1996b) and at 5000 m depths Le Pichon et al., 1990; Olu et al., 1997) in the Peru Trench (Fiala-Médioni et al., 1992; Olu et al., 1996a) in the Aleutian trench (Suess et al., 1998) and in the Eastern Mediterranean (Corcelli and Basso, 1996) revealed the existence of rich cold-seep communities down to a depth of 6000 m. Biological descriptions of seep communities have been based primarily upon underwater photographs, video recordings and faunal sampling obtained from submersible. They have provided information on species composition, abundance, and spatial distribution of cold-seep communities. Progressively, knowledge has been acquired on the geological contexts which control the expulsion of nutritive fluids, on the faunal distribution and the evidence for direct utilisation of reducing substances by typical species, either via symbiosis or indirect utilisation through an increase in food availability to classical or non vent abyssal species. Given the wide distribution and the high productivity of cold-seep ecosystems, their specificity and role in the deep sea are certainly not negligible and it is worth evaluating their main features. As already suggested by Aharon (1994) and Tunnicliffe et al. (1996), the domain of cold seeps has received considerably less attention compared to the investigations of the deep-sea hydrothermal vents; however, the diversity is generally considered to be greater in cold seeps than in hydrothermal vents, and the interactions between geological and biological systems are more

complex at low than at high temperature. Most of the megafauna living around cold seeps are generally considered closely related to those from hydrothermal vent communities in being dominated by a small number of megafaunal invertebrate species, and in high densities and biomass produced via chemosynthetic bacterial activity. However, cold-seep communities are mainly associated with sediment substrates and with fluids rich in methane of either thermogenic or biogenic origin (Kulm et al., 1986a, 1986b; Boulègue et al., 1987a; Gamo et al., 1988; Blanc et al., 1988; Bagley, 1994). The aim of this paper is a first review of the geographic distribution of seeps along margins, to analyse the main fluid characteristics and their variations, and to describe the geological and taxonomic diversity of cold seeps. From the existing scientific literature, we will analyse the trophic behaviour and fluid dependence of the major faunal component of cold-seep ecosystems, establish the species composition at each cold seep in order to identify patterns in biodiversity and biogeography and to compare the species composition of cold seeps with hydrothermal vents and with other chemosynthetic based ecosystems such as found near whale carcasses and a shipwreck.

2. Geographic and bathymetric distributions and geological setting of chemosynthetic communities along margins

Seep communities have been observed in twenty-four deep-sea areas located in the Atlantic, the Eastern and Western Pacific, and the Mediterranean Sea, on both passive and active margins at depths ranging between 400 and 6000 m (Fig. 1 and Table 1). Seeps are related to geological processes such as tectonically induced high-fluid pressures, petroleum or natural gas escape, artesian flow or catastrophic erosion and slides. The characteristic seep megafauna often serve as indicators of the location of methane or sulphide rich environments. The distribution of seep fauna has also been used, when possible, in parallel with geological observations to identify tectonic and sedimentologic features, and conduits of fluid, as well as to analyse fluid expulsion patterns.

2.1. Passive margins

The northern Gulf of Mexico continental margin is a rich oil and gas province (Brooks et al., 1986). Several cold-seep communities have been described between 88° and 95°W from 400 to 2200 m in depth. Chemosynthesis-based communities have been documented in three general regions, the upper continental slope (400–1000 m, off Louisiana), the Alaminos Canyon site on the lower continental slope (2200 m, off Louisiana) and the West Florida Escarpment site (3500 m) (Carney, 1994). Detailed biological descriptions of mytilids and pogonophoran tube worms exist principally for three sites on the upper continental slope off Louisiana: “Bush Hill” at 540 m depth (MacDonald et al., 1988, 1989), “Mussel Beach” at 630 m (MacDonald et al., 1990a) and Brine Pool NR1 at 650 m (MacDonald et al., 1990b). Very recently, polychaete worms (Hesionidae) have been discovered living in great densities on an unusual cold-seep habitat, the surface of exposed gas clathrates (methane hydrates) for which the

Table 1
List of the cold seep sites and references of geological and biological studies used in Table 2

Abbreviated name of the sites	Location of the sites	Depth (m)	References (numbers in brackets before references indicate studies on new species)
Bar. -N	Barbados prism (13–49°N)	4700–5000	(1) Bellan-Santini (1990); Le Pichon et al. (1990); (2) Vacelet et al. (1995, 1996); Olu et al. (1997)
Bar. -S	Barbados prism (10–11°N)	1000–2000	Faugères et al. (1987); Jollivet et al. (1990); (3) Kaas (1994); (4) Macpherson (1994); Olu et al. (1996b); (5) Bellan-Santini (1997); (6) von Cosel and Olu (in press); Sibuet (unpublished data on echinoderms); (7) Williams (1988); Carney (1994)
Lou-l	Gulf of Mexico, Louisiana lower continental slope (Alaminos canyon)	2200	
Lou-u	Gulf of Mexico, Louisiana continental slope	400 1000	Kennicutt et al. (1985); (8) Turner (1985); Brooks et al. (1987); (9) Erséus and Milligan (1989); MacDonald et al. (1989, 1990a, 1990b, 1990c); (10) McLean (1990); (11) Waren and Ponder (1991); (12) Waren and Bouchet (1993); Kaas (1993); (12b); Carney (1994); (13) Harrison et al. (1994); (14) Khol and Vokes (1994); Fisher, Carney, McDonald (pers. comm.)
Flo	Gulf of Mexico, Florida escarpment	3500	Pauli et al. (1984); (15) Turner and Lutz (1984); Hecker (1985); (16) Pettibone (1986); (17) Humes (1988); (18) Petrecca and Grassle (1987)
Car	North Carolina continental slope	2160	Pauli et al. (1995)
Lau	Laurentian fan	3800–3900	Mayer et al. (1988); Petrecca and Grassle (1987)
Gui	Gulf of Guinea	400–700	Boucher (pers. comm.)
Med	Eastern Mediterranean	1700 2000	Corselli and Basso (1996)
Ale	Aleutian trench	3200–5900	Suess et al. (1998)
Ore	Oregon prism	2000–2400	Suess et al. (1985)
Cal	North California continental shelf	450–600	Kennicutt et al. (1989)
Mon -b	Monterey bay	600–1000	Barry et al. (1996, 1997a); (19a) Barry et al. (1997b); (19b) Krilova and Moskalev (1996); (19c) Vrijenhoek (1994).
Mon-v	Monterey Fan Valley	3000–3600	Embley et al. (1990); Barry et al. (1996).
Cle	San Clemente fault	1800	Lonsdale (1979)
Gua	Sonoran margin near Guaymas basin	1600	Simoneit et al. (1990)

Mex	Mid American trench (off Mexico)	2500–4000	Macpherson (pers. comm.); Métiévier and Von Cosel (pers. comm.); Olu (unpublished data); Southward (pers. comm.)
Cos	Mid-American trench, Costa Rica prism	3500	Kahn et al. (1994)
Per	Peru trench, North peruvian margin	2300–5100	Kulm et al. (1986b); (20) Delaye and Toda (1994); Olu et al. (1996a)
Chi Jap.	Chili trench, Central Chili margin Japan subduction zones (Japan and Kurile trenches)	1400 3800–6000	Stuardo and Valdovinos (1988) Laubier et al. (1986); (21) Métiévier et al. (1986); (22) d'Hondt and Mawatari (1987); Juniper and Sibuet (1987); Ohia and Laubier (1987); Sibuet et al. (1988); (23) Miura and Laubier (1989); Warén and Bouchet (1993)
Nan- t	Eastern Nankai trough, (Tenryu canyon)	3600–3850	(24) Okutani and Métiévier (1986); Juniper and Sibuet (1987); Ohia and Laubier (1987); Sibuet et al. (1988); (25) Horikoshi (1989); (1) Bellan-Santini (1990); (13) Warén and Bouchet (1993); (26) Kojima et al. (1995)
Nan -p Sag	Nankai prism Sagami bay	2000 m 900–1200 m	Sibuet et al. (1990); Lallemand et al. (1992) (27) Okutani and Egawa (1985); Ohia and Hashimoto (1986), Hashimoto et al. (1988, 1989); (28) Miura and Laubier (1990); Ohia (1990); (29) Okutani and Fujikura (1990) (30); Miura and Hashimoto (1991); (31) Okutani et al. (1992); (32) Okutani and Fujikura (1992); (33) Toda et al. (1992); (34) Okutani et al. (1993); (13) Warén and Bouchet (1993); (35) Hashimoto and Okutani (1994); (36) Fujikura et al. (1995); (37) Hashimoto et al. (1995).



Fig. 1. Location of cold seeps in the world ocean on passive and active margins. The abbreviated names are listed in Table 1.

dependence on fluids is not clear. (C. Fisher, I. McDonald and R. Carney, 1997, personal communication). Along the Louisiana slope, the fluids are assumed to originate from petroleum or natural gas seepage (Kennicutt et al., 1985; Rosman et al., 1987). Indeed, the northern Gulf of Mexico slope is extensively faulted and fractured by salt tectonics; oil and gas are therefore expelled along conduits created by tectonic salt fracturing along the margin, and by salt diapirism (Bouma and Roberts, 1990; Kennicutt and Brooks, 1990). Hydrocarbon seeps also sustain communities on the continental slope off central California between 450 and 650 m depth (Kennicutt et al., 1989). Dense biological communities, dominated by mussels, have been photographed in association with gas hydrates on the passive margin of North Carolina at 2170 m depth over the Blake ridge diapir (Paull et al., 1995). A recent exploration of the Gulf of Guinea continental shelf indicates the existence of hydrocarbon seeps between 400 and 700 m (Cochonat, 1996, personal communication) corroborate by the presence of Thyasiridae and Lucinidae bivalves shells photographed and collected by box cores (Olu, 1996; P. Bouchet, 1996, personal communication).

