

The deepest chemosynthesis-based community yet discovered from the hadal zone, 7326 m deep, in the Japan Trench

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ABSTRACT: A dense community of benthic animals was discovered by the Japanese ROV 'Kaiko' in the hadal zone near the bottom of the Japan Trench, 7326 m deep. The community was dominated by a new species of thyasirid bivalve *Maorithyas hadalis*. This community appears to be sustained by chemosynthesis (nutrients being derived from reduced compounds within the sediment) for reasons including: a high concentration of sulfur contained in the thyasirid gills; the existence of numerous bacteria-like particles in the gill tissues; a sulfide smell from soft body parts and from collected sediment; the anoxic nature and high sulfide content of the sediments suggested by the dark gray to black color; the occurrence above geologic faults. Thyasirids have also been collected from other chemosynthesis-based communities around Japan, including the Japan Trench, Sagami Bay and the Nankai accretionary prism. Until now, the deepest chemosynthesis-based community known occurred on the Sanriku Escarpment of the Japan Trench, 6437 m deep. This site was dominated by the vesicomyid clam *Calyptogena phaseoliformis*. The discovery of a chemosynthesis-based community dominated by thyasirid clams from even deeper waters suggests a wider variety of chemosynthesis-based communities exists throughout deep-sea trenches. Additionally, the thyasirid species discussed here differs from other thyasirids by having circular symbionts which appear to exist intracellularly, and by living exposed above the sediment surface.

KEY WORDS: Chemosynthesis-based community · Thyasirid clams · Hadal zone · Japan Trench

INTRODUCTION

The discoveries of chemosynthesis-based communities at both cold seep areas and hydrothermal fields has enhanced our understanding of deep-sea ecosystems. Deep-sea cold seep communities have been observed in 24 areas worldwide at depths ranging from 400 to 6000 m (Sibuet & Olu 1998). Examples include subduction zones (Okutani & Egawa 1985, Kulm et al. 1986, Juniper & Sibuet 1987, Olu et al. 1996a,b,

Suess et al. 1998), groundwater seeps (Hecker 1985, Barry et al. 1996), hydrocarbon seeps (Kennicutt et al. 1985) and shallow methane seeps 150 m deep (Dando et al. 1991). Seep communities typically have high biomass. Dominant megafaunal species differ from site to site though they are often in the same families and genera. Descriptions of these communities have been based primarily upon video and still camera images and/or submersible-obtained specimens. Chemosynthesis-based communities are restricted to areas where hydrogen sulfide and/or methane rich water seeps out along geologic faults. The food webs of hydrothermal vent and cold seep communities rely on the production

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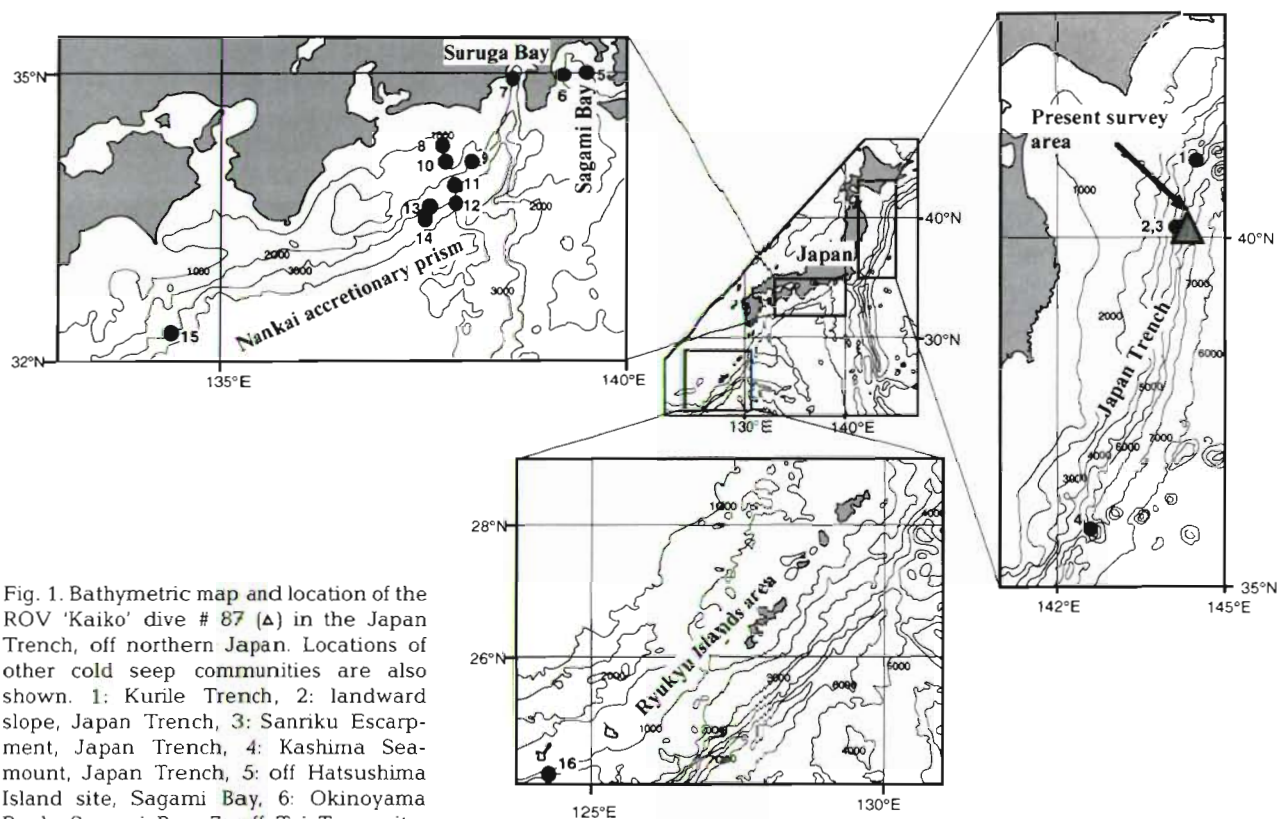


Fig. 1. Bathymetric map and location of the ROV 'Kaiko' dive # 87 (Δ) in the Japan Trench, off northern Japan. Locations of other cold seep communities are also shown. 1: Kurile Trench, 2: landward slope, Japan Trench, 3: Sanriku Escarpment, Japan Trench, 4: Kashima Seamount, Japan Trench, 5: off Hatsushima Island site, Sagami Bay, 6: Okinoyama Bank, Sagami Bay, 7: off Toi Town site, Suruga Bay, 8: Ryuyo Submarine Canyon, Nankai accretionary prism, 9: Tokai Thrust, Nankai accretionary prism, 10: Dai-ni Tenryu Submarine Canyon, Nankai accretionary prism, 11: Yukie Ridge, Nankai accretionary prism, 12: Dai-san Tenryu Submarine Canyon, Nankai accretionary prism, 13: Tenryu Submarine Canyon, Nankai accretionary prism, 14: Zenisu Ridge, Nankai accretionary prism, 15: Dai-ichi Minami Muroto Knoll, Nankai accretionary prism, 16: Kuroshima Knoll, Ryukyu Islands area

of organic matter via bacterial chemoautolithotrophy (Jannasch & Mottl 1985). The megafauna living at cold seeps is generally considered closely related to megafauna from hydrothermal vent communities. The principal bivalve families from chemosynthesis-based communities are Vesicomyidae, Mytilidae, Solemyidae, Lucinidae, and Thyasiridae. Members within these families have symbiotic bacteria in their gills (Fiala-Médioni & Felbeck 1990, Fisher 1990, Nelson & Fisher 1995).

