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Microdistribution pattern and biogeography of the hydrothermal vent communities of the Minami–Ensei Knoll in the Mid-Okinawa Trough, Western Pacific

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Abstract—From 1988 to 1992, a series of deep-sea surveys was conducted to characterize hydrothermal vent fields on the Minami–Ensei Knoll, approximately 140 km west of Amami–Ohshima Island, southwest Japan, with a multi-narrow beam mapping system (Sea Beam), deep tow observing systems and the submersible *Shinkai* 2000. The vent fields were centered around the depressions on the western slope of the knoll. The hydrothermal vents emitted superheated water over 269°C through chimneys. Diffuse fluid discharged from fissures in rocks. Numerous patches of grayish white hydrothermal stains were observed on the bottom of coarse sand. Vent-associated biological communities consisted of sponges, vestimentiferans, alvinellid and polynoid polychaetes, cerithiid and trochid gastropods, lepetrodrillid limpets, vesicomyid clams, mytilid bivalves, bresiliid and hippolytid shrimp, zoarcid and cynoglossid fish, and lithodid and galatheid crabs. The hydrothermal vent communities of the Minami–Ensei Knoll showed many similarities to those of the Kaikata Seamount, the Mariana Back-Arc Spreading Center, the North Fiji Basin and the Lau Basin, as well as the cold seep communities of Sagami Bay. There may be considerable interchange among the Minami–Ensei Knoll communities and other chemosynthetic communities in the Western Pacific despite the 1000 km distance separating these communities and the existence of Ryukyu Trench and Ryukyu Arc. These discoveries, as well as other more recent findings around Japan, contribute significantly to our understanding of the biogeography of the hydrothermal vent and cold seep communities in the Western Pacific.

INTRODUCTION

SINCE the first discovery of deep-sea chemosynthetically-based communities associated with hydrothermal vents along the Galapagos Rift off the coast of Ecuador (CORLISS and BALLARD, 1977; CORLISS *et al.*, 1979), numerous similar biological communities have been reported, not only in tectonically active areas, such as on the axis of the East Pacific Rise (RISE PROJECT GROUP, 1980; DESBRUYÈRES *et al.*, 1982), on the Gorda, the Juan de Fuca and Explorer Ridges (TUNNICLIFFE, 1991), in the Mariana Back-arc Basin (HESSLER and LONSDALE, 1991), on the Mid-Atlantic Ridge (TUNNICLIFFE, 1991), in the Lau Back-arc Basin (STACKELBERG and SHIPBOARD SCIENTIFIC PARTY, 1988; DESBRUYÈRES *et al.*, 1994),

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along the subduction zone off Oregon (SUESS *et al.*, 1985), and in the North Fiji Basin (HASHIMOTO *et al.*, 1989b; JOLLIVET *et al.*, 1989; DESBRUYÈRES *et al.*, 1994), but also in tectonically passive areas, such as the base of the Florida Escarpment (PAULL *et al.*, 1984), on the continental slope off Louisiana (KENNICUTT II *et al.*, 1985), on the Laurentian Fan (MAYER *et al.*, 1988) and in Monterey Bay (EMBLEY *et al.*, 1990).

Around Japan, chemosynthetic communities have also been found on the landward flanks of the Nankai Trough and the Japan Trench (OHTA and LAUBIER, 1987; JUNIPER and SIBUET, 1987; FIALA-MÉDIONI *et al.*, 1993), in Sagami Bay (OKUTANI and EGAWA, 1985; HASHIMOTO *et al.*, 1987, 1988a, 1989b) and in the vicinity of the central cone of the Kaikata Caldera (HASHIMOTO *et al.*, 1988b; HASHIMOTO and HORIKOSHI, 1989).

In 1986, numerous empty shells of a vesicomyid clam, *Calyptogena solidissima*, were dredged on the Minami–Ensei Knoll during geomorphological and geophysical surveys of the Mid-Okinawa Trough by the Hydrographic Department, Maritime Safety Agency of Japan, and recent active hydrothermalism was suggested by ^{14}C dating of those shells (KATO *et al.*, 1989; OKUTANI *et al.*, 1992). Active hydrothermal mounds have been found during the submersible survey of the Mid-Okinawa Trough (KIMURA *et al.*, 1988), and a dense actinian assemblage supposedly associated with warm-water seepage were photographed along the Yaeyama Graben in the southern Okinawa Trough (KATSURA *et al.*, 1986).

In June 1988 hydrothermal vents and special vent fauna were discovered on the Minami–Ensei Knoll through deep tow surveys conducted by Japan Marine Science and Technology Center. Subsequently, a series of surveys with R.V. *Kaiyo*, the submersible *Shinkai* 2000, and her mother ship *Natsushima* was made to clarify the distribution of the vent communities and their biological and geological characteristics. This paper describes the microdistribution pattern of the Minami–Ensei Knoll in the Mid-Okinawa Trough and summarizes some biogeographic knowledge on the hydrothermal vent communities of the western and southwestern Pacific.

GEOLOGICAL SETTING

The Okinawa Trough, located southwest of Japan, is a depression about 100 km wide and about 1000 km long. Tertiary unconformities, high heat flow, fresh igneous rock intrusion, remarkable graben structures and hydrothermal activities have been observed in the center of the trough (LEE *et al.*, 1980; KATSURA *et al.*, 1986; KIMURA *et al.*, 1988). Subsequent surveys have provided us with evidence that the trough is an active back-arc basin under extensional stress and in an incipient stage of back-arc spreading related to subduction of the Philippine Sea Plate along the Ryukyu Trench (KIMURA, 1985; JAPANESE DELP RESEARCH GROUP on back-arc basins, 1986; KATSURA *et al.*, 1986; SIBUET *et al.*, 1987). The age of the Okinawa Trough was estimated to be 1.9–2.0 Ma on the basis of magnetic anomalies and high heat flow (LU *et al.*, 1981; KIMURA, 1985). However, a recent study suggested that the Okinawa Trough is an overlapping area between the island arc and expansion belt continued from the Tunghai Shelf which has not yet developed into a back-arc basin, according to geomagnetic, gravitational and topographic data (KATO *et al.*, 1989). Thus, further studies appear to be required in order to more adequately interpret geologic features associated with this region (KIMURA, 1989).