Fluids may also arise from sulphide-rich brine seeps, as described from the Florida escarpment at a depth of 3270 m, located at the juncture of the escarpment base and the abyssal sediment plain (Paull et al., 1984; Hecker, 1985). Finally, cold seeps found along the Laurentian fan at 3850 m may be linked to a turbidite slide assumed to have been triggered by an earthquake (Mayer et al., 1988).

Seepage of methane and hydrocarbons of thermogenic origin (from young diatomaceous muds) were also discovered along a transform fault zone on the Sonoran margin bounding Guaymas Basin (Simoneit et al., 1990). Seepage occurs through shallow pockmarks along the eroding crest of a steep anticline belonging to the transform fault zone and located 1600 m below sea level. The seepage zone supports dense communities of clams (*Calypptogena* cf. *pacifica*) and vestimentifera (*Lamellibrachia* sp.). The pockmarks have been colonised by chemosynthetic animals similar to those found at other low-temperature continental margins seeps although the most common vesicomyid clam is the same species that clusters around high-temperature hydrothermal vents on the basin floor. These cold seeps are located a few kilometres from a high-temperature sulphide-precipitating vent system.

2.2. Active margins

Chemosynthesis-based communities have been observed along active margins on well-developed accretionary prisms and also along erosive margins.

On accretionary prisms, communities are generally sustained by methane-rich fluids expelled by sediment compaction. Communities of tube worms and giant clams were described from the compressive margins off Oregon at 2040 m depth on a fault-bend anticline (Suess et al., 1985; Kulm et al., 1986a, 1986b). On the Nankai Accretionary Prism off Japan, communities dominated by vesicomyid clams of the *Calypptogena* genus have been described near 3800 m depth (Juniper and Sibuet, 1987; Ohta and Laubier, 1987; Sibuet et al., 1988; Henry et al., 1992). The eastern Nankai accretionary wedge supports seep vesicomyid species, and vestimentiferan tube worms have been observed at the top of a 2000 m deep ridge (Lallemand et al., 1992). Several cruises

have explored cold-seep communities, dominated by mussels of the *Bathymodiolus* genus and containing vesicomyids and several species of vestimentiferans, in the southern part of the Barbados accretionary prism between 10°N and 11°N at 1000 and 2000 m water depths (Jollivet et al., 1990; Olu et al., 1996b). This region presents a complex network of anticlinal ridges and faults associated with numerous mud diapirs which feed mud volcanoes rising 250 m above the sea floor (Faugères et al., 1987). In the northern area seaward of the Barbados prism, close to the Trench at 13°N and at about 5000 m depth, a seep field with many types of mud volcanoes, diatremes, diapirs and intermediate structures is located (Le Pichon et al., 1990; Henry et al., 1990). These structures are colonised by chemosynthesis-based communities (Olu et al., 1997) including vesicomyid clams associated with sulphur-oxidising bacteria (A. Fiala, 1996, personal communication) and cladorhizid sponges associated with methantrophic bacteria (Vacelet et al., 1995, 1996). Recently, in the Eastern Mediterranean, coring on the top of the Napoli Dome, a mud volcano located at 1900 m, showed the existence of vesicomyid and lucinid shells and, therefore, the existence of fluid emission (Corselli and Basso, 1996).

In Monterey Bay, central California, cold-seep communities were also found in an accretionary-like prism on the continental slope between 990 and 1050 m depth, where fluid flow may have originated from hemipelagic sediments, in a region where mud volcanoes appear to have been formed (Green et al., 1993). Recent fluid expulsion may have arisen from over-pressuring of sediments due to transgression or hydrocarbon formation at depth (Barry et al., 1996). In the Monterey and Ascension Fan Valley systems, which are located on a former active margin, at the base of the slope-break, fluids rise in a complex system of channelled valleys. They sustained chemosynthesis-based communities located over depths ranging from 3000 to 3600 m on channel floors or walls (Embley et al., 1990).

Fluid emission also occurs at convergent margins in the absence of well developed accretionary prism. In Sagami Bay, a large cold-seep community lies at about 1000 m depth (Hashimoto et al., 1989). In the Japan and Kurile Trench, fluid venting and associated clam communities occur along normal faults and large-scale slides (Cadet et al., 1987a, 1987b; Sibuet et al., 1988). Cold-seep communities dominated by vesicomyid clams and serpulid worms along the erosive margin off northern Peru have been described over a large bathymetric range and are also associated with a large debris slide (Fiala-Médioni, et al., 1992; Duperret et al., 1993; Olu et al., 1996a). Cold-seep communities dominated by Vesicomyidae, Solemyidae and Serpulidae have been also observed along scarps between 3000 and 4200 m depth in the Mid-American trenches off Mexico between 18° and 21°N (Michaud et al., 1996; Olu, 1996, and personal observations). In the Aleutian trench off Alaska, vesicomyid clams arranged in clusters and alignments, as well as solemyids, pogonophorans and buccinid gastropods allowed the visual detection of active vent sites at the base of steps or in depressions at the accretionary ridge between 4500 and 5000 m depth (Suess et al., 1998). Finally, the San Clemente fault zone, which was explored earlier than the Florida escarpment, was first considered a hydrothermal site (Lonsdale, 1979), but the geological context and faunal composition (the vestimentiferan *Lamelibrachia barhami* and clams) are more like cold seeps.

From the observed subduction areas it is now possible to indicate two major types of geological setting for cold seeps:

- (1) Compressional forces within accretionary prisms yield two different types of structures that allow the formation of chemosynthesis-based communities: diapiric structures like mud volcanoes (Barbados prism) and active thrust faults near the deformation front (Nankai prism).
- (2) Erosion, landslides yield habitats for typical chemosynthetic fauna on: (1) the head scars of large-scale debris slides probably linked to earthquake occurrences as on the Peru margin or on the Japan Trench, (2) along canyon walls where sediment piles have been removed by tectonic motions -and faults on seamounts entering subduction zones (Japan).

3. Composition and origin of fluids

Cold seeps are characterised by small temperature anomalies in the bottom waters. In general, no clear evidence for positive temperature anomalies in the bottom water have been reported. Similar anomalies have been observed near biological communities in the Nankai trough (0.1–0.45°C), (Boulègue et al., 1987b) and Oregon (0.35°C), (Kulm et al., 1986a) subduction zones. In the Aleutian subduction zone there is only a small positive anomaly (+0.010°C) (Suess et al., 1998). However, at the centre of some mud volcanoes of the Barbados, at a few tenths of meters from the vesicomid beds, the water–gas mixture is expelled through a convective mud lake at a constant temperature of 21°C (Henry et al., 1996).

Fluids are mainly characterised by high methane concentration and generally without sulphide. Sulphide is however present in the fluid at the Florida escarpment (Paull et al., 1984) and Monterey Bay seeps (Barry et al., 1997a). Vertical profiles of sulphide in pore waters along transects crossing seep communities indicated that sulphide levels were higher towards central seep locations and deeper in the sediment as shown in clam beds dominated by *Calyptogena kilmeri* and *C. pacifica* at Monterey Bay (Barry et al., 1997) and at cold seeps inhabited by *Calyptogena soyoeae* in Sagami bay (Hashimoto et al., 1995). The ability of clams to extend their foot several centimetres into the sediment provides access to sulphide as shown for *C. magnifica* (Arp et al., 1984). When sulphide, which is necessary for the thiotrophic species is not available in the expelled fluid, sulphide may be produced in sediments by sulphate reduction coupled with methane oxidation as shown at the Sagami Bay (Masuzawa et al., 1992) and at the Barbados mud volcanoes (Martin et al., 1996). Methane concentrations have been measured from water sample collected at active sites, near or just over clam colonies. At the Oregon site for example, CH₄ concentrations one meter above the seafloor (180–420 nll⁻¹) are three to six times greater than the CH₄ concentration found in the ambient sea water (Kulm et al., 1986a, 1986b). In the Monterey fan, the CH₄ concentration is one order of magnitude higher than normal (Embley et al., 1990). At the Hatsushima cold-seep in Sagami Bay, the bottom waters above the communities contained one order of magnitude higher CH₄ concentrations (360–4200 nll⁻¹) than those away from the communities (Gamo et al., 1988). At the

Gulf of Mexico, the highest concentration of methane (1.5 ml l^{-1}) were obtained in bubbling water near mussel beds (MacDonald et al., 1989). In pore fluids from mud volcanoes, even if methane concentrations can only be measured with limited precision because of the strong dependence of methane solubility on pressure and temperature, CH_4 concentrations are very high with approximately 22.4 ml l^{-1} (Martin et al., 1996). However, these authors have not indicated the distance of sediment sampling from biological communities found in the Barbados mud volcanoes and have not measured the methane in the water just above the bivalves. In the Monterey bay, methane concentrations measured in the pore water can reach 14 ml l^{-1} ; nevertheless, the chemolithoautotrophic vesicomyid clams relies on sulphide as methylotrophic metazoans are absent from seeps in Monterey Bay (Barry et al., 1997a). Because of large dilution of pore water by ambient sea water during sampling and because the sampling is seldom undertaken just near or beneath the biological communities, it is difficult to estimate the error in concentrations and to compare the composition and concentration of the fluids within and between sites. However, from qualitative informations on the composition of the fluids and from the geological context, the origin of the fluid can be more or less deduced: it is either biogenic, due to microbial organic matter decomposition in anoxic sediment layers, or thermogenic, where high temperature induces fast transformation of deep buried organic matter (references cited below).