The Japan Trench was formed by the subduction of the Pacific plate beneath the North American or Okhotsk plate (Seno & Sakurai 1996). A broad-based study of geologic and biologic features within the Japan Trench was started under a Japan-French cooperative program (the KAICO Project) using surveys from the French manned submersible 'Nautil' (KAICO I Research Group 1986, Juniper & Sibuet 1987, Ohta & Laubier 1987, Sibuet et al. 1988). The deepest chemosynthesis-based community known prior to this report was discovered during a dive of the Japanese submersible 'Shinkai 6500', on the Sanriku Escarpment

slope of the Japan Trench at a depth of 6437 m (Ogawa et al. 1996) (Fig. 1). Distribution of chemosynthesis-based communities in the hadal zone is very difficult to ascertain, as submersible dive time is limited and expensive. Thus each new chemosynthesis-based community discovered provides valuable data for comparing faunal compositions between chemosynthesis-based communities. This is important in order to understand the biogeography and biodiversity of chemosynthesis-based communities in the deep sea. During a recent survey using the ROV 'Kaiko' in the Japan Trench, a dense aggregation of thyasirid clams was discovered at a depth of 7326 m.¹ The purpose of this paper is to present this chemosynthesis-based community as the deepest in the world to date.

¹During the review process of this paper, several aggregations of *Maorithyas hadalis* were found at slightly deeper sites, 7336 m and 7434 m, near the present study area using the ROV 'Kaiko'. Although these communities could not be fully investigated for this manuscript, initial observations suggest these communities were similar in nature to those reported here

MATERIAL AND METHODS

A sea floor survey near the bottom of the northern Japan Trench was conducted on August 5, 1998, using the ROV 'Kaiko' of the Japan Marine Science and Technology Center. The dive site was located at 40° 02.85' N latitude, 144° 16.50' E longitude, and the bottom depth ranged from 7300 to 7330 m (Fig. 1). This site was chosen after a multichannel seismic survey suggested the existence of a geologic fault. Observations were made with a high quality color TV camera (PHOTOSEA TV3100XD), 3 additional TV cameras (PHOTOSEA TV2200XD), and 35 mm photographs (SUBSEA OFFSHORE LIMITED ABERDEEN CI801T). Positioning of the 'Kaiko' was recorded by a Super Short Base Line (SSBL) using a GPS. Bivalve specimens were collected by the ROV manipulator. Water temperature and salinity were measured by a CTD (SEABIRD SBE-9).

The presence of symbiotic bacteria in the gills of the bivalves was determined by transmission electron microscopy (TEM). Gills were excised on board ship and sliced into 2 mm sections in a droplet of 8% glutaraldehyde, and preserved in cacodylate buffer. Thin-sections were viewed by TEM (JEOL JEM-1210). Gill tissue was frozen at -80°C for sulfur analysis. After defrosting, the tissue was diced into 3 mm sections and desiccated at 60°C for 12 h, and coated by carbon vapor deposition. Gill tissue was not critical point dried. Elemental analyses were conducted using an Energy Dispersive X-ray Spectrometer (OXFORD LINK ISIS 200I), and detector (JEOL SUPERMINI CUP). Thyasirid mantle tissue, gill tissue from the shallow-living short-necked clam *Ruditapes philippinarum* which lives in non-chemosynthesis-based communities, and gill tissue containing symbiotic bacteria from the vesicomyid clam *Calyptogena soyoeae* were also analyzed to compare the composition of dominant inorganic elements (mainly sulfur) of bivalves from the Japan Trench.

RESULTS

During the survey, 3 dense bivalve aggregations were discovered

at 7326 m (Fig. 2). The community was dominated by a single thyasirid species *Maorithyas hadalis* (Okutani et al. 1999) (Fig. 3). Aggregations were circular, approximately 0.7 to 1 m in diameter. Three aggregations were observed in the survey area, which was approximately 400 m². The total numbers of living bivalves in each aggregation were approximately 50, 80 and 100. Burrow trails of bivalves were not present in or around the thyasirid aggregations. Almost all living specimens were buried with about 20% of shell exposed in a vertical position in the muddy sediments. Dead or dissolving shells were scattered sparsely within the aggregations (Fig. 2A). Two living specimens and many disarticulated shells were collected. Most of the collected *M. hadalis* were of the same size, approximately 3 cm in shell length. The thyasirid aggregations occurred on a muddy seafloor made of soft debris deposited by downslope movements or by bottom cur-

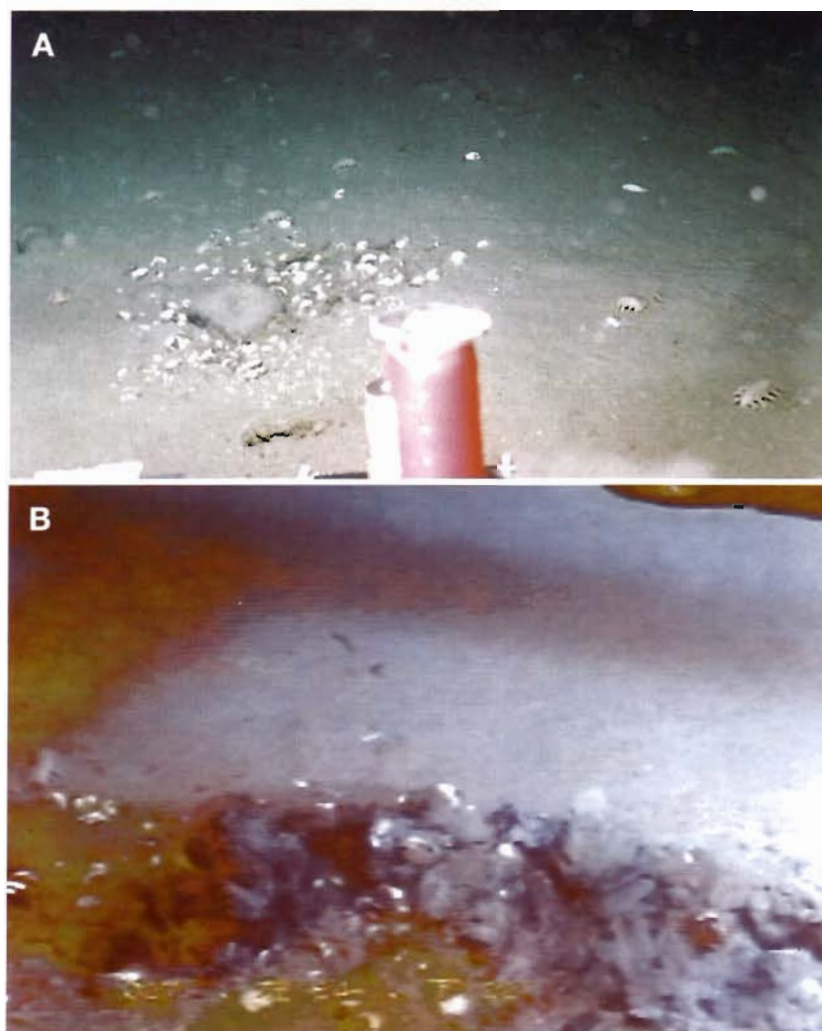


Fig. 2. (A) Photograph of an aggregation of *Maorithyas hadalis* (Thyasiridae), showing dead shells scattered over the bed. (B) Video still of black sediment suspended after core sampling. The blackish color suggests a reducing environment