The biological communities were discovered on the western slope of the Minami–Ensei Knoll located approximately 140 km west of Amami–Ohshima Island (Fig. 1). The knoll is

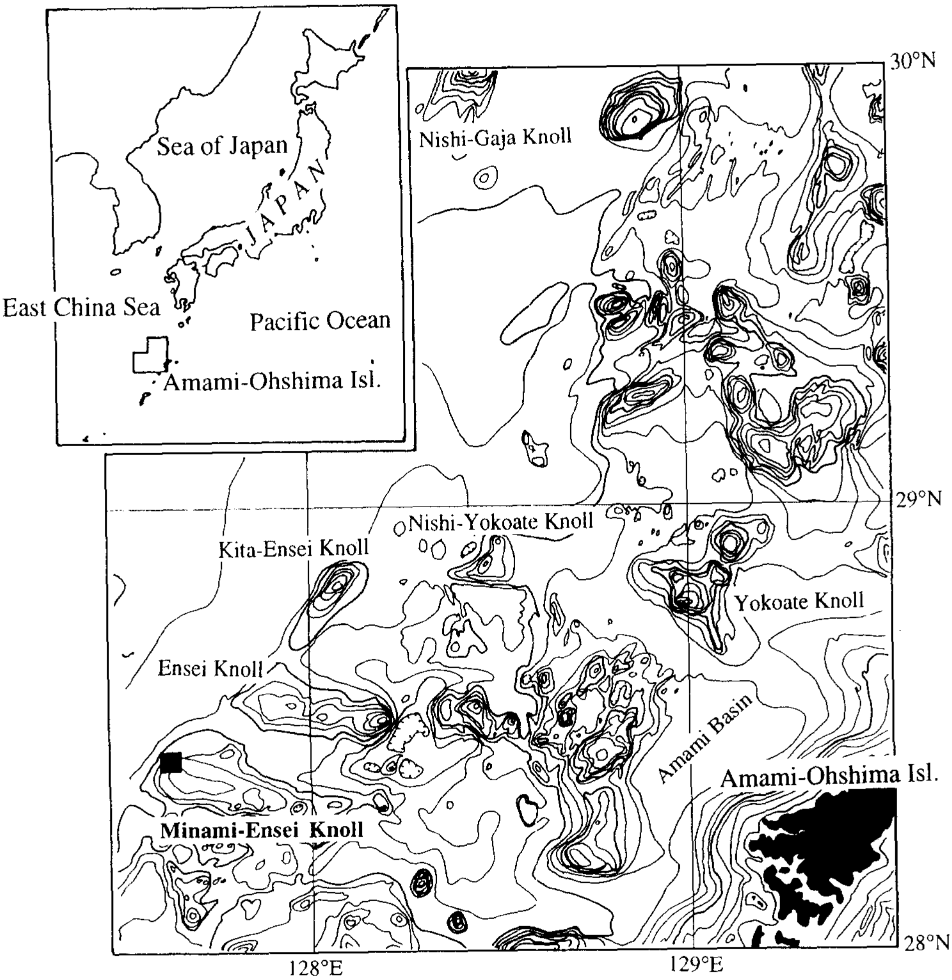


Fig. 1. Location of survey area.

situated at the northern part of the central graben of the Okinawa Trough, referred to the Torishima Central Graben. Many small knolls and several depressions are scattered to the south of the Minami-Ensei Knoll. An active volcano, Ioh-Torishima Island, is located southeast of the knoll. The ages of acidic rock samples from the Torishima Central Graben and its vicinity showed volcanism younger than 0.1 Ma (Kimura *et al.*, 1992). Explosive events were suggested by the analysis of collected volcanic rocks and hydrothermal ore deposits (Nedachi, personal communication). Thus, it appears that many of the observed depressions may be small calderas formed by volcanic activity. The Minami-Ensei Knoll shows an elliptical outline with the top situated at a depth of 550 m. The western part of the knoll is cut into three divisions by two ENE-WSW trending structural lines. Reverse faults trending NE or ENE were revealed by continuous seismic profilings made by the Geological Survey of Japan in the study area (Tamaki *et al.*, 1976).

Quartz diorite, hornblende granite, mudstone and dead shells of vesicomyid clams were collected from one of the depressions. The collected shells were estimated to be 1170 ± 80

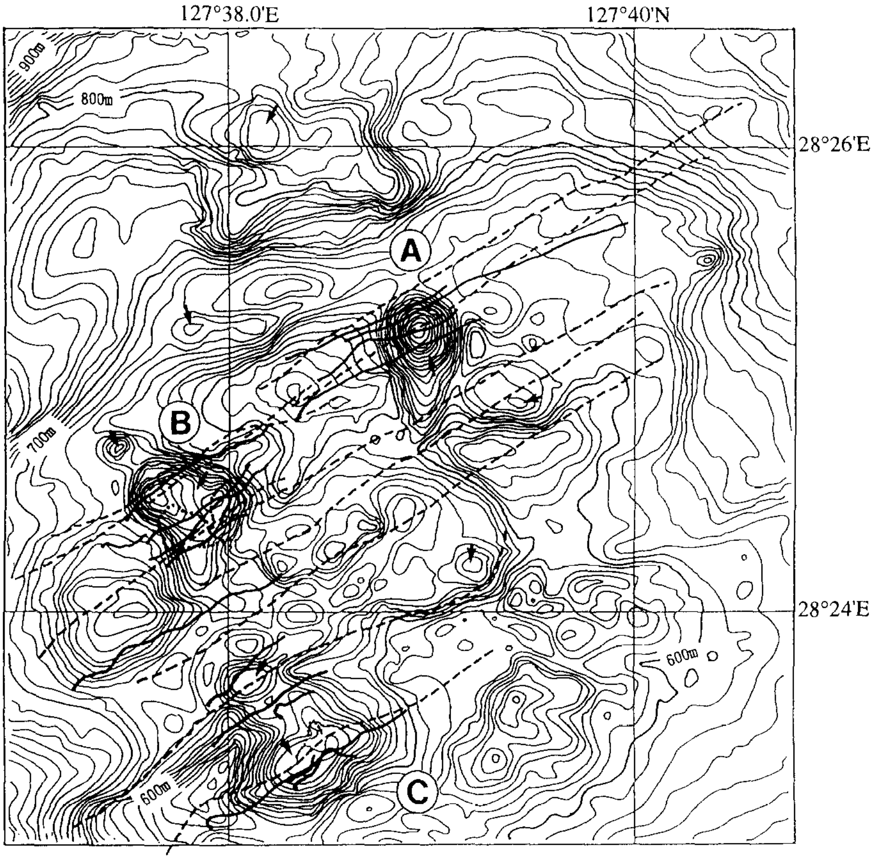


Fig. 2. Submarine topographic map of the western slope of the Minami–Ensei Knoll with deep tow tracks. Thick solid line: deep tow TV track, Dashed line: deep tow sonar track, Arrow: depression.

years old by ^{14}C dating. Therefore, hydrothermal activities were shown to be events of the Recent epoch (KATO *et al.*, 1989).

SURVEY RESULTS

In 1988, prior to other surveys, a detailed topographic map of the Minami–Ensei Knoll was prepared by a multi-narrow beam mapping system (Sea Beam: General Instruments Co.) fitted to the R.V. *Kaiyo*. Several small depressions, about 100–1000 m in diameter, were dotted on the western slope of the knoll (Fig. 2). Those depressions, which appeared to be small calderas formed by volcanic activity, were skirted by steep escarpments, approximately 100 m high. Three depressions (A, B and C shown in Fig. 2) were chosen as the main detailed survey sites. From 1988 to 1989, 10 side scanning sonar survey lines and 16 TV lines were set parallel to the ENE–WSW trend (Fig. 2). After these deep tow surveys, a total of 10 *Shinkai* 2000 dives were carried out in and around depressions B and C; these dives were intended to clarify geological and geomorphological controls on the distribution of the communities and their biological and geochemical characteristics.