On passive margins, the nature, the composition and the origin of fluids are various. In the Gulf of Mexico, seeps of biogenic and/or thermogenic origin occur in liquid (crude oil), gas and solid (hydrate) forms (Aharon, 1994). At the North California margin seeps, the chemical environment is characterised by the presence of gas hydrates and high concentrations of biogenic and thermogenic methane in near surface sediment and can be considered to be relatively similar to the Louisiana seeps (Kennicutt et al., 1989). At the Florida escarpment, hypersaline fluids rich in sulphides are seeping from the adjacent carbonate platform (Paull et al., 1984). At the North Carolina margin, methane and hydrogen sulphide are transported in a plume upward into the water column; methane is either of microbial origin in superficial sediment or coming from deeper gas hydrates charged sediment (Paull et al., 1995). At the Sonoran margin of Guaymas Basin, seepage of methane and heavier hydrocarbons occurs through shallow pockmarks. Based on the hydrocarbon composition, the methane which escapes from the Guaymas seeps is mainly thermogenic (Simoneit et al., 1990).

On active margins, methane rich fluids are due to the thermogenic or biogenic decomposition of organic matter. Both thermogenic or biogenic origins are proposed for the compressive margin off Oregon (Suess et al., 1985; Kulm et al., 1986a, 1986b), and for the Sagami Bay seeps (Gamo et al., 1988). A thermogenic origin of fluids coming from great depth is proposed for compressive contexts at Nankai Trough (Boulègue et al., 1987b) and at the Barbados prism (Le Pichon et al., 1990). Along the Peru convergent margin, vent fluids expelled by large scale slides could be directly issued, either from continental aquifers or from continental material removed by subduction erosion (Dia et al., 1993). Sulphide-rich fluids occur in the accretionary-like wedge at the Monterey region which was formerly an active margin. In the

deepest part of the canyon, the sulphide source is probably biogenic and seeps migrate along thrust faults from a deeply buried organic-rich source; in the shallower part, sulphide or both methane- and sulphide-rich (via hydrocarbon degradation) fluids are expelled either via tectonic compression or from an aquifer driven flow that percolates in some case through organic rich deposits (Green et al., 1993; Barry et al., 1996).

4. Fluid flow rates and biomass of cold-seep communities

The biological production at cold seeps can be related to the intensity of the fluid flow. This has been demonstrated by the relationship between the linear flow velocity, deduced from temperature gradients, and (1) species composition, densities and biomass of clam aggregates in the Nankai trough (Sibuet et al., 1990; Henry et al., 1992), (2) densities and species composition of mussel beds in the South Barbados volcanoes (Olu et al., 1996b), and (3) clam densities and biomass (reaching 30 kg m^{-2} in an exceptional large clam field of about 1000 m^2) in the Peru Trench (Olu et al., 1996a). Direct and indirect measurements of fluid flow have been realised on some active seep sites. From direct measurements with flowmeters, venting rates varied from 86 to $1765 \text{ l m}^{-2} \text{ d}^{-1}$ at the Cascadia margin off Oregon (Carson et al., 1990; Linke et al., 1994). At an active seep on the Peru slope, the fluid flow is in the same range ($441 \text{ l m}^{-2} \text{ d}^{-1}$) (Linke et al., 1994) as well as in the Aleutian zone, with a value of $240 \pm 200 \text{ l m}^{-2} \text{ d}^{-1}$ (Suess et al., 1998). Indirect measurements deduced from barium concentration variations (Suess et al., 1998) and temperature gradients on the most active sites of the northern Peruvian margin (Olu et al., 1996a) give similar flow rate estimates: the 'barium-flux' gives a flow rates of $970 \text{ l m}^{-2} \text{ d}^{-1}$; considering a total surface of fluid emission (= surface covered by clam communities) of 60 m^2 , the estimated 400 m year^{-1} linear flow velocity gives a flow rate of $1100 \text{ l m}^{-2} \text{ d}^{-1}$ (Olu, 1996).

Large variations of fluid flow rates within a single cold-seep area and between different sites have been observed (Henry et al., 1992). Spatial variation in the fluid supply is an important factor which explains the patchy distribution of cold-seep communities within a single locality. Most of the very high biomass reported in the Japan Trench (50 kg m^{-2}) (Ohta and Laubier, 1987) and at Sagami Bay ($16\text{--}51 \text{ kg m}^{-2}$) (Hashimoto et al., 1989) occurs on spatially restricted or discontinuous areas. Like hydrothermal vents (Hessler et al., 1985; Fustec et al., 1987), the patchy and ephemeral occurrence of chemosynthetic fauna can be attributed to spatial and temporal variations in the fluid supply (Juniper and Sibuet, 1987; Olu et al., 1996b, 1997). Patch size is generally less than 20 m^2 and frequently of about $0.5\text{--}2 \text{ m}^2$ which means that the fluid emission is restricted to simple conduits. However, some exceptions exist at Sagami Bay, the Gulf of Mexico and in one area called 'Paita' at the Peru trench, where clam beds which include patches of various size can reach $1000\text{--}6000 \text{ m}^2$. Consequently, the existence of such large and continuous fields are consistent with regular and diffuse expulsion (Olu et al., 1996a).

It remains difficult to relate biological production to flow rates together with the chemical composition of the fluids because the biological and geochemical analyses,

and measurement of fluid flow are seldom undertaken together for a single study site. In the future, there is a need for comprehensive studies to relate chemical concentration, fluid flow intensity and biological activity.

5. Faunal composition and geographic distribution

The biological descriptions from different cold-seep areas (Table 1) allow us to present a synthesis of the species found in cold-seeps, their geographic distribution, and their trophic behaviour. As some species benefit directly from fluids by endosymbiosis of chemoautotrophic bacteria, we will separate 'symbiont containing species' from 'non-symbiotic' deep-sea fauna associated with cold-seep communities (Table 2). Formal descriptions and identifications are not always available and many new species remain to be described. For some sites, community descriptions rely only on photographs which give limited information concerning the species composition. Twenty areas have been explored by submersibles, whereas the others are known only from sampling with geological corer or underwater photographs. Table 2 shows the data available in the literature for 24 areas, for the 'symbiont-containing' and 'non-symbiotic' fauna. A total of 211 species has been inventoried.

5.1. 'Symbiont-containing species' and fluid dependence

The more frequent species, largely dominant in terms of abundance and biomass, are large bivalves belonging to the families Vesicomidae and Mytilidae. But in some places, other known or assumed symbiont-containing species occur, for example species in other bivalve families (Solemyidae, Thyasiridae, Lucinidae), Pogonophora worms, and sponges. From the literature, we were able to list 64 known or assumed 'symbiont-containing' species (Table 2) and to analyse their distribution and fluid dependence according to environmental conditions. Several species are new to science or remain undescribed.

5.1.1. *Vesicomidae*

The Vesicomidae (genera *Vesicomya* and *Calyptogena*) have been observed on all cold-seep sites, except the North Carolina slope, which has been relatively less explored or less investigated for biological studies (Paull et al., 1995). At seeps, vesicomid clams live in soft sediment usually with the anterior part buried in mud. Species of the genus *Calyptogena* reach shell lengths of 20 cm. A total of 20 species of Vesicomidae (Table 2) have been identified including six new species, *Calyptogena* (*Ectenagena*) *phaseoliformis*, *C. (E) laubieri*, *C. (E) nautilei*, *C. (E) kaikoi* (all three species, from Japan cold-seeps), *C. (E) australis* (Chili Trench), *Calyptogena* (*Ectenagena*) *extenta* and *Calyptogena packardana* (both from Monterey cold-seeps). Moreover, *Calyptogena* sp. and *Vesicomya* sp. (Table 2) include several species (probably more than 10) new to science which remain to be described. However, these two genera are not well defined and need to be revised as they may consist of many cryptic species (Vrijenhoek et al., 1994).

The Vesicomysidae are extremely diverse. Several species of *Calyptogena* and species of *Vesicomys* can be present at a single site and even in a single aggregate. For example, in the Nankai prism (Sibuet, 1989, personal observation; Metivier, 1990, personal communication) and in Monterey Bay (Barry et al., 1996), up to five species live close together. However, some bathymetric restriction in species distribution probably occurs: in the Peru Trench three species occur but only one, *Calyptogena* sp., below 3500 m and in the Japan and Kurile Trench at depths below 3800 m only *Calyptogena* (*Ectenagena*) *phaseoliformis* is observed (Fig. 2a); in the mud volcanoes of the northern Barbados prism at 4800 m depth, only *Calyptogena* n. sp. occurs in large beds (Fig. 2b). Similarly, *Calyptogena* cf. *phaseoliformis* (Barry et al., 1996), now considered to be *Calyptogena* (*Ectenagena*) *extenta* (Vrijenhoek et al., 1994; Krylova and Moskalev, 1996; Barry, 1997a, personal communication), is the only species in the Monterey fan valley. The limited bathymetric range of these species may be due to non-planktotrophic larvae or to effects of pressure on larval stages which may restrict the larval dispersal of these deep-sea species across topographic barriers.