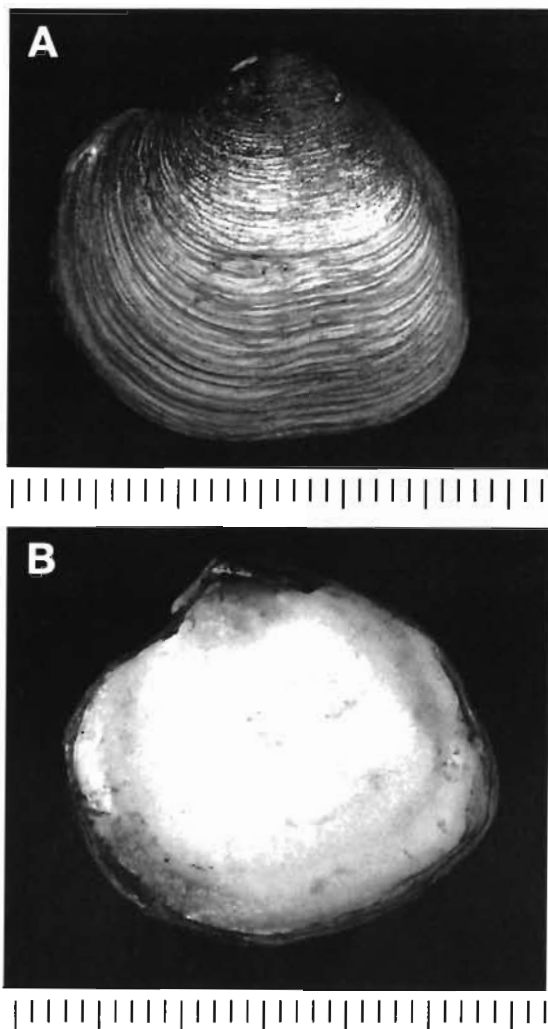


Fig. 3. *Maorithyas hadalis* (Thyasiridae) collected from the Japan Trench, 7326 m deep. Scale divisions = 1 mm. (A) External surface of a valve. (B) Inner surface of a valve

rents. A rock (approx. 40 cm in diameter) was in the center of 1 aggregation (Fig. 2A). The surface layer of mud near the thyasirid aggregations was olive-gray colored, while the surface sediment within the thyasirid aggregations was dark gray to black (Fig. 2B), suggesting an anoxic environment with high sulfide levels. No bacterial mats were seen in or around the thyasirid aggregations. A sulfide smell was easily detectable from the soft parts of *M. hadalis* and collected sediments. *In situ* water temperature was 1.79°C; salinity was 3.47‰.

Within the thyasirid aggregations, there were 2 tubes approximately 1 cm in diameter and 8 cm in length. These were presumably polychaetes. Additionally, there were Eurycopidae-like isopods approximately 6 to 7 cm in length, and *Scotoplanes*-like holothurians approximately 8 to 9 cm long. The Eurycopidae-like isopods

and *Scotoplanes*-like holothurians were also common outside the thyasirid aggregations. The densities of the Eurycopidae-like isopods and the *Scotoplanes*-like holothurians within the thyasirid aggregations were higher than without the aggregations. Vesicomyid clams, *Bathymodiolus* spp. (Mytilidae) and vestimentiferan (Pogonophora) tube worms, which are the principal members of most chemosynthesis-based communities, were not found within these *Maorithyas hadalis* dominated communities.

TEM analysis of *Maorithyas hadalis* gill tissue showed densely packed assemblages of round bacteria-like particles, 0.3 to 0.7 microns in diameter, within vacuoles in cells of the gill tissues (Fig. 4). The distribution of these assemblages was not even, but rather concentrated near the ciliated gill epithelium.

Elemental analysis showed sulfur (K = 2.3 KeV) was the dominant inorganic element in the gill tissues of *Maorithyas hadalis* (Fig. 5). The sulfur peak in *M.*

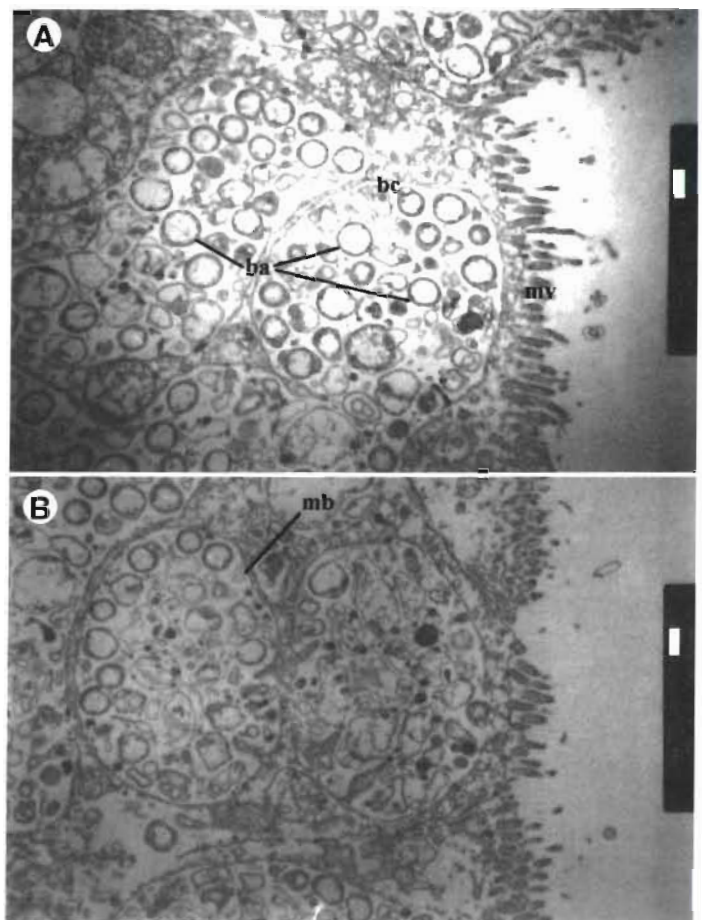


Fig. 4. Gill section (TEM) of *Maorithyas hadalis* (Thyasiridae). (A) ba: particles resembling bacteria; bc: structures similar to bacteriocytes; mv: microvilli on the external surface of the cell. White scale bar = 0.5 μm. (B) mb: membrane bound vacuoles. A structure similar to bacteriocytes is surrounded by a membrane