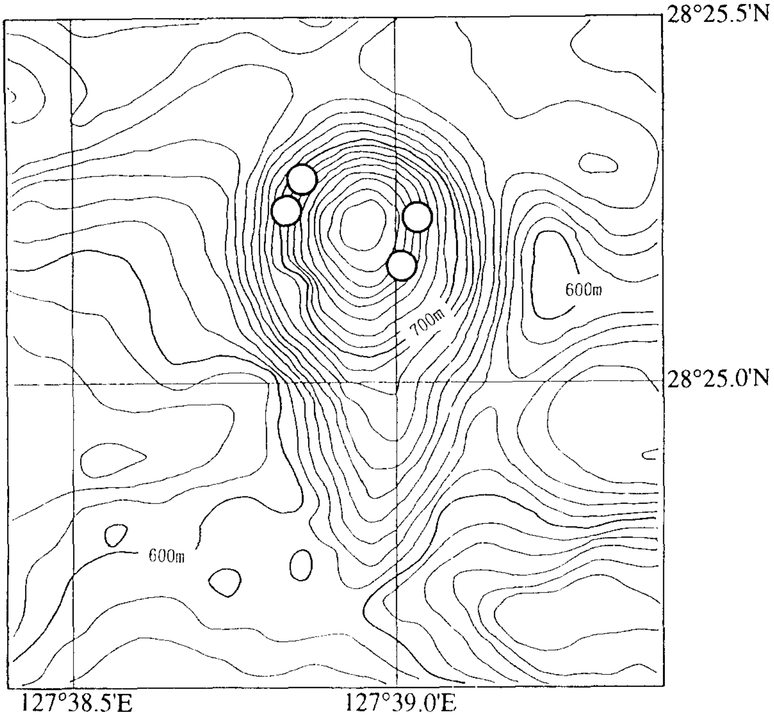


Fig. 3. Distribution of dead shells of *Calyptogena solidissima* in depression A. Open circle: heap of dead shells.

Depression A

In 1986, dead shells of *Calyptogena solidissima* were collected from depression A (Fig. 3) by the Hydrographic Department of the Maritime Safety Agency of Japan. This cone-shaped depression was about 600 m in diameter. The water depths of the central and marginal parts were 780 m and 670 m, respectively. Scattered huge rock outcrops, several meters in diameter, were observed around depression A. The central part was covered with thick fine sediments. Along the foot of the marginal steep escarpment, 700–750 m deep, many deposits of altered sediment with a yellowish brown and grayish white color were observed, as were empty shells of vesicomyid clams. The empty shells were easily recognized, because almost all of their valves gaped widely [Fig. 8(1)]. Several shells were collected by a small dredge installed in the deep tow TV frame. No biological community was seen by the deep tow TV at this site (Fig. 3).

Depression B

This pear-shaped depression about 1000 m in diameter, the deepest western part being 770 m deep, was found through the Sea Beam survey (Fig. 4). Large outcrops covered with thin sediments were exposed around the outside of the depression, as around depression A. Breccia and coarse sand filled the space between outcrops. Depression B was also encircled by a steep escarpment approximately 100 m high. Enormous breccia ranging in

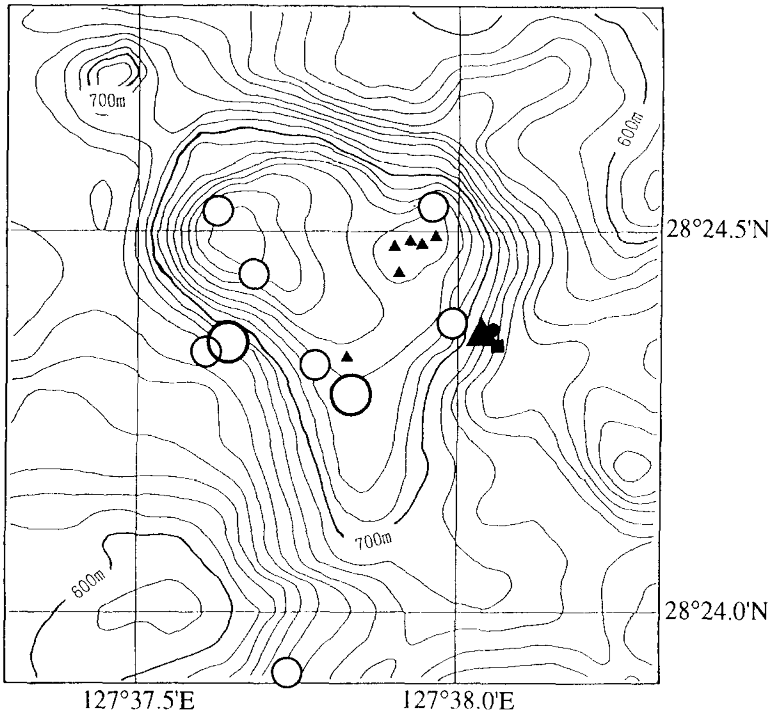


Fig. 4. Distribution of vent animals in depression B. Open circle: heaps of dead vesicomyid clams, closed circle: living vesicomyid clams, triangle: vestimentiferans, rectangle: deep-sea mussels.

size from tens to hundreds of centimeters across were piled, like a stone wall, in the middle part of the escarpment. The toe of the escarpment, at 720 m depth, consisted of gullies continuing into flat bottom covered with thick fine sediments and coarse sand. The bottom had many scattered grayish white stains. Those deposits increased in density toward the escarpment. The floor was covered mostly with thick sediment scattered with small pumice pieces, several millimeters in diameter.

Small-scale heaps (2–3 m in diameter) of dead vesicomyid clam shells were found along the foot of the steep escarpment and along the marginal part. A few living clams were observed in the vicinity of some thanatocenoses. A vast field of vestimentiferans, over 200 m in diameter, was observed on the flat bottom. Individual vestimentiferans were positioned vertically on the sediment with two-thirds of their tube length in the sediment [Fig. 8(2)]. The density was estimated by stereographic analysis of bottom photographs to be over 10 individuals per square meter. A positive temperature anomaly of over 0.1°C was measured 30 cm below the sediment surface, suggesting low temperature seepage out of the sea floor. Several individuals of the buccinid gastropod *Neptunea insularis* were found on and around the skirt of the escarpment (OKUTANI *et al.*, 1993).