Vesicomysidae may be able to survive temporal variations in fluid flow: even with a reduced fluid flow, and after fluid expulsion ceased, live vesicomysids have been found at an old field of gas expulsion in the Gulf of Mexico (Sassen et al., 1994) and at the top of a mud dome in the southern Barbados where temperature measurements revealed the absence of fluid activity (Olu et al., 1996b). Vesicomysids can also survive with variable concentrations in sulphide (Hashimoto et al., 1995), although sulphide-binding capacities differ between species (Barry et al., 1997a). This may explain the occurrence of *Calyptogena* and *Vesicomys* in several cold seeps and the large geographic distribution at the level of genus.

The Vesicomysidae thriving in cold seeps live in symbiosis with chemoautotrophic bacteria. *Calyptogena* (*E.*) *phaseoliformis* (which was collected in the Japan trench) hosts endosymbiotic chemoautotrophic sulphur-oxidising bacteria (Fiala-Médioni and Le Pennec, 1988; Fiala-Médioni et al., 1993). As it is a methane-rich fluid which fuels the Japan cold seeps, sulphate reduction and methane oxidation may provide sulphide (Boulègue et al., 1987a; Suess and Whiticar, 1989; Masuzawa et al., 1992; Fiala-Médioni, 1993). At mud volcanoes, hydrogen sulphide is not contained in the fluid expelled through the volcano but is produced in the subsurface sediments (Martin et al., 1996). Methane is assumed to be oxidised by methanotrophic bacteria which supply a carbon source for sulphate-reducing bacteria and sulphide is likely produced from sulphate by the sulphate reducers; the sulphate being provided by sea water as its concentration in the fluid is very low (Fig. 3) (Martin et al., 1996; Olu et al., 1997). In the case of the Barbados mud volcano, methanotrophic and presumably sulphate-reducing bacteria were detected in sediment cored from a mud volcano (Guézennec and Fiala-Médioni, 1996).

5.1.2. Mytilidae

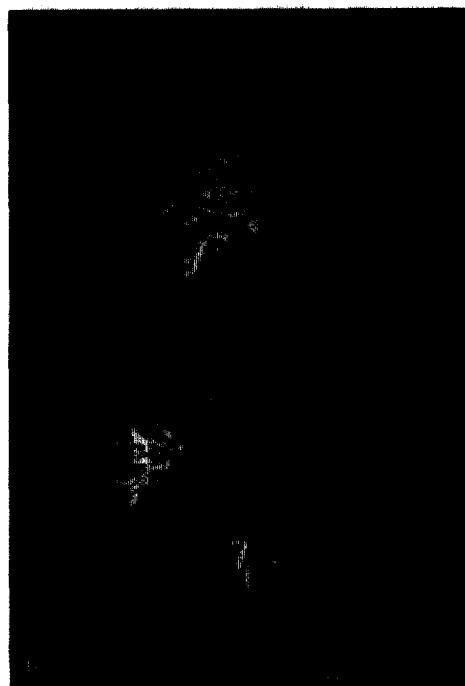
The cold-seep Mytilidae represented by one genus, *Bathymodiolus*, have more restricted geographic and bathymetric distributions than vesicomysids. They have been observed only in Atlantic and Western Pacific cold-seep areas at depths ranging from 400 to 2000 m except at Florida escarpment at 3270 m water depth. Mytilids

have been observed in dense aggregates in areas with relatively high methane rich-fluid flow in the Gulf of Mexico (MacDonald et al., 1989). In the southern Barbados prism, one of the *Bathymodiolus* sp. B is densely distributed (mean density 900 individuals per m²) in large mussel beds (Fig. 2c). It is associated with high temperature gradients, high methane concentrations and carbonate concretions (Olu et al., 1996b). Aharon (1994) has observed that the high-flow seep sites are colonised solely by methanotrophic mussels, while vesicomys and vestimentiferans occur in areas of low seepage.

Even if the taxonomic study is incomplete, eletrophoretic study of cold-seep mytilids allowed the distinction of seven, or more probably eight, undescribed species of *Bathymodiolus* showing large genetic distances, in the Gulf of Mexico and Florida escarpment (Craddock et al., 1995). Two species A (von Cosel and Olu, in press) and B (von Cosel and Olu, personal communication) at the Barbados prism and three known *Bathymodiolus* species (*B. adaloides*, *B. japonicus*, *B. platifrons*) in Sagami Bay indicate a high diversity of this genus at single locations (Table 2). The genus *Bathymodiolus* (Mytilidae) is diverse in cold seeps, yet less so than the genus *Calypptogena* (Vesicomysidae); it is less widespread.

These mussel species inhabit regions of cold seeps where natural gas, composed primarily of methane, is expelled through the sediments or directly through faults to oxygenated bottom water. Their chemoautotrophy has been studied and their ability to use methane has been demonstrated by Childress et al. (1986) and Cavanaugh, (1987). They may even use methane as the sole source of carbon and energy (Cary et al., 1988) as they harbour methanotrophic endosymbionts (Fig. 3). The study of an undescribed hydrocarbon-seep mussel from the Louisiana slope indicates that this mytilid primarily uses a methanotrophic endosymbiont and probably also an external symbiont to oxidise thiosulphate and fix carbon via the Calvin Benson cycle (Fisher et al., 1987). Fisher et al. (1993) later proved the co-occurrence of methanotrophic and sulphur-oxidising endosymbiotic bacteria in a mytilid from Alaminos Canyon in the Gulf of Mexico. In the southern part of the Barbados seep field, the two

Fig. 2. (a) Active seep site in the Japan Trench at 5900 m depth, with clam aggregates consisting of live *Calypptogena phaseoliformis* in clusters and few shells. Size of clams is about 20 cm. In the vicinity, abundant polychaetes tubes are vertically implanted in the mudstone substratum (density of nearly 100 ind m⁻²), and endemic species of actinians and caprellid amphipods live on the clam communities. Photograph taken during the KAIKO cruise with the submersible Nautille (X. Le Pichon, chief scientist). (b) Active seep site in the northern Barbados prism at 4700 m depth with clam bed of *Calypptogena* n. sp. and the galatheid *Munidopsis* sp., cladorhizid sponges, and the actinarian *Monactis vestita*. Photograph taken during the MANON cruise with the Nautille (Le Pichon et al., 1990a). (c) Active seep site in the southern Barbados prism (El Pilar site) at 1240 m depth with a huge community dominated by dense concentration of *Bathymodiolus* sp B (individuals reaching 85 mm in length, mean density of 900 individuals per m²) and bacterial mats. The lithodid crab is likely *Lithodes manningi* and the gastropods, *Bathynnerita naticoides*. Photograph taken during the DIAPISUB cruise with the Nautille (J.C. Faugères, chief scientist; Olu et al., 1996b). (d) Active seep site in the southern Barbados prism (Orenoque B, dome 13 site) at 1950 m depth with small clumps of *Bathymodiolus* sp. A. (250 mm in length size) mainly buried in the diapiric mud associated with a few *Vesicomys* sp. and nearly Pogonophora/Obturator (Vestimentifera) *Lamellibrachia* sp. Photograph taken during the DIAPISUB cruise (Olu et al., 1996b).



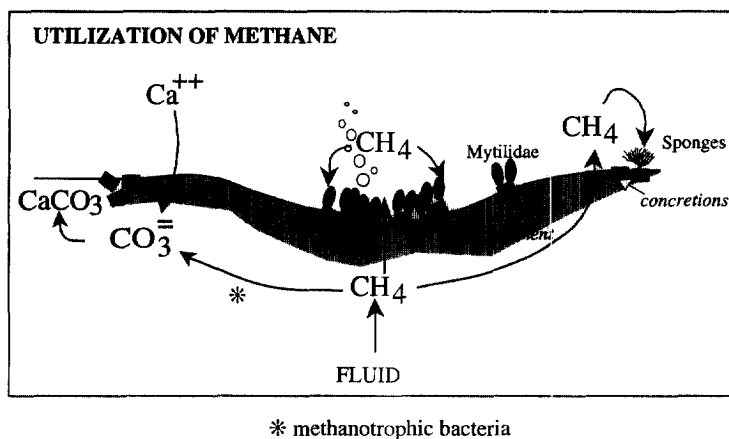
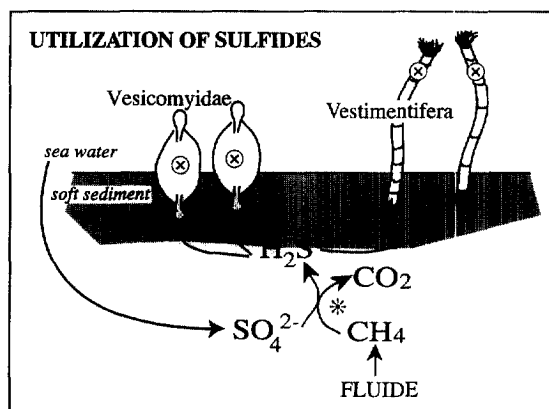


Fig. 3. Schematic representation of the chemical processes in the first few meters of seep sediments. The utilisation of sulphides by Vesicomyidae and Pogonophora (Vestimentifera) tube worms and of methane by Mytilidae and Cladorhizidae sponges are indicated. The activity of both methanotrophic bacteria and sulphate-reducing bacteria in the sediments results respectively in the oxidation of methane from pore fluid to CO_2 , and in the reduction of seawater sulphate to sulphide (Hasuzawa et al., 1992; Guezenee and Fiala-Médioni, 1996; Olu, 1996; Suess and Whiticar, 1989), sulphide that can be used by Vesicomyidae and Vestimentifera.