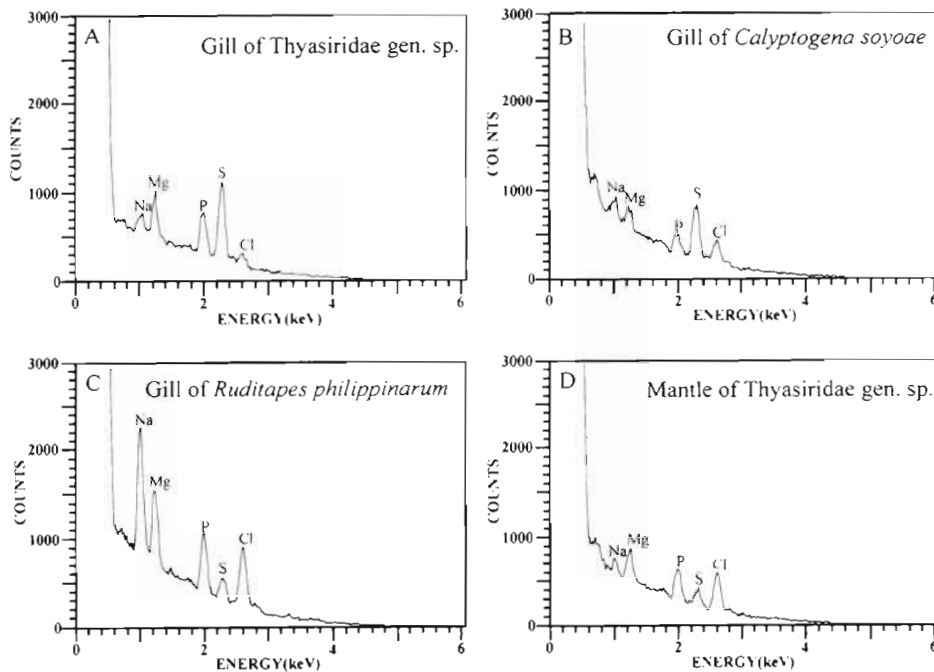


Fig. 5. Elemental composition analysis, as determined by an Energy Dispersive X-ray Spectrometer. (A) Gills from thyasirid clam *Maorithyas hadalis* collected from the Japan Trench, 7326 m. (B) Gills of the vesicomyid clam, *Calyptogena soyoe* collected from a deep-sea chemosynthesis-based community in Sagami Bay, 1200 m. (C) Gills from the short-necked clam, *Ruditapes philippinarum* collected from a non-chemosynthesis-based community area in shallow water. (D) The mantle of thyasirid clam *M. hadalis*

hadalis was at almost the same level as that in *Calyptogena soyoe* collected from a bathyal chemosynthesis-based community in Sagami Bay, and both species had much higher sulfur peaks than that of *Ruditapes philippinarum* collected from a non-chemosynthesis-based community. Conversely, the sulfur peak from mantle tissue of *M. hadalis* was very low.

DISCUSSION

Dense aggregations of the thyasirid clam, *Maorithyas hadalis*, were found at depths greater than 7300 m near the bottom of the Japan Trench. This biological community is probably sustained by chemosynthetic processes, for reasons that include: (1) the concentration of sulfur in gills of *M. hadalis* was much higher than in the gills of *Ruditapes philippinarum* from a non-chemosynthesis-based community, while almost the same level as in the gills of *Calyptogena soyoe* from a chemosynthesis-based community (Fig. 5); (2) the existence of numerous particles in the gill tissue which appeared to be symbiotic bacteria (Fig. 4). Symbiotic bacteria in a few thyasirid species are rod-shaped, 0.18 to 0.5 μm in diameter and 0.5 to 2.0 μm in length (Fisher 1990), while symbionts in *Calyptogena phaseoliformis* from the Japan Trench were round with diameters from 0.6 to 1.0 μm (Fiala-Médioni & Le Pen-

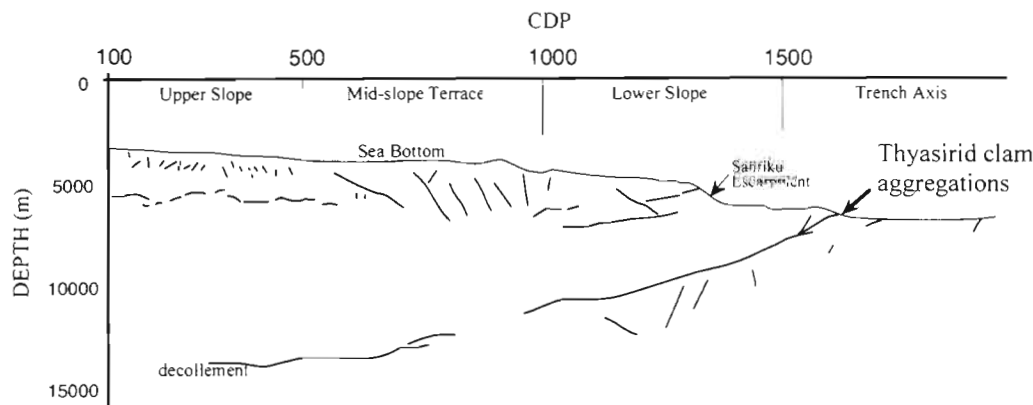
nec 1988). Thus the particles in *M. hadalis* appear more similar to symbionts in *C. phaseoliformis* than to other thyasirid species; (3) a hydrogen sulfide (H_2S) smell was easily detected from the soft parts of *M. hadalis* and collected sediments; (4) the sediments within the aggregations were locally dark gray to black, suggesting an anoxic and high sulfide environment; (5) many species belonging to the family Thyasiridae have symbiotic bacteria in their gills (Dando & Southward 1986, Southward 1986, Distel & Wood 1992); (6) thyasirid bivalves have been reported from cold seeps at various depths along active and passive margins of the Atlantic, East Pacific and West Pacific oceans (Dando & Southward 1986, Southward 1986, Zonenshayn et al. 1987, Mayer et al. 1988, Lallemand et al. 1992, Fujikura et al. 1995, Olu et al. 1996b); (7) thyasirid species have been collected from cold seeps around Japan including: *Conchocele disjuncta* from the off Hatsushima site at 830 to 1230 m depth and from the Okinoyama Bank at 1040 to 1180 m depth in Sagami Bay (Fujikura et al. 1995), *Conchocele* sp. from the Yukie Ridge at a depth of 2050 m in the Nankai accretionary prism (Lallemand et al. 1992), and *Parathyasira kaireiae* from the landward slope at 5790 m and from the Sanriku Escarpment at 6390 m in the Japan Trench (Okutani et al. 1999) (Table 1).