A tangled cluster consisting of hundreds of vestimentiferans attributed to two different species was encountered at the eastern margin [Fig. 8(3)]. Their tubes were 0.5–1 cm in diameter and 20–60 cm in length. The site was covered with many large breccia of unknown composition. Grayish white stains were observed on breccia 15–20 m away from the vestimentiferan cluster. Gaps among breccia were thickly filled with coarse, grayish sand. At the center of the vestimentiferan cluster, "shimmering" water was observed, venting from the sandy bottom and from fissures on the rocks. The temperature just above the effluent was 9.9°C, compared to 7.0°C at the same depth about 3 m outside of the cluster, which was similar to ambient bottom seawater temperature. Water collected from the warm seepage gave a strong odor of hydrogen sulfide; a hydrogen sulfide level of 2.6 ppm and a methane value of 2200 nl kg^{-1} were measured from the retrieved seawater (GAMO, personal communication). The cluster of vestimentiferans was about 3 m in diameter and roughly spherical in shape. Sponges, filamentous bacteria (probably *Beggiatoa*) and a turbinid gastropod, *Cantrainea jamsteci* [*Thermocollonia jamsteci* has been replaced by the genus *Cantrainea* recently by WAREN and BOUCHET (1993)], were attached to the outer surface of the vestimentiferan tube (OKUTANI and FUJIKURA (1990)). Three limpet species (*Puncturella parvinobilis*, *Bathyacmaea secunda* and *Lepetodrilus japonicus*) and two species of cerithiid gastropods, including *Provanna glabra*, were collected on scattered outcrops and on sandy bottom in close proximity to the vent fluid. Two living specimens of *Calyptogena solidissima* were buried approximately one-third to one-half of their shell length into the coarse sand. Two mussel specimens (*Bathymodiolus aduloides*) were attached to a breccia in the center of the cluster, where shimmering water was observed (HASHIMOTO and OKUTANI (1994)). The mussel differed from *Bathymodiolus thermophilus* of Galapagos Rift by the absence of inner mantle fusion in the antero-ventral region, a different shell form, and a different orientation of muscle scars. The species was also collected at the Izena Caldron and the Iheya Ridge, in the Mid-Okinawa Trough. A zoarcid fish species, a cottid fish (*Psychrolutes inermis*) and a lithodid crab of genus *Paralomis* were creeping on or lying amongst the mussel assemblage. Many specimens of an asteroid, *Ceramaster misakiensis*, were found on breccia. The distribution of vent communities at depression B is depicted in Fig. 4.

Depression C

Depression C was irregular in shape 5. As in the case of the other depressions, this depression was also encircled by a steep escarpment approximately 100 m high. Breccia ranging in size from tens to hundreds of centimeters was piled as talus in the middle part of the escarpment. The deepest part of the depression was 720 m. The rather flat bottom of the depression was approximately 1000–1200 m across, with approximately 10 m in relative altitude. A group of black and white smokers vigorously emitted superheated water (Fig. 5). Enormous dense aggregations of a deep-sea mussel (*Bathymodiolus japonicus*) were discovered at the center (HASHIMOTO and OKUTANI (1994)). Shimmering water and hot vents with small bubbles were found at various places including fissures on outcrops and sandy bottom. More than twenty chimneys 50–250 cm in height and consisting of Kuroko-type sulfide ore and gypsum-anhydrite blocks (NEDACHI *et al.*, 1992) appeared like tree trunks in a dense forest on mounds with heights of approximately 5–6 m. These vents were trending in a north–south direction over the center of the bottom.

One of the active smokers, approximately 70 cm in height and 15 cm in diameter, stood on a huge rock covered with enormous mussels ranging in shell length from approximately 5 to 100 mm [Fig 8(4)]. Clear hydrothermal fluid up to 269°C was gushing out from the surface of this chimney. Water samples from other chimneys kept at *in situ* pressure effervesced furiously when the sample was exposed to the atmospheric pressure. The pH

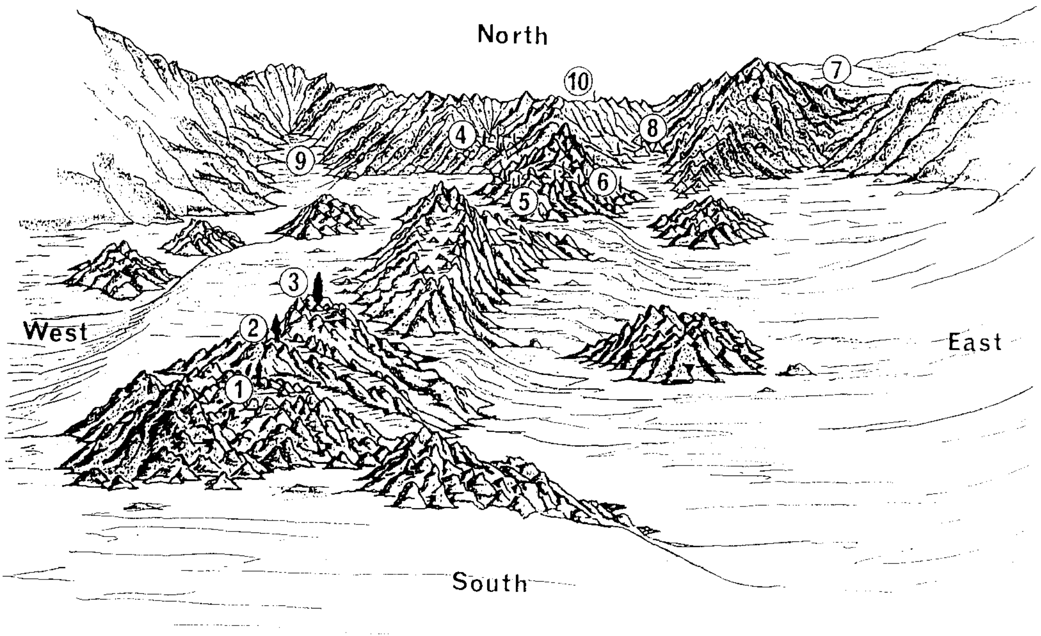


Fig. 5. A general view of the hydrothermal vents in depression C. (1) Yunoi (hot spring in Japanese) Chimney [Fig. 8. (4)] (2) Taimatsu (torch in Japanese) Chimney (3) Yajiri (arrowhead in Japanese) Chimney (4–5) small crowd of chimneys (6) large crowd of extremely active chimneys (7) White Clam Hill (numerous living specimens of *Calyptogena solidissima* inhabit the coarse sand bottom) (8) Mussel Valley (a steep escarpment is covered with enormous living deep-sea mussels) (9) thanatocoenoses of *Calyptogena solidissima* (10) large chimney, approximately 25 cm in outer diameter, 3.5 m in height.

value of these samples registered approximately 5; CO_2 concentration was 630 ppm. Concentrations of Zn, Cu and Mn in 258°C hydrothermal fluid were approximately 0.74–0.79 mg kg^{-1}, 0.14–0.33 mg kg^{-1} and 0.06–0.80 mg kg^{-1}, respectively. These values were two to three orders of magnitude higher than those found in normal seawater. The concentrations of Fe and Al were also two orders of magnitude higher. The concentration of CO_2 in the surrounding bottom water was 1700 ppm (NOGAMI, personal communication). Clear and cloudy gas bubbles rich in CO_2 [like the gas bubbles of the Izena Caldron (SAKAI *et al.*, 1990)] were observed to emerge from whitish, metachromatic, sandy bottom and dense mussel beds along the crowded chimneys. Sherbet-like substances, probably CO_2 hydrate, emerged intermittently out of the seafloor. However, this phenomenon was inclined to decrease with distance from the most active vent.