Bathymodiolus species A and B show different distributions on the diapiric structures: the methanotrophic mussel *Bathymodiolus* sp. B is associated with high fluid flow, high methane concentrations, and requires a hard substratum, while *Bathymodiolus* sp. A is largely buried (Fig. 2d), requires soft sediment and possesses two types of endosymbionts (Fiala-Médioni et al., 1994; Olu et al., 1996b; von Cosel and Oue, in press). The latter species is able to take methane in sea water and sulphide produced in the sediments and can survive at low fluid flow. The dependence of these two bivalve species on reducing substances is thus different (Fig. 3).

5.1.3. Solemyidae, Thyasiridae, Lucinidae

The bivalve families, Solemyidae, Thyasiridae and Lucinidae are mostly deep burrowers and are not easy to observe or to sample with the submersible manipulator or cores. Solemyidae (mainly empty shells) of the genus *Solemya* and *Acharax* have been observed in low numbers, but may be relatively common in the different areas investigated. The genus *Acharax* has mainly been observed below a water depth of 2000 m. Species of this family are observed at the Peru Trench cold seeps in areas of relatively low fluid flow, as indicated by the low density of living vesicomys and the presence of their empty shells (Olu et al., 1996a). Indeed, fluid flow measured at the Oregon subduction site colonised by Solemyidae showed a lower rate than at sites colonised by Vesicomysidae (Carson et al., 1990).

Thyasiridae and Lucinidae were observed at shallow seep sites in the Gulf of Mexico (Carney 1994), in Sagami Bay (Hashimoto et al., 1988) and south Barbados (Olu et al., 1996b) and at one deeper cold-seep site at 3800 m depth, on a turbidite deposited on the Laurentian fan (Mayer et al., 1988).

All three families are likely dependent on chemoautotrophy but this has not been demonstrated for deep sea cold-seep species. In coastal sulphide-rich habitats, species of these families are characterised by a reduced digestive tract and various studies suggest that they get most of their carbon from chemoautotrophic bacterial endosymbionts (Fiala-Médioni and Felbeck, 1990; Prieur et al., 1990). Shallow-water Solemyidae are known to host sulphur-oxidising bacteria (Reid and Barnard, 1980; Cavanaugh, 1983; Felbeck, 1983; Kusnetsov et al., 1990) as are Thyasiridae (Dando and Southward, 1986; Dando and Spiro, 1993) and Lucinidae (Cary et al., 1989b; Dando et al., 1994a). In hydrothermal vents, the new species *Acharax alinae* also lacks a digestive system and probably hosts chemosynthetic bacteria, in gill tissues (Métivier and von Cosel, 1993). The ability to host intracellular symbiotic bacteria is considered to be widespread in bivalves, which have adapted to live solely or partly from chemoautotrophic production (Fiala-Médioni and Felbeck, 1990).

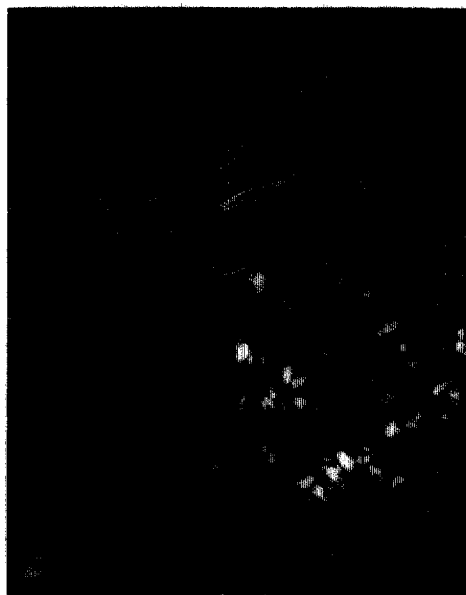
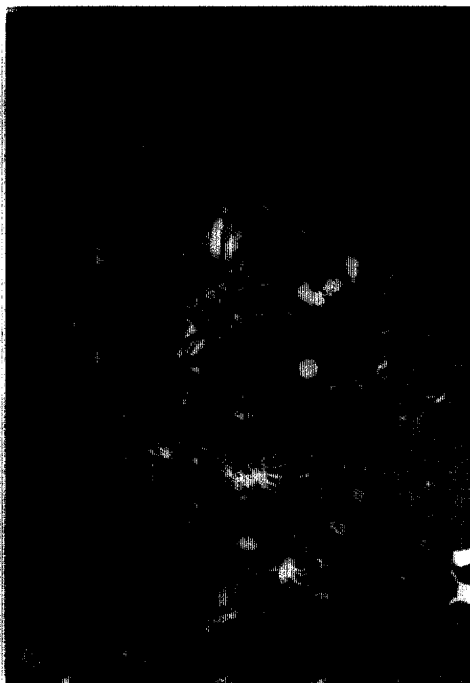
5.1.4. Pogonophora (including Vestimentifera)

According to Southward (1988), the phylum Pogonophora contains three subdivisions: Perviata, Obturata, Monilifera. Jones (1985) had proposed phylum status for Obturata, under the name Vestimentifera. Perviata live in reducing sediments; Obturata live close to hydrothermal vents and cold seeps; Monilifera live in decaying wood, and sometimes in reducing sediments in shallow water and near deep cold seeps.

Pogonophora are relatively widespread and known from 17 of the 24 deep cold seeps investigated, where they generally live in small groups. The genera *Sclerolinum* (Monilifera) *Polybrachia* (Perviata), and others assigned to the Perviata have been observed only rarely at the seeps and live even at great depth as they have been collected at the deepest cold seeps (Peru Trench, Monterey fan valley, Laurentian fan, Aleutian Trench). The subphylum Obturata (Vestimentifera), represented by the genera *Lamellibrachia* (Fig. 4a) and *Escarpia* (Jones, 1985) (Fig. 4b), are widespread and more frequent at the shallower sites. Near Monterey, *Lamellibrachia barhami* (Pogonophora/Obturata or Vestimentifera) was collected at the shallow cold-seep site of Monterey Bay (600–1000 m) (Barry et al., 1996), while at the deeper site at Monterey fan valley (3000–3600 m) *Polybrachia* sp. (Pogonophora/Perviata) was collected (Embley et al., 1990). At the southern Barbados seep site, *Escarpia laminata* and *Lamellibrachia* sp. (Obturata) were collected (Olu et al., 1996b), whereas at the deeper cold seep site, near northern Barbados, *Sclerolinum* sp. (Pogonophora/Monilifera) was collected (Olu et al., 1997). In the cold seeps near Japan, vestimentiferans were collected at Sagami Bay (900–1200 m) (Hashimoto et al., 1989) while there is no record of the other subphyla of Pogonophora at the deeper cold-seep sites (Ohta and Laubier, 1987). The shallow distribution of vestimentiferan seems to appear as a general trend. The type locality of *L. barhami* is off southern California (Webb, 1969). According to Suess et al. (1985) hydrocarbon seepages are a common phenomena in slope sediments in this region. *L. barhami* is relatively widespread and has been found at various types of reducing environments and distinct geographic areas in the Atlantic and the Pacific oceans, such as the Louisiana lower continental slope, the Oregon prism, Monterey Bay, and at San Clement fault cold seeps.

Pogonophora are all dependent on internal symbiotic chemoautotrophic bacteria (Southward, 1997, personal communication). Evidence for sulphide-fuelled chemoautotrophy first came from studies of the hydrothermal vent *Riftia* (Cavanaugh et al., 1981; Felbeck, 1981). Similar dependence on sulphur oxidation has been shown in the cold-seep genera *Escarpia* and *Lamellibrachia* (Felbeck, 1981; Cavanaugh, 1983; Cary et al., 1989a; and see Southward, 1987; Nelson and Fisher, 1995 for reviews). While no demonstration of chemoautotrophy has been undertaken for deep-sea

Fig. 4. (a) Active seep site in the eastern Nankai accretionary wedge at 2000 m depth with tube worms Pogonophora/Obturata (Vestimentifera) *Lamellibrachia* sp. Photograph taken during the KAICO-NANKAI cruise (Henry et al., 1992; X. Le Pichon, chief scientist). (b) Active seep site in the southern Barbados prism at 1700 m depth. From left to right successively: *Bathymodiolus* sp. B, *Vesicomys* sp. (living and dead animals) and a large bush of Pogonophora/Obturata *Escarpia* cf. *laminata* (E. Southward pers. comm.) of about 1 m length. Photograph taken during the DIAPISUB cruise (Olu et al., 1996b). (c) Bush of *Caldorhiza* sp. sponge of about 1 m width, near the eye of the diatreme Atalante in the northern Barbados prism at 5000 m depth. Photograph taken during the MANON cruise. (d) Main active seep site at the Peru Trench at 3520 m. Extended thickets of serpulid worms *Neovermilia* sp. within *Calyptogena* n. sp. 2 field. Galatheididae are *Munidopsis crassa*. Photograph taken during the NAUTIPERC cruise with the Nautile (J. Bourgois, chief scientist, Olu et al., 1996a). (e) Active seep site in the eastern Nankai prism at 3850 m depth. Dense field of aggregates of several *Calyptogena* sp. (living and dead animals) accompanied by actinians, holothuroid, galatheididae. Study site for in situ heat flow measurements. Photograph taken during the KAICO-NANKAI cruise (Henry et al., 1992; Le Pichon et al., 1992).



cold-seeps specimens of perviate Pogonophora, it is worth observing that methanotrophic bacteria are used by one species of perviate pogonophore living at a shallow-water methane seep (Schmaljohann and Flügel, 1987), while all other perviates investigated use sulphur-oxidising (thiotrophic) bacteria (Southward et al., 1986).