Chemosynthesis-based communities in subduction zones are distributed along geologic faults via tectonic

Table 1. Endemic species from deep-sea cold seeps around Japan. *Not enough biological data. 1: Okutani & Egawa (1985), 2: Okutani & Métivier (1986), 3: Juniper & Sibuet (1987), 4: Ohta & Laubier (1987), 5: Sibuet et al. (1988), 6: Hashimoto et al. (1989), 7: Miura & Laubier (1989), 8: Lallemant et al. (1992), 9: Fujioka et al. (1993), 10: Okutani et al. (1993), 11: Fujikura et al. (1995), 12: Ogawa et al. (1996), 13: Okutani et al. (1996), 14: Ashi (1997), 15: Iwai & Momma (1997), 16: Okutani et al. (1997), 17: Kojima & Ohta (1997a), 18: Kojima & Ohta (1997b), 19: Kuramoto & Joshima (1998), 20: Matsumoto et al. (1998), 21: Fujikura (unpubl. data), 22: Fujikura et al. (unpubl. data), 23: Okutani et al. (unpubl. data)

<p>Nankai accretionary prism Dai-ni Tenryu Submarine Canyon *^{19, 22} 600 m Pogonophora Unidentified vestimentifera Mollusca <i>Calyptogena solidissima</i></p> <p>Ryukyu Islands area Kuroshima Knoll *^{20, 22, 23} 680–810 m Pogonophora Unidentified vestimentifera Mollusca <i>Vesicomya</i> sp. <i>Calyptogena solidissima</i></p> <p>Sagami Bay off Hatsushima Island site ^{1, 6, 11, 17} 830–1230 m Annelida <i>Protomystides hatsushimaensis</i> <i>Nicomache ohtai</i> <i>Shinkai sagamiensis</i> <i>Natsushima bifurcata</i> Nautiliniellidae gen. sp. Unidentified polychaeta Pogonophora <i>Lamellibrachia</i> sp. Unidentified vestimentifera Mollusca <i>Serradonta vestimentifericola</i> <i>Bathymacra nipponica</i> <i>Margarites shinkai</i> <i>Provanna glabra</i> <i>Oenopota sagamiana</i> <i>Phymorhynchus buccinoides</i> <i>Acharax johnsoni</i> <i>Bathymodiolus japonicus</i> <i>Bathymodiolus platifrons</i> <i>Lucinoma yoshidai</i> <i>Conchocele disjuncta</i> <i>Calyptogena soyoe</i> <i>Calyptogena okutanii</i></p> <p>Arthropoda <i>Neolepas</i> sp. <i>Alvinocaris longirostris</i> <i>Lebbeus</i> sp.</p> <p>Nankai accretionary prism Ryuyo Submarine Canyon *^{13, 14} 1000 m Mollusca <i>Calyptogena okutanii</i> <i>Calyptogena nankaiensis</i></p>	<p>Sagami Bay Okinoyama Bank ^{11, 17} 1040–1180 m Annelida <i>Nicomache ohtai</i> <i>Natsushima bifurcata</i></p> <p>Pogonophora <i>Lamellibrachia</i> sp. Unidentified vestimentifera Mollusca <i>Bathymacra nipponica</i> <i>Margarites shinkai</i> <i>Provanna glabra</i> <i>Acharax johnsoni</i> <i>Bathymodiolus japonicus</i> <i>Bathymodiolus platifrons</i> <i>Bathymodiolus adaloides</i> <i>Conchocele disjuncta</i> <i>Calyptogena soyoe</i> <i>Calyptogena okutanii</i></p> <p>Suruga Bay off Toi Town site *^{10, 21} 1490 m Pogonophora Unidentified vestimentifera Mollusca <i>Calyptogena fausta</i></p> <p>Nankai accretionary prism Yukie Ridge ^{8, 18} 1940–2180 m Mollusca <i>Solemya</i> sp. <i>Conchocele</i> sp. <i>Calyptogena similis</i> <i>Calyptogena fausta</i></p> <p>Tokai Thrust *^{14, 15} 2080 m Pogonophora Unidentified vestimentifera Mollusca <i>Calyptogena similis</i></p> <p>Dai-ichi Minami Muroto Knoll *^{15, 22} 3620 m Mollusca <i>Calyptogena nautilei</i></p> <p>Dai-san Tenryu Submarine Canyon ^{22, 23} 3760 m Mollusca <i>Vesicomya</i> sp. <i>Calyptogena nautilei</i> <i>Calyptogena kaikoi</i> <i>Calyptogena laubieri</i> <i>Calyptogena</i> sp.</p>	<p>Nankai accretionary prism Tenryu Submarine Canyon ^{2, 3, 4, 5} 3760–3840 m Cnidaria Unidentified actinian Annelida Serpulid polychaeta Mollusca <i>Calyptogena nautilei</i> <i>Calyptogena kaikoi</i> <i>Calyptogena laubieri</i></p> <p>Zenisu Ridge *⁴ 4020 m Mollusca <i>Calyptogena</i> spp.</p> <p>Kurile Trench *^{4, 5} 4980–5780 m Mollusca <i>Calyptogena phaseoliformis</i></p> <p>Japan Trench Kashima Seamount ^{3, 4, 5} 5130–5770 m Cnidaria Unidentified actinian Annelida Tube-dwelling polychaetes Mollusca <i>Calyptogena phaseoliformis</i></p> <p>Arthropoda Caprellid amphipod landward slope ^{3, 4, 5, 7, 23} 5640–5940 m Cnidaria Unidentified actinian Annelida <i>Nautilina calyptogenicola</i> Tube-dwelling polychaetes Mollusca <i>Parethyasira kaireiae</i> <i>Calyptogena phaseoliformis</i></p> <p>Arthropoda Caprellid amphipod Sanriku Escarpment ^{9, 12, 23} 6270–6440 m Cnidaria Unidentified actinian Annelida Tube-dwelling polychaetes Mollusca <i>Parethyasira kaireiae</i> <i>Calyptogena phaseoliformis</i> <i>Calyptogena</i> sp.</p> <p>Arthropoda Caprellid amphipod</p> <p>Present study site 7326 m Mollusca <i>Maorithyas hadalis</i></p>
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Fig. 6. Geologic structure recorded by a multichannel seismic reflection system on the landward slope of the Japan Trench (modified from von Huene & Culotta 1989). Bold solid lines below the sea bottom show geologic faults. Thyasirid aggregations occurred above a geologic fault. One CDP (common depth point) = 25 m



compression or extension. Seismic data for the region (von Huene & Culotta 1989) revealed that the thyasirid aggregations occurred above a geologic fault near the bottom of the Japan Trench (Fig. 6). Fluids seep out of these faults, providing nutrients for chemosynthesis-based species. Seep fluid is generally characterized by high methane concentrations and is often low in sulfide (Sibuet & Olu 1998). Sulfide is produced in sediments from microbial sulfate reduction (Masuzawa et al. 1992). Sulfide for these thyasirid aggregations may be produced in this way, using methane as an energy source.

The distribution of this community seems more restricted than seep communities in other areas, such as Sagami Bay (Hashimoto et al. 1989, Fujikura et al. 1995), the Nankai accretionary prism (Juniper & Sibuet 1987, Ohta & Laubier 1987, Sibuet et al. 1988), Monterey Bay (Barry et al. 1996), the Peruvian active margin (Olu et al. 1996a) and the Barbados prism (Olu et al. 1996b). Detailed observations show that the newly discovered communities differ in other aspects as well. Each aggregation of *Maorithyas hadalis* was very small and contained no other commonly endemic chemosynthetic taxon (for example vestimentiferan tube worms, vesicomyids and *Bathymodiolus* bivalves, or provannid gastropods). In shallower (from 4981 to 5938 m) cold seep communities in the Japan Trench (dominated by *Calyptogena phaseoliformis*), numerous actinians, buccinid and rissocean gastropods, tube-dwelling polychaetes, caprellid amphipods, and swimming holothurians (*Peniagone* sp.) are consistently associated with *Calyptogena* aggregations (Juniper & Sibuet 1987, Ohta & Laubier 1987, Sibuet et al. 1988), but they were not observed in these thyasirid aggregations. The tubes observed at this site were curved and sparsely distributed, while those tubes commonly observed within *Calyptogena*-dominated sites are straight and densely packed. The Eurycopidae-like isopods and *Scotoplanes*-like holothurians were similar to the *Storhyugura*-type isopods and *Scotoplanes globosa* ob-

served near *Calyptogena* aggregations (Ohta & Laubier 1987).