Small assemblages and dead remains of *Calyptogena solidissima* were found on the rim and at the base of the encircling steep slope [Fig. 8(5)]. Although no active venting or shimmering water was observed in this area, a temperature anomaly of +0.3°C was recorded at 30 cm below the white-stained bottom surface. Living clams buried themselves about one half to two-thirds of their shell length into the sediment. Progressing towards the center of the depression, whitish metachromatic sediments and whitish bacterial mats were increasingly apparent. Abundant specimens of *Cantrainea jamsteci* and a lithodid crab of the genus *Paralomis* (different from the species encountered in depression B) and several specimens of *Neptunea insularis* were crawling around bacterial mats. Closer to the center of the depression, approximately 100–150 m away from venting areas, shimmering water with small gas and liquid bubbles was identified in all directions. Large breccia, outcropping rocks and mounds were covered with numerous sponges. There were dozens of specimens of a cynoglossid fish, *Symphurus* cf. *orientalis*, around the whitish metachromatic sediment [Fig. 8(6)]. Additionally five or more species of gastropods, *Provanna glabra* and limpets, *Lepetodrilus japonicus*, *Puncturella parvinobolis* and *Bathyacmaea secunda*, were found or captured near the stained bottom. Many specimens of fish and shrimp were found among crevices between breccia and outcrops covered with tremendous numbers of unidentified sponges. There were two hagfish, *Eptatretus okinoseanus* and *Myxine garmani*, a cottid fish, *Psychrolutes inermis*, a hippolytid shrimp, *Lebbeus washingtonianus* and an undescribed crangonid shrimp of the genus *Paracrangon*.

One of the most abundant and conspicuous organisms in the vicinity of the observed hydrothermal vent was a mussel, *Bathymodiolus japonicus*. Each mussel assemblage was composed of various size-classes, ranging from juveniles to adults. A polynoid polychaete, *Branchipolynoe pettiboneae* and a nautiliniellid, *Mytilidiphila okinawaensis*, were found in the mantle cavity of the mussel (MIURA and HASHIMOTO, 1991, 1993). The surfaces of the shells abutting on vent openings were covered thickly with filamentous bacteria probably belonging to the genus *Beggiatoa*. Three species of limpet, *Lepetodrilus japonicus*, *Puncturella parvinobilis* and *Bathyacmaea secunda*, were attached to the shell surface of the mussel. A large number of larvae and juveniles of harpacticoid copepods inhabited the mats of filamentous bacteria (TODA, personal communication). An alvinellid polychaete, *Paralvinella hessleri*, was captured from the surface of active chimneys and in the vicinity of active vent openings. Numerous bresiliid shrimp, probably belonging to the genus *Alvinocaris* and a bythograeid crab were found in the small hollows of chimneys and among the mussel beds bathing directly in the hydrothermal fluids. *Paralomis jamsteci* and a galatheid crab close to the genus *Munidopsis* (the same species was collected from the Izena Caldron and the Iheya Ridge) were observed resting or creeping among the mussels in the vicinity of vent openings (TAKEDA and HASHIMOTO, 1990). Zoarcid fishes were seen less frequently, partially because they sometimes hide among the mussels.

A burrowing mussel of the subfamily Bathymodiolinae was found on the sandy bottom in the depression as well as on the western rim of the depression, which may be related to the species collected at the Kaikata Seamount (HASHIMOTO and HORIKOSHI, 1989). In the mantle cavity of the mussel, *Branchipolynoe pettiboneae* and *Mytilidiphila enseiensis* were found frequently (MIURA and HASHIMOTO, 1993).

Another small depression (connected via a flat corridor 670 m deep) was observed to the northwest of depression C. The central portion of this small depression was covered with coarse sand and breccia. Sponges consisting of *Pheronema* sp., *Euplectella* sp. and an unidentified species were attached to outcrops along the surrounding steep slope. Around the small depression, however, there was no indication of hydrothermal activity other than grayish white flecks on the coarse sand along the flat corridor connecting to depression C. A strong bottom current was suggested by ubiquitous ripple marks over the regions. Thanatocenoses of *Calyptogena solidissima* were recognized along the base of the slope of the surrounding steep escarpment and at the margin of this small depression. Bacterial mats, small assemblages of *C. solidissima* and a few solitary tube-worms were seen at the

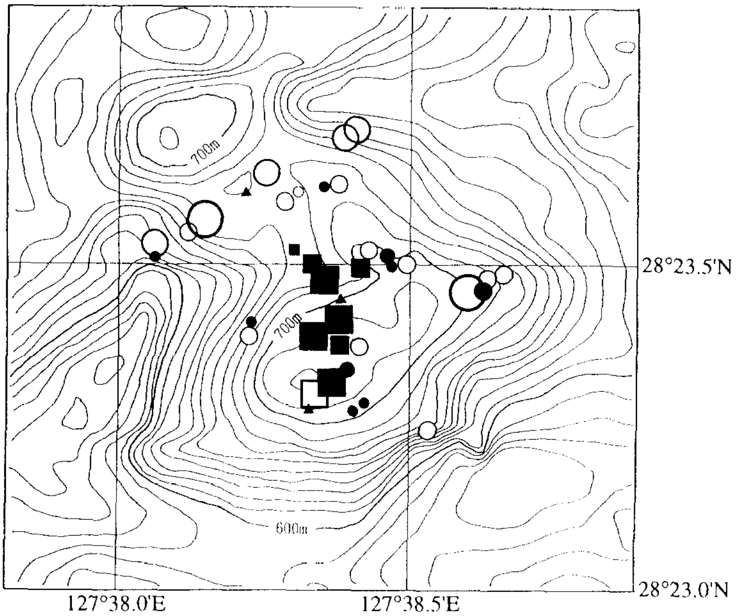


Fig. 6. Distribution of vent communities in depression C. Open circle: heaps of dead vesicomyid clams, closed circle: living vesicomyid clams, triangle: vestimentiferans, open rectangle: heaps of dead deep-sea mussels, closed rectangle: deep-sea mussel assemblage.

periphery of small outcrops along the central flat bottom. The distribution of the vent communities in depression C is shown in Fig. 6.

DISCUSSION AND CONCLUSIONS

Microdistribution pattern

At least 48 species of deep-sea organisms were collected from the Minami-Ensei Knoll and six additional species were observed (Table 1). The organisms tended to segregate according to the habitat influenced by the different hydrothermal activities. The hydrothermal habitat can be roughly categorized into two types: (1) rocky or exposed field with active superheated vents and/or low-temperature vents; and (2) sedimentary or covered field where low-temperature hydrothermal fluid approximately 5–10°C higher than the ambient seawater percolates from the sandy bottom.