5.1.5. *Porifera*

An unexpected symbiosis between methane-oxidising bacteria and a new species of deep-sea carnivorous sponge of the genus *Cladorhiza* (Demospongiae, Poeciloscleria, Cladorhizidae) has been discovered (Vacelet et al., 1995, 1996) at 4700–4900 m in the Barbados Trench. This species lives in dense, bush-like clumps of several hundred individuals (Olu et al., 1997), (Fig. 4c). Apparently, similar associations between sponges and methanotrophic bacteria have been reported in a preliminary paper on *Hymedesmia* sp.. This sponge encrusts vestimentiferan tube worms at hydrocarbon seep communities in the Gulf of Mexico, 600 m deep (Harrison et al., 1994).

5.2. 'Non symbiont-containing' species and indirect utilisation of fluid

Because the exploration of cold-seep environments is relatively recent and mostly undertaken for geological purposes, faunal sampling is often not a priority. Thus, there is a lack of knowledge of the composition of the fauna (especially meiofauna and small macrofauna) living in the immediate vicinity of seeps. It appears that at some seeps only symbiont-containing species are present in high densities, whereas at others the symbiont-containing species are accompanied by non symbiont-containing species at exceptional densities as at the Nankai prism cold seeps (Juniper and Sibuet, 1987), at the southern (Olu, 1996b) and the northern Barbados (Olu et al., 1997), in Sagami Bay (Hashimoto et al., 1989; Ohta, 1990) and in Monterey Bay (Barry et al., 1996). This accompanying fauna, composed of species known from more typical deep-sea habitats, is likely to be attracted by the local organic enrichment; some species may be feeding on free bacteria present in the fluid or on bacterial mats, while some are carnivorous and feed on bivalves, and others are detritivores. The list of the common species already identified from cold-seep environments includes at least 147 non-symbiont-containing species (Table 2). They belong mainly to visible fauna belonging to the macro- and megabenthos.

5.2.1. *Meiofauna*

The sampling of meiofauna has rarely been undertaken at seeps. At Sagami Bay off Hatsushima, sediments have been collected near dense beds of the giant clam *Calypotogena soyoae* (Shirayama and Ohta, 1990). No difference in meiofaunal abundance between seeps and control areas has been observed, suggesting that the abundance of meiofauna is not influenced by the thiobiotic conditions in this area (Shirayama and Ohta, 1990). More recently, in the northern Barbados prism, meiobenthos were sampled from sediments within and surrounding seeps; on one mud volcano named Atalante, abundance reached 11 300 individuals per 10 cm² near *Calypotogena* sp. and cladorhizid sponge beds (Olu et al., 1997). This exceptionally high density, mainly of

unusual large nematodes (Dinet 1996 personal communication), is two orders of magnitude higher than those recorded at similar depth from the Demerara abyssal plain, where meiofaunal densities reached means of 279 individuals per 10 cm² and 145 individuals per 10 cm² at the two deep-sea stations investigated (Sibuet et al., 1984). In comparison, the density of meiofauna at hydrothermal vents has been reported to be one or two orders of magnitude lower than the figure in the non-vent deep-sea (Dinet et al., 1988). The observation at the Barbados mud volcanoes suggests a local organic enrichment of the surrounding sediment apparently utilised by the infauna (Olu et al., 1997). Two hypothesis may explain these enhanced faunal abundances: the local enrichment in the sediment by chemosynthetic production may be due (1) to free-living chemoautotrophic bacteria or (2) detrital organic matter from clusters of symbiotic fauna.

The bacterial endosymbiosis of the gutless nematode *Astomonema southwardorum* was demonstrated from shallow-water North Sea methane seeps (Giere et al., 1995). Considering that the worm is living in a deep layer of sediment where reduced sulphur compounds are available, Giere et al. (1995) suggested that it may be a suitable environment for sulphur-oxidising bacteria which support the hypothesis that the *Astomonema* symbiosis is thiotrophic. Nematods with endosymbionts could also occur in deep cold seeps.

5.2.2. Macrofauna and Megafauna

Table 2 shows that most of the phyla of marine invertebrates and fishes have been identified at seeps. We notice the absence from cold seeps of the subphylum Urochordata, which is mainly composed of Ascidiacea and Sorberacea in the deep-sea. Tunicates have never been observed at hydrothermal vents as well (M. Segonzac, 1997, personal communication). The most common non-symbiont-containing invertebrates collected with the submersible and observed on deep-sea photographs are suspension and deposit feeders. As no large sample of sediment has been taken with a box corer (USNEL type), no *sensu stricto* macrofauna studies can be compared with typical deep-sea environments. However, typical taxa of macrofauna have been observed, although of large size, visible in photographs at unusually high densities. For example, polychaetes may cover extensive areas around clam communities in sites such as the Japan Trench (Juniper and Sibuet, 1987), and the deep mud volcanoes (Olu et al., 1997). Some macrofaunal species of relatively large size and megafaunal species may be colonists from the surrounding benthos, and have higher densities in the seep community than outside. Others may be vagrants, with the same abundance inside as outside seep areas (Carney, 1994). The distinction between 'colonists' and 'vagrants' is usually deduced from video and photographic records. In addition to these categories, one can consider that some commensal species of polynoid and nautiliniellid polychaetes that live in the mantle cavities of synthesis-based mytilidae and Vesicomidae bivalves, are endemic to the chemosynthesis-based ecosystems. Polychaetes of such families are known to live in association with numerous hydrothermal-vent (Pettibone, 1984) and cold-seep bivalves (Pettibone, 1986; Miura and Laubier, 1989, 1990a; Miura, 1990b); Polynoid polychaetes also live near whale carcasses (Pettibone, 1993). Some species like the gastropod *Bathynnerita naticoides*

and the shrimp *Alvinocaris* cf. *muricola* are very likely to be endemic to seeps as they are abundant at Louisiana upper slope hydrocarbon seeps (Carney, 1994) and southern Barbados seeps at 1000 and 1700 m depth (Olu et al., 1996b), but absent from the surrounding benthos.

Filter feeders, such as the serpulid polychaetes *Neovermilia*, a widespread genus in the deep sea, have been reported from Nankai prism, Peru Trench (Fig. 4d) and the Mexico Trench and the southern Barbados prism (Table 2). Some species can be relatively abundant around mussel beds (Olu et al., 1996b) and clam beds (Olu et al., 1996a) and be considered as colonist or even endemic of seeps because they were not observed outside seeps. At the PAITA area in the Peru Trench, aggregations of the serpulid (*Neovermilia* sp.) can reach 20 m² and cover a total area of 200 m² in a large clam field of 1000 m²; individuals are unusually longer than 20 cm (Olu et al., 1996a). Suspended particulate organic matter produced by chemosynthetic activity is the most probable food source. As bacterial mats of the filamentous chemosynthetic *Beggiatoa* sp. have been observed near serpulid clumps, they may also contribute to the nutrition of the serpulids (Olu et al., 1996a). In the southern Barbados prism as well, *Neovermilia* sp. are concentrated at all sites colonised by mussels where bacterial mats are also abundant (Olu et al., 1996b). Sponges (*Geodia* sp., *Stelletta* sp.) are also frequent at seeps; the presence of numerous bacteria in their tissues (Vacelet et al., 1996, personal communication) tends to confirm that these species rely on filtration of free-living bacteria.

Most of the detritivorous species at seeps are vagrants, with the exception of holothurians which may occasionally be colonists; e.g. *Scotoplanes* sp. observed in high densities near Kashima seamount in the Japan Trench (Juniper and Sibuet, 1987; Sibuet et al., 1988) and in the Peru Trench (Olu et al., 1996a). Suspension feeders and detritivores can be relatively abundant in areas colonised by chemosynthetic fauna, being established for a relatively long time and indicating more or less a level of maturity of the ecosystem composed of various trophic groups (Fig. 4e).