Species occurring in chemosynthesis-based communities are classified into 3 types: endemic, colonists, and vagrants (Carney 1994). Endemic species are completely restricted to cold seep environments; colonist species are more abundant in cold seep areas than in surrounding areas; vagrant species may profit from the organic enrichment around seeps, but remain common beyond the influence of seep areas. Using these definitions, species within the thyasirid aggregations may be classified. *Maorithyas hadalis* is an endemic species, while the Eurycopidae-like isopods and *Scotoplanes*-like holothurians are colonists. There were not enough of the tube-dwelling species to afford classification. Sibuet & Olu (1998) suggested that species richness of chemosynthesis-based communities tends to decrease with increasing depth. Data from the present study support this idea as only 1 endemic species occurred at this deepest known site. A summary of data on endemic species collected from cold seep sites around Japan, however, is inconclusive (Table 1). Of the 3 major regions surveyed sufficiently for comment, it does appear that the number of endemic species generally decreases with depth. There are more endemic species reported from Sagami Bay than from the Nankai accretionary prism, and more from both these areas than from the Japan Trench. Moreover, the number of endemic species from the best studied individual sites within each region generally decreases with depth. The exceptions listed in Table 1 appear in areas which are not well studied. Therefore these areas need to be more fully explored before a conclusive statement regarding endemic diversity at chemosynthetic sites can be made for all cold seep sites around Japan.

Five bivalve families have some species known to be endemic to chemosynthetic environments, including the Solemyidae (Métivier & von Cosel 1993, Fujikura et al. 1995, Olu et al. 1996a,b), Mytilidae (Cavanaugh

1983, Hashimoto & Okutani 1994, Ohno et al. 1996, Olu et al. 1996b), Lucinidae (Fisher & Hand 1984, Corselli & Basso 1996), Thyasiridae (Dando & Southward 1986, Southward 1986, Zonenshayn et al. 1987, Mayer et al. 1988, Fujikura et al. 1995, Okutani et al. 1999) and Vesicomidae (Cavanaugh 1983, Okutani & Egawa 1985, Brooks et al. 1987, Fisher et al. 1988, Barry et al. 1996, Ogawa et al. 1996). Members in these families occur in both vent and seep habitats and depend on chemosynthesis, using symbiotic bacteria in their gills (Reid & Bernard 1980, Cavanaugh 1983, Fisher & Hand 1984, Dando & Southward 1986, Fiala-Médioni & Felbeck 1990, Fisher 1990, Distel & Wood 1992, Dando et al. 1994, Nelson & Fisher 1995). Vertical distribution ranges of these species-rich families are summarized in Table 2. This report extends the known range of thyasirid clams from chemosynthetic environments, nearly doubling it (it is unclear if thyasirids reported deeper than 10 000 m [Belyaev 1966] had chemosynthetic symbionts). The deepest previously-known report for the family was from 3840 to 3890 m in the Laurentian Fan (Mayer et al. 1988), and they have been reported from near the surface at 15 m (Southward 1986), and many depths in between (in Sagami Bay from 830 to 1230 m (Fujikura et al. 1995), west of Paramushir Island at 770 m (Zonenshayn et al. 1987), the Barbados prism at 1300 m (Olu et al. 1996b), and the Nankai accretionary prism at 2000 m (Lallemant et al. 1992).

This community also extends the range for all chemo-synthesis-based bivalves, replacing the previous record of 6437 m for *Calyptogena phaseoliformis* which was also collected from the Japan Trench (Ogawa et al. 1996). It is interesting to speculate why *C. phaseoliformis* does not occur at these thyasirid aggregation sites. One possibility is that the vertical range for *C. phaseoliformis* is more restricted as these thyasirids were collected nearly 900 m deeper than the deepest *C. phaseoliformis*. However, unlike any previously reported case for deep-sea thyasirid bivalves, almost all living *Maorithyas hadalis* were observed with 20 % of the shell exposed. The typical case for thyasirids is to live buried completely within the sediment, reaching depths 8 to 9 times their shell length (Dando & Southward 1986). This suggests that the available sulfide layer at the present site is relatively thin and near the surface. If so, *C. phaseoliformis* may be excluded from the site due to limited sulfide levels, either due to a thin sulfide layer near the surface, or by very low sulfide concentrations within the sediment. A thin sulfide layer might inhibit *Calyptogena* spp., as it has been

Table 2. Vertical ranges of the principal families of bivalvia which occur in chemosynthetic environments or have chemoautotrophic symbionts in the gills

Family	Shallowest habitat	Deepest habitat
Solemyidae	Eelgrass beds near Woods Hole (Cavanaugh 1983)	4776–4949 m Aleutian Subduction Zone (Suess et al. 1998)
Lucinidae	0.25 m St. Joseph's Bay, Florida (Fisher & Hand 1984)	1950 m Napoli Mud Volcano (Corselli & Basso 1996)
Thyasiridae	15 m Loch Etive, Scotland (Southward 1986)	7326 m Japan Trench (present study)
Mytilidae	432 m Kaikata Seamount, Ogasawara Islands area (Ohno et al. 1996)	3660 m Mariana Back-arc Basin (Hessler & Lonsdale 1991)
Vesicomidae	400 m Louisiana Slope (Brooks et al. 1987)	6437 m Japan Trench (Ogawa et al. 1996)

suggested that vesicomids gain an advantage over other seep taxa (Barry et al. 1996) based in part on their ability to acquire sulfide through a burrowing foot separately from oxygen brought in through an incur-rent siphon from overlying seawater (Fisher 1990). Thyasirids are often found in areas with free sulfide levels less than 1.0 μM (Fisher 1990). Conversely, sulfide levels from *Calyptogena* spp. habitats have relatively high sulfide levels including: *C. magnifica* at 35 μM , the highest level at the vent in the Galapagos Rift (Fisher et al. 1988); *C. pacifica* at 0.09 mM and *C. kilmeri* at 10.9 mM to 11.3 mM in the Monterey Bay (Barry et al. 1996), *C. soyoe* at 0.05 to 0.6 mmol kg^{-1} in Sagami Bay (Hashimoto et al. 1995), some species of vesicomids (including 2 *Calyptogena* species) at 50 to 70 μM in the Nankai accretionary prism at a depth of 3950 m (Fiala-Médioni et al. 1993), and *Calyptogena* sp. at 43 to 183 μM in the Laurentian Fan (Mayer et al. 1988). Only 1 exception, an unknown *Calyptogena* species from the Nankai accretionary prism occurred at 0.1 μM (Fiala-Médioni et al. 1993). It remains unclear whether sulfide concentration levels or a thin near-surface sulfide layer or both are acting to restrict *C. phaseoliformis* from the present site. Future dives will examine the underlying sediment more carefully to ascertain how deep the thyasirid bivalves dwell. If thyasirids are found well below the surface, as is the normal case for the family, this would suggest low sulfide concentration is limiting *C. phaseoliformis*.