Deep-sea mussels, with symbiotic bacteria living in the unusually thick gill, were dominant in the rocky field habitat. Filamentous bacteria (a primary producer in the hydrothermal ecosystem) and limpets (a primary consumer) were attached to the surface of the mussel. *Paralvinella hessleri* may be a primary consumer in the same manner as *Alvinella caudata* and *A. pompejana* (GAILL *et al.*, 1988). *Paralomis jamsteci*, *Alvinocaris* sp., an unidentified bythograeid crab and a munidopsid galatheid are thought to be predators in the rocky field habitat. Alvinocarid shrimp is thought to be a primary

Table 1. List of collected and observed species and habitat in which species was found at the Minami-Ensei Knoll. *, *uncollected specimens*; ×, *present*; ××, *abundant*

		Habitat	
	Species	Rocky field	Sedimentary field
Porifera	*_Euplectella_	×	
	*_Pheronema_	×	
	unidentified sp.	×	
Vestimentifera	unidentified spp. (2 species), new species (?)	×	×
Polychaeta	_Eunice masudai_	×	
	Eunice northioidea	×	
	Eunice spp. (4 species)	×	
	Schistomeringos sp.		×
	Ophryotrocha sp.		×
	Syllidae or Hesioniidae gen. sp.	×	
	Paraonidae gen. sp.		×
	Capitella sp.		×
	Ampharetidae gen. sp.		×
	Maldanidae gen. sp.		×
	Branchipoynoe pettibonaeae	×	
	Polynoidae gen. sp.	×	
	Sabellidae gen. sp.	×	×
	Terebellidae gen. sp.		×
	Paralvinella hessleri	×	
	Mytilidiphila enseiensis, new species	×	
	Mytilidiphila opkinawaensis, new species	×	
	Nautiliniellidae gen. sp.	×	×
Mollusca			
	Gastropoda		
	Neptunea insulalis		×
	Cantrainea jamsteci, new species	×	××
	Provanna glabra, new species	××	×
	Cerithiidae gen. sp. new species (?)	×	
	Lepetodrilus japonicus, new species	×	×
	Puncturella parvinobilis, new species	×	×
	Bathyacmaea secunda, new species	×	×
	Bivalvia		
	Calyptogena solidissima, new species		×
	Bathymodiolus japonicus, new species	××	
	Bathymodiolus aduloides, new species	×	
	Bathymodiolinae gen. sp. new species		×
Arthropoda			
	Copepoda		
	Extinosomidae gen. sp.	×	×(?)
	Cerviniidae gen. sp.	×	×(?)
	Hyphalion sp.	×	×(?)
	Malacostraca, Decapoda		
	Alvinocaris sp.	××	
	Lebbeus washingtonianus	××	×
	Paracrangon sp., new species	×	
	*Bythograeidae gen. sp.	×	
	Paralomis jamsteci, new species	×	×
	Paralomis spp. (2 species)	×	×
	Munidopsidae gen. sp., new species	×	
Asteroidea	_Ceramaster misadiensis_	×	×
Pisces	Zoarcidae gen. sp., new species(?)	×	
	Psychrolutes inermis	×	
	*_Symphurus_ cf. _orientalis_		×
	*_Myxine garmani_	×	
	*_Eptatretus okinoseanus_	×	

consumer at vent fields (see also VAN DOVER and FRY, 1989). Zoarcid fish were found to feed on small specimens of *Lebbeus washingtonianus*. Bresiliid shrimp living in the small hollows among the mussel beds and bathing directly in high-temperature vent fluids, however, were not included in the stomach contents of sampled zoarcids. Sponges, an undescribed crangonid shrimp and two species of hagfish occupied the outer margin of the rocky field, approximately 100–150 m away from active smokers. *Psychrolutes inermis*, a cottid fish of the rocky field, fed on small crustaceans such as young specimens of *Lebbeus washingtonianus*, harpacticoid copepods living among the filamentous bacterial mats and unidentified amphipods.

Lebbeus washingtonianus is one of the most aggressive predators inhabiting both the rocky and sedimentary fields (OHTA, 1990a). Many gastropods and limpets found in both fields may graze on chemosynthetic bacteria and their secretion on the surface of the rocks, vestimentiferan tubes and bivalve shells by their rhipidoglossate radula. *Cantrainea jamsteci* is thought to be a grazer. *Provanna glabra*, which occurs in both fields, may be a carnivore because of its taenioglossate radula.

Calyptogena soldissima, two vestimentiferan species and a burrowing deep-sea mussel occupied the sedimentary field. In this field, an undescribed lithodid crab of the genus *Paralomis* was observed roaming the sandy bottom. *Symphurus* cf. *orientalis* was seen to feed on polychaetes in the same manner as observed on the Kaikata Seamount (HASHIMOTO, unpublished data). Furthermore, non-vent organisms, such as a buccinid gastropod, *Neptunea insularis* and an asteroid, *Ceramaster misakiensis*, were also present in the sedimentary field.

The presence of *Calyptogena soldissima* and vestimentiferan species means that a sufficient supply of hydrogen sulfide exists within the warm vent fluids to sustain the associated symbiotic bacteria. However, many non-vent organisms were also present in the sedimentary field. The concentration of hydrogen sulfide in the sedimentary field was lower than that measured in the rocky field. The hydrogen sulfide which can be toxic to non-vent organisms in high concentrations might be diffused outside of the warm vent field by the strong bottom current over the sedimentary field. Therefore, non-vent organisms, usually concentrated in the peripheral zone of the vent site, may enter the sedimentary field in order to use the rich organic production of the vent system. Predation by fish, crabs and shrimp may prompt transfer of vent productivity to the surrounding deep-sea community. An overwhelmingly dominant species of the hydrothermal vent communities at the Minami–Ensei Knoll is a deep-sea mussel, *Bathymodiolus japonicus*. The sedimentary field occupies more of this vent area. The fact that the hydrothermal vent fluids contain high concentrations of carbon dioxide implies an island-arc volcanism type. From such a viewpoint, the microdistribution pattern of vent fauna of the Minami–Ensei Knoll is seen to differ from that of the Galapagos Spreading Center (HESSLER and SMITHEY, 1983; HESSLER *et al.*, 1988) and the East Pacific Rise (RISE PROJECT GROUP, 1980).

The trophic structure of the hydrothermal vent ecosystem at the Minami–Ensei Knoll is similar to that of other vent fields in the Okinawa Trough (KIM *et al.*, 1989; OHTA, unpublished data). Although direct information is limited, this ecosystem appears to be different from that of the Galapagos Spreading Center, the East Pacific Rise, the Juan de Fuca Ridge (TUNNICLIFFE, 1991; JUNIPER *et al.*, 1992), the Mariana Back-Arc Basin (HESSLER and LONSDALE, 1991), the North Fiji Basin, and the Lau Basin (DESBRUYÈRES *et al.*, 1994), in having a more complicated trophic structure due to the presence of many non-vent organisms. Comparative studies of sulfur, carbon and nitrogen isotopic ratios in organisms collected at both the rocky and sedimentary fields are required for a better understanding of food web dynamics in these ecosystems.