Carnivores are present generally in small numbers except in the shallow Gulf of Mexico where crustaceans and fishes are abundant (Carney, 1994). Some carnivorous gastropods, e.g., Trophoninae and Turridae, which are known from the typical deep sea, are also colonists of seep areas. *Cataegis meroglypta* (Trochidae) is abundant at the Louisiana slope hydrocarbon seeps (Carney 1994) and at some domes in the southern part of the Barbados prism (Olu et al., 1996b). Buccinids feed on living and dead clams as observed at Monterey Bay (Barry et al., 1996) and Sagami Bay (Hashimoto et al., 1989) cold seeps. Occasionally, carnivorous asteroids are abundant near vesicomys in Sagami Bay (Ohta, 1990) or mussels on the Louisiana slope (Carney, 1994) but are more frequently vagrants. Large carnivores such as octopods, shrimps, lithodids, brachyuran crabs and macrourid fishes observed occasionally in seep communities can be considered vagrant species, while galatheids are frequently seen and likely to be colonists (Barry et al., 1996; Hashimoto et al., 1989; Olu et al., 1996b) (Plates 1b and 2d, e). Unlike hydrothermal vents, specialised carnivores have not been reported in high abundance, which implies that they do not play a particular role in structuring cold-seep communities and particularly not at the very deep cold seeps.

6. General patterns in biodiversity and in geographic distributions

Species richness is here considered to be the number of species observed in each cold-seep area. It is used to analyse the variation of species richness between the 24 seeps (Table 2). The species richness of the total seeps considered is high and certainly underestimated. From the total of 211 known species, of which 147 are non-symbiont-containing species, only 116 have been identified with a species name. From the 64 symbiont-containing species living at cold seeps, only 26 are described or named. We underestimate the real number of species because 'gen. sp.' in the Table 2, may lump several species which remain to be identified and because seep areas were not sufficiently explored. Despite the fact that different areas received different level of investigation and that taxonomic identifications must be treated with caution, some general patterns can be discerned.

There is a general trend of decreasing symbiont-containing species richness with depth. In the deepest cold seeps, only a small number of symbiont-containing species are living: only one species at the Japan and Kurile trenches at 6000 m depth. This small number of species could be explained by limited larval dispersal in deep waters. In shallower depths, the diversity is higher with a maximum of 15 symbiont-containing species at the Louisiana upper slope, 10 at Sagami Bay and nine at the southern Barbados prism. In these sites, the total species richness is also the highest (between 39 and 42 species). We will not analyse here the diversity within a site, although variations and examples of high species richness within a single cluster exist: with up to five symbiont-containing species living together in a single aggregate at the Barbados prism (Olu et al., 1996b). Within a depth range, higher diversity of cold seep communities has been observed on sediment substrates than on hard substrates (Olu, 1996; Sibuet et al., 1988). Variations of diversity could be also linked to variability between sites of fluid flow. In the shallower cold seeps on passive margins as well as on active margins, the relatively high species richness may be due to better environmental conditions depending for example on the duration of the fluid source, the fluid flow rate and the methane and/or sulphide concentrations in the fluid. Indeed, higher rates of speciation may depend on the recent history of cold-seeps and the more or less ephemeral venting activity. The number of species and trophic behaviour can be used to characterise the level of maturity of seep communities. As proposed by Frontier and Pichod-Viale (1991), the maturity of an ecosystem can be expressed by species richness, diversity of feeding strategies, complexity of the trophic structure, biomass and size distribution. For seep communities, the maturity has been shown by the diversity of symbiont-containing and non-symbiont-containing species, by the proportion of living and dead animals and by the presence of various trophic groups (Juniper and Sibuet, 1987; Olu et al., 1996a). The least mature community consists of small, sparse symbiont-containing species with very few accompanying species. The most mature systems such as those found in the Gulf of Mexico, in the southern Barbados prism, in the Paita area of the Peru Trench, in Monterey Bay, as well as in Tenryu canyon in the Nankai prisms, have large aggregations containing several symbiont-containing species, and numerous endemic and colonists non symbiont-containing species of various trophic strategies (filter and deposit feeding and

scavenging). Establishment of a mature ecosystem is probably possible only if the field is sustained by constant fluid flow over a long time. Compared to the hydrothermal vent communities dominated by a small number of species (seldom more than one species of one genus) and where the accompanying species are more scattered, cold seeps show a relatively high species richness. The high number of mytilids (13), vesicomyids (20) and pogonophorans (14) at seeps, compared to those found at hydrothermal vents, where these taxa are respectively represented by eight *Bathymodiolus* species, only three *Calymene*, and 10 pogonophoran species is remarkable. The presumed stability of the seep habitats might create different selection pressures, providing more opportunity for local diversification and speciation (Craddock et al., 1995). While seepage is believed to provide a relatively stable source of nutrients, hydrothermal venting is known to be unpredictable and ephemeral. Moreover, the Craddock et al. (1995) study on mytilids supports the hypothesis also considered by (Tunnicliffe, 1991) that the evolution of cold-seep sulphide/methane mytilids was a critical antecedent to the evolution of hydrothermal vent mytilids.

The general trends of the geographic distribution of cold-seep species is deduced in our study from their occurrence at the 24 explored cold-seep areas (Table 2). The geographic distribution shows that symbiont-containing species are mostly endemic to a seep site: each species is known in most cases only at one or two cold seeps and exceptionally in both Pacific and Atlantic oceans. Each Mytilidae species is only known from one cold-seep area. Each Vesicomyidae species is known from one or two seeps in geographic proximity. As an exception, the pogonophoran (vestimentiferan) species *Lamellibrachia barhami*, the most widespread species, occurs at four cold-seep areas of the Atlantic and the Pacific oceans. Atlantic connection with eastern Pacific may occurred through an open Isthmus of Panama area (Tunnicliffe et al., 1996; Barry et al., 1997a). At the generic and familial levels, the geographic range of chemosynthetic fauna is larger. The genus *Calymene* is the most widespread and most families and genera occur in the Atlantic and eastern and western Pacific, except for the sponges (*Cladorhiza* and *Hymedesmia*) known only in the Atlantic ocean, and the genus *Bathymodiolus* which is absent from the eastern Pacific. The absence of methanotrophic Mytilidae from eastern Pacific seeps is remarkable considering that several different areas along the American and south American margins have been explored. The genus *Bathymodiolus* is absent from all 11 cold-seep areas investigated in the eastern Pacific, even though species of this genus are elsewhere represented by large populations. This absence may be related to larval migration barriers or insufficient migration from an origin in the Atlantic despite past connection through the Isthmus of Panama. It may also be related to the absence of suitable habitats (i.e. insufficient methane concentrations in sea water) in eastern Pacific. Despite the presence of relatively high CH_4 concentration in interstitial water for example at Monterey Bay (Barry et al., 1997), similar to Atlantic seeps, the rate of expulsion in the Eastern Pacific seeps may be too slow: the lower expulsion rate (1 cm s^{-1}) measured in the Pacific at Oregon seeps (Carson et al., 1990) compared to the rate measured (10 cm s^{-1}) in the northern Barbados seeps (Olu et al., 1997) may not create suitable habitat. Moreover no evidence of fluid discharge in seawater was observed in the Pacific as in the Gulf of

Mexico seeps (Aharon, 1994). Another hypothesis proposed by Barry et al. (1996, 1997a) is unstable CH_4 seepage due to the rarity of evaporitic deposits in the Pacific. High salinity brines or methane hydrates, common at Atlantic seeps, and slow mixing rates near the sea floor may stabilise methane concentration at seeps.

The non-symbiont-containing species commonly found near aggregates of seep species, also show restricted geographic distributions, when comparisons are made between the known seeps, and not with the non-seep deep-sea, where most of these species may also occur. Some species can be considered to be endemic to seep ecosystems as they are not known from the typical deep-sea, for example the gastropods *Bathynnerita naticoidea*, *Cataegis meroglypta*, some amphipods, and the decapod *Alvinocaris muricola*. At the level of species, if we consider only the 90 identified non-symbiont containing species (57 species are only indicated with a genus name and cannot be distinguished between sites), each occurs at a single cold seep with a few exceptions. Only the following three species are widespread at cold seeps: *Bathynnerita naticoidea* is found in the Gulf of Mexico and the Atlantic ocean at the southern Barbados seep, the shrimp *Alvinocaris muricola* occurs in three areas in the Gulf of Mexico and at the Barbados prism, and the fish *Coryphaenoides acrolepis* is found in Monterey Bay and Sagami Bay cold seeps. Most of the non-symbiont-containing are known from the non-seep deep-sea environment, however, mainly from the geographic area surrounding the seeps. Greater between-seep similarity is observed at the level of family and genus. However more sampling and taxonomic studies of seep communities, including the environment immediately surrounding the typical aggregations of cold-seep fauna, are essential to evaluate the degree of endemism of all the components of seep communities and the similarities between sites.