Fisher (1990) comments on the dispute as to whether or not thyasirid symbionts are intracellular as in all other bivalves with chemoautotrophic symbionts. His reluctance to accept claims to the contrary (see Herry

& Le Pennec 1987 and Reid & Brand 1986) is based mainly on inconclusive micrographs showing no clear membrane separating symbionts from the external environment. We believe symbionts in *Maorithyas hadalis* are indeed intracellular based on our micrographs showing more complete membrane bound vacuoles (Fig. 4B). Thus the case for extracellular symbionts as a distinguishing feature of thyasirids has to be reconsidered. If other members of the family do prove to have extracellular symbionts, then the intracellular symbionts of *M. hadalis* are the exception.

The existence of various types of chemosynthesis-based communities within the relatively restricted range of the Japan Trench has implications for biogeographic distribution and speciation in the deep sea. Deep-sea trenches (deeper than 6000 m) created by plate convergence exist in more than 20 areas around the world ocean. Chemosynthesis-based communities are likely distributed widely throughout the world, and their role in marine ecosystems is not yet well known.

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LITERATURE CITED

- Ashi J (1997) Distribution of cold seepage at the fault scarp of the eastern Nankai accretionary prism. *JAMSTEC J Deep-Sea Res* 13:495–501
- Barry JP, Greene HG, Orange DL, Baxter CH, Robison BH, Kochevar RE, Nybakken JW, Reed DL, McHugh CM (1996) Biologic and geologic characteristics of cold seeps in Monterey Bay, California. *Deep-Sea Res* 43:1739–1762
- Belyaev GM (1966) Hadal bottom fauna of the world ocean. *Izdatel'stvo 'Nauka', Moskva*, 1972. Translated from Russian, Israel Program for Scientific Translations, Jerusalem
- Brooks JM, Kennicutt MC II, Fisher CR, Macko SA, Cole K, Childress JJ, Bidigare RR, Vetter RD (1987) Deep-sea hydrocarbon seep communities: evidence for energy and nutritional carbon sources. *Science* 238:1138–1142
- Carney RS (1994) Consideration of the oasis analogy for chemosynthetic communities at Gulf of Mexico hydrocarbon vents. *Geo-Mar Lett* 14:149–159
- Cavanaugh CM (1983) Symbiotic chemoautotrophic bacteria in marine invertebrates from sulphide-rich habitats. *Nature* 302:58–61
- Corselli C, Basso D (1996) First evidence of benthic communities based on chemosynthesis on the Napoli mud volcano (Eastern Mediterranean). *Mar Geol* 132:227–239
- Dando PR, Southward AJ (1986) Chemoautotrophy in bivalve molluscs of the genus *Thyasira*. *J Mar Biol Assoc UK* 66: 915–929
- Dando PR, Austen MC, Burke RA Jr, Kendall MA, Kennicutt MC II, Judd AG, Moore DC, O'Hara SCM, Schmaljohann R, Southward AJ (1991) Ecology of a North Sea pockmark with an active methane seep. *Mar Ecol Prog Ser* 70:49–63
- Dando PR, Ridgway SA, Spiro B (1994) Sulphide 'mining' by lucinid bivalve molluscs demonstrated by stable sulphur isotope measurements and experimental models. *Mar Ecol Prog Ser* 107:169–175
- Distel DL, Wood AP (1992) Characterization of the gill symbiont of *Thyasira flexuosa* (Thyasiridae: Bivalvia) by use of polymerase chain reaction and 16S rRNA sequence analysis. *J Bacteriol* 174:6317–6320
- Fiala-Médioni A, Felbeck H (1990) Autotrophic processes in invertebrates nutrition: bacterial symbiosis in bivalve molluscs. In: Mellingør J (ed) *Animal nutrition and transport processes 1, Vol 5. Nutrition in wild and domestic animals*; Kinne RKH, Kinne-Saffran E, Beyenbeck KW (eds). Karger, Basel, p 49–69
- Fiala-Médioni A, Le Pennec M (1988) Trophic structural adaptations in relation to the bacterial association of bivalve molluscs from hydrothermal vents and subduction zones. *Symbiosis* 4:63–74
- Fiala-Médioni A, Boulégué J, Ohta S, Felbeck H, Mariotti A (1993) Source of energy sustaining the *Calyptogena* populations from deep trenches in subduction zones off Japan. *Deep-Sea Res* 40:1241–1258
- Fisher CR (1990) Chemoautotrophic and methanotrophic symbioses in marine invertebrates. *Aquat Sci* 2:399–436
- Fisher CR, Childress JJ, Arp AJ, Brooks JM, Distel D, Favuzzi JA, Felbeck H, Hessler R, Johnson KS, Kennicutt MC II, Macko SA, Newton A, Powell MA, Somero GN, Soto T (1988) Microhabitat variation in the hydrothermal vent mussel, *Bathymodiolus thermophilus*, at the Rose Garden vent on the Galapagos Rift. *Deep-Sea Res* 35:1769–1791
- Fisher MR, Hand SC (1984) Chemoautotrophic symbionts in the bivalve *Lucina floridana* from sea grass beds. *Biol Bull* 167:445–459
- Fujikura K, Hashimoto J, Fujiwara Y, Okutani T (1995) Community ecology of the chemosynthesis-based community at Off Hatsushima site, Sagami Bay, Japan. *JAMSTEC J Deep-Sea Res* 11:227–241 (in Japanese with English abstract)
- Fujioka K, Takeuchi A, Horiuchi K, Okano H, Murayama M, Hori Y (1993) Contrasted nature between landward and seaward slopes of the Japan Trench off Miyako, northeast Japan. *Proc JAMSTEC Symp Deep-Sea Res* 9:1–26
- Hashimoto J, Okutani T (1994) Four new mytilid mussels associated with deep-sea chemosynthetic communities around Japan. *Venus* 53:61–83
- Hashimoto J, Ohta S, Tanaka T, Hotta H, Matsuzawa S, Sakai H (1989) Deep-sea communities dominated by the giant clam, *Calyptogena soyoeae*, along the slope foot of Hatsushima Island, Sagami Bay, central Japan. *Palaeogeogr Palaeoclimatol Palaeoecol* 71:179–192
- Hashimoto J, Ohta S, Fujikura K, Fujiwara Y, Sukizaki S (1995) Life habit of vesicomyid clam, *Calyptogena soyoeae*, and hydrogen sulfide concentration in interstitial waters in Sagami Bay, Japan. *J Oceanogr* 51:341–350
- Hecker B (1985) Fauna from a cold sulfur-seep in the Gulf of Mexico: comparison with hydrothermal vent communities and evolutionary implications. *Biol Soc Wash Bull* 6: 465–473
- Herry A, Le Pennec M (1987) Endosymbiotic bacteria in the gill of the littoral bivalve molluscs *Thyasira flexuosa* (Thyasiridae) and *Lucinella divaricata* (Lucinidae). *Symbiosis* 4:25
- Hessler RR, Lonsdale PF (1991) Biogeography of Mariana Trough hydrothermal vent communities. *Deep-Sea Res* 38:185–199
- Iwai M, Momma H (1997) Deep-tow camera observation