Biogeography

The compiled list of the hydrothermal vent organisms of the Manami–Ensei Knoll (Table 1) offers a key to the discussion on the meso-scale biogeography of the vent fauna in the western and southwestern Pacific. Eighteen out of 54 documented taxa collected from the Minami–Ensei Knoll are new or probably new species. However, the hydrothermal vent communities on the Minami–Ensei Knoll bear some resemblance at the familial and/ or generic level to the fauna described from the Izena Caldron (1400 m) and the Iheya Ridge (1400 m) in the Mid-Okinawa Trough (Ohta, 1990a; Kim and Ohta, 1991), as well as to faunal communities associated with the cold seep site off Hatsushima (1150 m) in Sagami Bay (Hashimoto *et al.*, 1989a; Ohta, 1990b). Vestimentiferans, vesicomyid clams, mussels, bresiliid and hippolytid shrimp, lithodid crabs, and zoarcid fish were encountered at all of the above sites, although the hydrothermal vent communities of the Minami–Ensei Knoll, Izena Caldron and Iheya Ridge are dominated by deep-sea mussels, while the seep communities of Sagami Bay are dominated by vesicomyid clams. The Minami–Ensei Knoll communities differ from those of southwestern Pacific areas, such as at the Mariana Back-Arc Basin (Hessler and Lonsdale, 1991), the North Fiji Basin, and the Lau Basin (Desbruyères *et al.*, 1994), in the absence of two gastropod species, *Alviniconcha hessleri* and *Ifremeria nautilei*, which are dominant and key species of the latter. Vesicomyid clams, which were present at the Minami–Ensei Knoll site, were not reported from the other hydrothermal sites studied to date in the southwestern Pacific. A primitive scalpellid species of *Neolepas* was present on the Iheya Ridge and in Sagami Bay. A primitive barnacle species of *Neoverruca* was dominant in the surroundings of vent openings of the Kaikata Seamount vent site located near the Bonin Islands and the Izena Caldron. However, neither primitive scalpellid nor barnacle have been encountered to date at the Minami–Ensei Knoll.

Three species of deep-sea mussels, *Bathymodiolus aduloides*, *B. japonicus* and an undescribed species belonging to the subfamily Bathymodiolinae, are recognized from the Minami–Ensei Knoll. The first species is characterized by a slender, rather thick, light-brown shell and had been found at the seep communities of the Okinoyama Bank in Sagami Bay and at vent communities of the Iheya Ridge in the Okinawa Trough. The second is dark-brown and is found also in Sagami Bay (Hashimoto and Okutani, 1994). The third species is a burrowing species and resembles that from the Kaikata Seamount. Furthermore, a provannid gastropod, *Provanna glabra*, is found also at the Izena Caldron and the Iheya Ridge in the Okinawa Trough and in Sagami Bay (Okutani *et al.*, 1993). Three or more species of the genus *Paralomis* (including *P. jamsteci*) were observed in the vent environments of the Minami–Ensei Knoll. *Paralomis multispina* was common in Sagami Bay (Hashimoto *et al.*, 1989a) and *P.* cf. *verrilli* in the Iheya Ridge (Kim and Ohta, 1991). *Symphurus* cf. *orientalis* also populates the coarse sand bottom of the Kaikata Seamount near the Bonin Island (Hashimoto *et al.*, 1988b) and similar bottom sediments of the Nikko Seamount near the Minami–Iohjima Island (Hashimoto, personal observation). This cynoglossid fish appears to be one of the constituents of the vent fauna. Four eunicid polychaetes of the genus *Eunice* from the exposed rocky field may be vent organisms, while two non-vent eunicid species were also recorded (Miura, 1992).

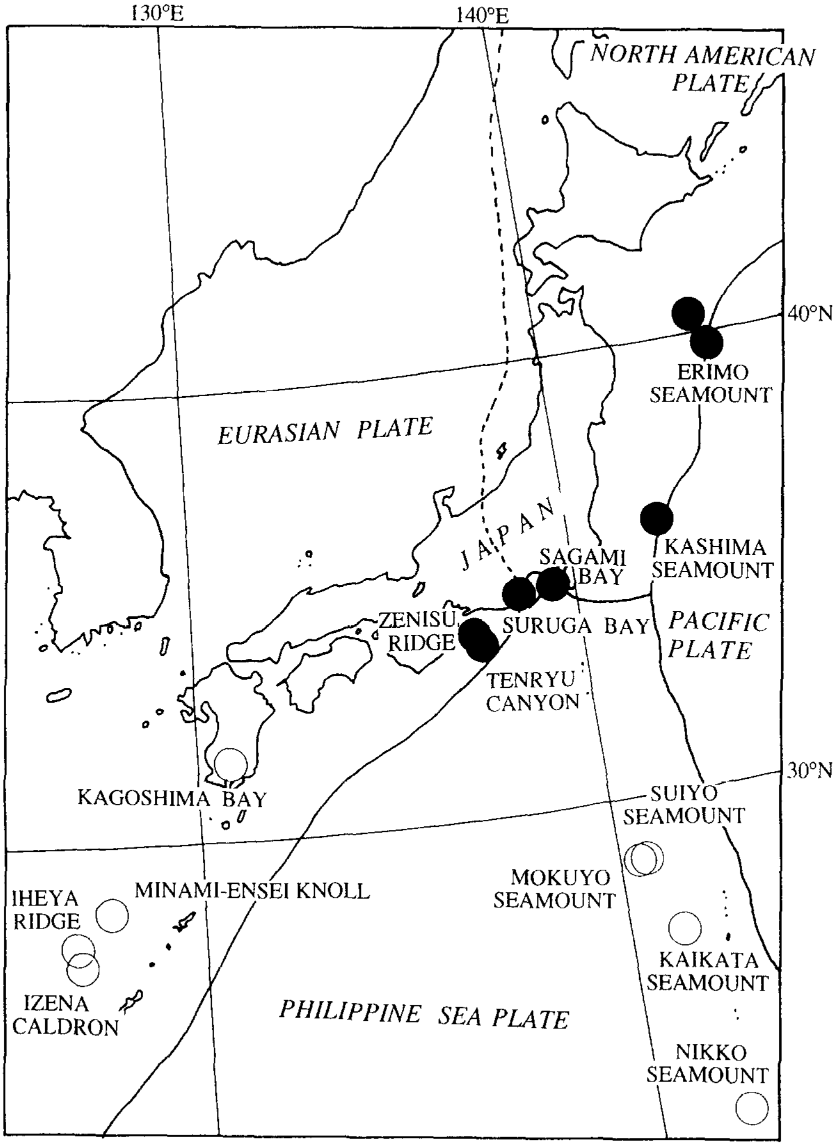


Fig. 7. Plate boundaries and deep-sea chemosynthetic communities around Japan. Ornamented line: plate boundaries. Closed circle: cold seep communities. Open circle: hydrothermal vent communities.