7. Comparison of species of cold seeps and other chemosynthetic based environment

We have compared phyla, families, genera and species, which are common to seeps and hydrothermal vents, and those which are common to seeps and other deep-sea chemoautotrophic habitats (Table 3). We have made these comparisons using all the known species living (1) on hydrothermal vents in Atlantic and Pacific oceans (Tunnicliffe, 1991; M. Segonzac 1997, personal communication; Desbruyères and Segonzac, 1997), (2) on whale bones from the deep north east Pacific at 1240 m in the Catalina Basin off southern California (Smith et al., 1989; Bennett et al., 1994) and on whale bones at the Torishima seamount, 4037 m deep, in the forearc slope of the Izu-Bonin Arc near Japan (Fujioka et al., 1993; Fujikura, 1997, personal communication), and (3) on organic-rich shipwrecked cargoes found in the east Atlantic, where just two symbiont-containing species have been reported, *Lamellibrachia barhami* (pogonophora/vestimentifera) and *Idasola* sp.(bivalve) (Dando et al., 1992). In all these reducing habitats, the dominant fauna and the majority of the biomass is mainly due to species which depend on reduced compounds by endosymbiotic chemoautotrophic bacteria. However, the geological and environmental context and the nature and origin of reduced compounds are different. Although taxonomic uncertainties

Table 3

List of common taxa (at the level of family, genus and species) between cold-seeps and hydrothermal vents; between cold-seeps and whale carcasses or shipwreck^a and between the three types of ecosystems^b

Phylum or Class	Family	Genus	Species
Porifera	Cladorhizidae		
Cnidaria	Sertulariidae	Sertularella	
	Hormathiidae		
	Actinostolidae		
Polychaeta	Ampharetidae	Amphisamytha	<i>A. galapagensis</i>
	Chaetopteridae ^a		
	Hesionidae	Hesiospina	<i>H. vestimentifera</i>
	Maldanidae	Nicomache	<i>N. arwidssoni</i>
	Nereididae ^b	Nereis ^b	
	Polynoidae ^b	Branchipolynoe	<i>B. seepensis</i>
	Nautiliniellidae	Shinkai	
	Phyllodocidae	Protomystides	
	Serpulidae ^b		
Pogonophora/Obturata (Vestimentifera)	Lamellibrachiidae ^b	Lamellibrachia ^b	<i>L. barhami^b</i>
Gastropoda	Acmaeidae	Bathyaacmaea	
	Buccinidae ^b	Buccinum	
		Neptunea ^b	<i>N. amianta^a</i>
	Collumbellidae ^a	Mitrella ^a	<i>M. permodesta^a</i>
	Neolepetopsidae	Neolepetopsis	
		Paralepetopsis	
	Provannidae	Provanna	<i>P. glabra</i>
	Trochidae		
Bivalvia	Conidae	Phymorhynchus	
	Nuculanidae	Nuculana	
	Solemyidae	Acharax	
	Mytilidae ^b	Bathymodiolus	<i>B. aduloides</i> <i>B. japonicus</i> <i>B. platifrons</i>
	Thyasiridae ^a	Thyasira ^a	
	Vesicomysidae ^b	Calypptogena ^b	<i>C. pacifica (?)^b</i>
		Vesicomys ^a	<i>V. gigas (?)^a</i>
Copepoda	Clausidae	Hyphalion	
Cirripedia	Eolepadidae	Neolepas	
Amphipoda	Lysianassidae	Orchomene	
	Phoxocephalidae		
Decapoda	Alvinocarididae	Alvinocaris	<i>A. longirostris</i>
	Lithodidae	Paralomis	<i>P. verrilli</i> <i>P. sp</i> <i>M. crassa</i>
	Galatheididae ^b	Munidopsis ^b	
		Munida	
Holothuroidea	Majidae		
	Elpidiidae	Scotoplanes ^a	<i>S. globosa^a</i>
	Synaptidae	Chiridota	
Vertebra/Pisces	Zoarcidae ^b		
	Macrouridae		
	Synphobranchidae	Synphobranchus	
	Scorpaenidae	Sebastolobus ^a	<i>S. altivelis^a</i>
	Chaunacidae	Chaunax	

remain for polychaetes like *Amphisamytha galapagensis* (D. Desbruyères, 1996, personal communication), for decapods, like *Munidopsis crassa* and *Paralomis verrilli* (Chevaldonné and Olu, 1996), which may be considered as distinct species between seeps and vents, we use the known literature for our comparison. We found only 13 species common between cold-seeps and hydrothermal vents, where a total of 472 species (from vents and surroundings) are known (Segonzac 1997, personal communication; Desbruyères and Segonzac, 1997). Six species are common between cold-seeps and whale carcasses environments, and one (*Lamellibrachia barhami*) is common between cold seeps and the shipwreck. If we now compare only the symbiont-containing species, only five species are common between cold seeps and hydrothermal vents: one Pogonophora *Lamellibrachia barhami*, which is widespread in cold-seeps and known only at the Juan de Fuca hydrothermal vent in the North Eastern Pacific, three species of *Bathymodiolus* (*B. adaloides*, *B. japonicus* and *B. platifrons*) all found at the Sagami Bay cold seep and at hydrothermal vent sites near Japan, one Vesicomidae, *Calyptogena pacifica* which occurs at Monterey Bay and northern California continental shelf cold seeps and at Guaymas hydrothermal vents. Two symbiont-containing species and four genera are common between whale carcasses or shipwreck reducing habitats and cold seeps (however *Calyptogena pacifica* and *Vesicomya gigas* have to be confirmed in the whale carcass habitat). *Calyptogena pacifica* is the only species known in the three types of habitats, i.e. cold seeps, hydrothermal vents and whale carcasses. The geographic distribution of these bivalve species, which are shared between cold seep and hydrothermal-vents or whale-carcass habitats, is however limited as these species are known from a single geographic region. Moreover, the taxonomic identification has to be treated with caution until further morphological and molecular studies clarify the systematic relationships (Vrijenhoek et al., 1994). At the genus level, only five 'symbiont-containing' genera are shared between the 13 known 'symbiont-containing' genera at hydrothermal vents and 20 such genera at cold seeps. Some subphyla, families, even genera of 'symbiont-containing' species are not known from hydrothermal vents and appear to be endemic to seeps (if we just compare with hydrothermal vents) but are also encountered on whale carcass and shipwreck reduced habitats. Escarpidae (Obturata), Perviata and Monilifera pogonophorans, Lucinidae and Thyasiridae bivalves are not found at hydrothermal vents. The echinoderms had been long considered to be absent from hydrothermal vents, until the sampling of *Echinus alexandri* (Sibuet, 1996, identification) and the discovery of the new ophiuroid genus *Ophioctenella* (Tyler et al., 1995), which reaches high densities at 14°45'N on the Mid Atlantic Ridge (M. Segonzac, 1997, personal communication). The echinoderms are well represented at seeps, with high abundances of holothuroids, for example, at the Florida Escarpment (Paull et al., 1984), in the Japan Trench, and in the Nankai trough (Sibuet et al., 1988; Sibuet, 1989, personal observations) and in the Peru trenches. The probable occurrence of organically enriched cold-seep sediment may explain the presence of detritivorous holothuroids, ophiuroids and asteroids. Extensive dense populations of filter feeders (sponges and serpulids) are also a characteristic of cold-seep environments.

Relationships between cold seeps with other chemosynthetic based ecosystems appear very restricted at the level of species, however at the level of genera and families

the similarity reflects some evolutionary connection through common ancestors as already suggested (Tunicliffe et al., 1996).

8. Conclusion

This review of the existing knowledge from 24 cold seeps in the Atlantic and Pacific oceans has allowed us to highlight major faunal and environmental features of deep cold seeps, to analyse the faunal distribution, trophic behaviour and fluid dependence of the major species, and to identify trends in biogeography and biodiversity which are summarised as follows.

Cold seeps have a wide geographic and bathymetric distribution along different types of passive and active margins. Methane rich fluid of thermogenic and/or biogenic origin is the principal source of energy, however, production of sulphide by sulphate reduction in the sediment also plays a major role.

Productivity, expressed in terms of biomass, is high and recent studies shows that it varies with fluid flow and possibly with methane and sulphide concentrations. However, these relationships require more investigation to analyse and quantify the relationships, and to better understand the role in the ocean of these highly productive ecosystems.

Different symbiont-containing species rely on sulphide or methane oxidation, or both, via chemoautotrophic endosymbiotic bacteria. Non-symbiont-containing species are diverse and very abundant. This highlights the spatial influence of a local enrichment which modifies the composition and productivity of the surrounding ecosystem. However, ecological studies remain to be undertaken both inside and outside seeps to quantify the impact of seeps on the deep ocean.

From this review, we were able to list a total of 211 species from which 64 are considered to be symbiont-containing species or dependent on symbiotic chemoautotrophy, a majority of them are endemic to single seep sites and to the cold-seep ecosystem.

The species richness of cold-seep communities decreases with depth. High diversity (unusual for chemosynthetic based ecosystems) of symbiont and non-symbiont containing-species found in several seeps can be explained by—the duration and intensity of fluid flow,—the sediment substrate which may favour long-term stability, and enough methane and sulphide accumulation in pore fluids to maintain chemosynthetic processes. The species richness at a single site is higher at cold seeps than at hydrothermal vents.

From the known literature, only 13 seep species are shared with hydrothermal vents; five symbiont-containing species are shared with hydrothermal vents, where 23 species depend on symbiotic chemoautotrophy. However, this result has to be taken with caution as more studies are needed: taxonomic studies are essential to understand the relationship between seeps and between other chemosynthesis based ecosystems. Molecular phylogeny can help to demonstrate the recent hypothesis, shown for mytilids, that the evolution of cold seep, sulphide/methane dependent species was a critical antecedent to the evolution of hydrothermal-vent fauna. Did other components of the seep fauna play an ancestral source to hydrothermal-vent species?

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