- around the long-term deep sea floor observatory off Muroto, Nankai Trough: results from K96-09 cruise. JAMSTEC J Deep-Sea Res 13:521–533
- Jannasch HW, Mottl MJ (1985) Geomicrobiology of deep-sea hydrothermal vents. Science 229:717–725
- Juniper SK, Sibuet M (1987) Cold seep benthic communities in Japan subduction zones: spatial organization, trophic strategies and evidence for temporal evolution. Mar Ecol Prog Ser 40:115–126
- KAIKO I Research Group (1986) Topography and structure of trenches around Japan—data atlas of France-Japanese KAIKO Project, Phase I: Ocean Research Institute, University of Tokyo, Tokyo
- Kennicutt MC II, Brooks JM, Bidigare RR, Fay RR, Wade TL, McDonald TJ (1985) Vent type taxa in a hydrocarbon seep region on the Louisiana Slope. Nature 317:351–353
- Kojima S, Ohta S (1997a) *Calyptogena okutanii* n. sp., a sibling species of *Calyptogena soyoe* Okutani, 1957 (Bivalvia: Vesicomysidae). Venus 56:189–195
- Kojima S, Ohta S (1997b) Bathymetrical distribution of the species of the genus *Calyptogena* in the Nankai Trough, Japan. Venus 56:293–297
- Kulm LD, Suess E, Moore JC, Carson B, Lewis BT, Ritger SD, Kadko DC, Thornburg TM, Embley RW, Rugh WD, Massoth GJ, Langseth MG, Cochrane GR, Scamman RL (1986) Oregon subduction zone: venting, fauna and carbonates. Science 231:561–566
- Kuramoto S, Joshima M (1998) Precise gravity measurement for gas hydrate layer. JAMSTEC J Deep-Sea Res 14: 371–377
- Lallemant SE, Glaçon G, Lanriat-Rage A, Fiala-Médioni A, Cadet JP, Beck C, Sibuet M, Iiyama JT, Sakai H, Taira A (1992) Seafloor manifestations of fluid seepage at the top of a 2000-metre-deep ridge in the eastern Nankai accretionary wedge: long-lived venting and tectonic implications. Earth Planet Sci Lett 109:333–346
- Masuzawa T, Handa N, Kitagawa H, Kusakabe M (1992) Sulfate reduction using methane in sediments beneath a bathyal 'cold seep' giant clam community off Hatsushima Island, Sagami Bay, Japan. Earth Planet Sci Lett 110: 39–50
- Matsumoto T, Kimura M, Nishida S, Nakamura T, Ono T (1998) Chemosynthetic communities and surface ruptures discovered on the Kuroshima Knoll south of Yaeyama Islands (NT97-14 cruise). JAMSTEC J Deep-Sea Res 14: 477–491
- Mayer LA, Shor AN, Hughes Clarke J, Piper DJW (1988) Dense biological communities at 3850 m on the Laurentian Fan and their relationship to the deposits of the 1929 Grand Banks earthquake. Deep-Sea Res 35:1235–1246
- Métivier B, von Cosel R (1993) *Acharax alinae* n. sp., solemyidae (Mollusca: Bivalvia) géante du bassin de Lau. C R Acad Sci Paris, Sér III 316:229–237
- Miura T, Laubier L (1989) *Nautilina calyptogenicola*, a new genus and species of parasitic polychaete on a vesicomysid bivalve from the Japan Trench, representative of a new family Nautilinidae. Zool Sci 6:387–390
- Nelson DC, Fisher CR (1995) Chemoautotrophic and methanotrophic endosymbiotic bacteria at deep-sea vents and seeps. In: Karl DM (ed) The microbiology of deep-sea hydrothermal vents. CRC Press, Inc, Boca Raton, p 125–167
- Ogawa Y, Fujioka K, Fujikura K, Iwabuchi Y (1996) En echelon patterns of *Calyptogena* colonies in the Japan Trench. Geology 24:807–810
- Ohno T, Fujikura K, Hashimoto J, Fujiwara Y, Segawa S (1996) The hydrothermal vent community at the Kaikata Seamount near Ogasawara (Bonin) Islands, south Japan. JAMSTEC J Deep-Sea Res 12:221–230 (in Japanese with English abstract)
- Ohta S, Laubier L (1987) Deep biological communities in the subduction zone of Japan from bottom photographs taken during 'nautilé' dives in the Kaiko project. Earth Planet Sci Lett 83:329–342
- Okutani T, Egawa K (1985) The first underwater observation on living habitat and thanatocoenoses of *Calyptogena soyoe* in bathyal depth of Sagami Bay. Venus 44: 285–289
- Okutani T, Métivier B (1986) Descriptions of three new species of vesicomysid bivalves collected by the submersible *Nautilé* from abyssal depths off Honshu, Japan. Venus 45: 147–160
- Okutani T, Fujikura K, Hashimoto J (1993) Another new species of *Calyptogena* (Bivalvia: Vesicomysidae) from bathyal depth in Suruga Bay, Japan. Venus 52:121–126
- Okutani T, Kojima S, Ashi J (1996) An unusual vesicomysid bivalve, *Calyptogena nankaiensis* n. sp. from bathyal depth off Honshu, Japan. Venus 55:257–263
- Okutani T, Kojima S, Ashi J (1997) Further discovery of new taxon of vesicomysid clam from the Nankai Trough, off Honshu, Japan. Venus 56:185–188
- Okutani T, Fujikura K, Kojima S (1999) Two new hadal bivalves of the family Thyasiridae from the plate convergent area of the Japan Trench. Venus 58:49–54
- Olu K, Duperret A, Sibuet M, Foucher JP, Fiala-Médioni A (1996a) Structure and distribution of cold seep communities along the Peruvian active margin: relationship to geological and fluid patterns. Mar Ecol Prog Ser 132:109–125
- Olu K, Sibuet M, Harmegnies F, Foucher JP, Fiala-Médioni A (1996b) Spatial distribution of diverse cold seep communities living on various diapiric structures of the southern Barbados prism. Prog Oceanogr 38:347–376
- Reid RGB, Bernard FR (1980) Gutless bivalves. Science 208: 609–610
- Reid RGB, Brand DG (1986) Sulfide-oxidizing symbiosis in Lucinaceans: implications for bivalve evolution. Veliger 29:3–24
- Seno T, Sakurai T (1996) Can the Okhotsk plate be discriminated from the North American Plate? J Geophys Res 101: 11305–11315
- Sibuet M, Olu K (1998) Biogeography, biodiversity and fluid dependence of deep-sea cold-seep communities at active and passive margins. Deep-Sea Res II 45:517–567
- Sibuet M, Juniper SK, Pautot G (1988) Cold-seep benthic communities in the Japan subduction zones: geological control of community development. J Mar Res 46:333–348
- Southward EC (1986) Gill symbionts in thyasirids and other bivalve molluscs. J Mar Biol Assoc UK 66:889–914
- Suess E, Bohrmann G, von Huene R, Linke P, Wallmann KW, Lammers S, Sahling H (1998) Fluid venting in the eastern Aleutian subduction zone. J Geophys Res 103:2597–2614
- von Huene R, Culotta R (1989) Tectonic erosion at the front of the Japan Trench convergent margin. Tectonophysics 160: 75–90
- Zonenshayn LP, Murdmaa IO, Baranov BV, Kuznetsov AP, Kuzin VS, Kuz'min MI, Avdeyko GP, Stunzhas PA, Lukashin VN, Barash MS, Valyashko GM, Demina LL (1987) An underwater gas source in the Sea of Okhotsk West of Paramushir Island. Oceanology 27:598–602