Fig. 8. (1) Thanatocoenoses of *Calyptogena solidissima* in depression A, along the slope foot of a steep escarpment, 28°25.15'N, 127°39.02'E, at a depth of 750 m. (2) Living specimens of a solitary vestimentiferan tube-worm in depression B, rising from the coarse sand bottom, 28°24.50'N, 127°37.90'E, at a depth of 740 m. (3) Cluster consisting of hundreds of vestimentiferan specimens at the marginal part of depression B, 28°24.40'N, 127°38.00'E, at a depth of 670 m, where *Calyptogena silidissima* and a deep-sea mussel were also collected. (4) Yunoi Chimney gushing out clear hot water of 269°C in depression C, 28°23.37'N, 127°38.38'E, at a depth of 705 m, covered with numerous deep-sea mussels. (5) A small assemblage of *Calyptogena solidissima* in depression C, 28°23.50'N, 127°38.22'E, at a depth of 712 m. (6) *Symphurus* cf. *orientalis* and *Paralomis jamsteci* in depression C, 28°23.30'N, 127°38.40'E, at a depth of 715 m.

8.(1)

8.(2)

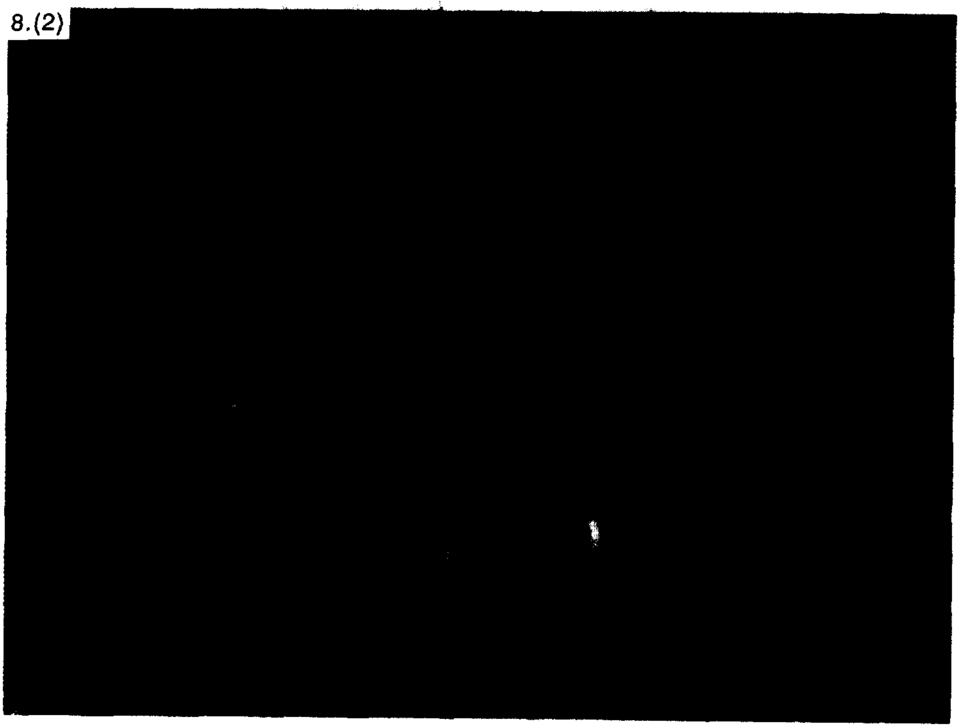
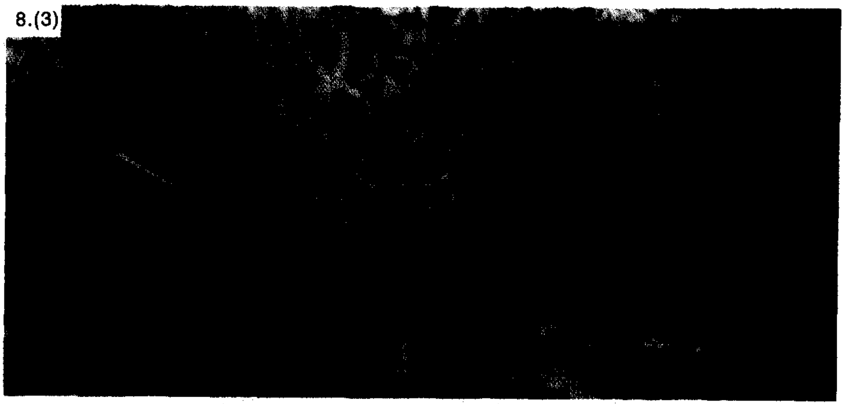


Fig. 8. (*Continued overleaf.*)

8.(3)



8.(4)

Fig. 8. (continued)

8.(5)

8.(6)

Fig. 8. (continued)

Branchipolynoe pettiboneae was also encountered on the Iheya Ridge and the Kaikata Seamount (MIURA and HASHIMOTO, 1991). This polynoid species has been found at the vent communities of the Mariana Back-Arc Basin, the North Fiji Basin and the Lau Basin (DESBRUYÈRES *et al.*, 1994). These vent species may have a high dispersal capability. Certainly, a few vent organisms, such as *Bathymodiolus thermophilus*, *Bythograea thermydron* and *Alvinocalis lusca*, distributed widely in geographically separated hydrothermal sites in the Eastern Pacific, undergo a planktotrophic, high dispersal mode of development. However, most of the vent species studies to date appear to have a free-swimming, lecithotrophic larval stage with a relatively low dispersal capability (LUTZ, 1988). Few reproductive data are available for vent species sampled around Japan, but those species are expected to have similar adaptations.

Ocean circulation in the deep western Pacific has been characterized by MANTYLA and REID (1983); the deep waters of the East Mariana Basin originate in the Southwest Pacific Basin spreading northward or northwestward in the Shikoku Basin and then extending southward to the Philippine Basin. Such deep water circulation patterns may well play a significant role in the dispersal and distribution of hydrothermal vent animals along the eastern edge of the Philippine Sea Plate. In any case, there may be significant faunal exchange between the Minami-Ensei Knoll communities and other chemosynthetic communities in the western Pacific, despite their different water depths, a gap of over 1000 km among them and such barriers as the Ryukyu Trench and the Ryukyu Arc.

From 1992 to 1993, new hydrothermal vent sites with deep-sea biological communities were discovered by a deep tow, the R.O.V. *Dolphin 3K*, the *Shinkai* 2000 and the *Shinkai* 6500 on the Suiyo Seamount, the Mokuyo Seamount and the Nikko Seamount located along the eastern edge of the volcanic front of the Philippine Sea Plate (HASHIMOTO and FUJIKURA, 1992), and in Kagoshima Bay (HASHIMOTO *et al.*, 1993). New cold seep sites dominated by vesicomyid bivalves were also found in Suruga Bay (OKUTANI *et al.*, 1993) and on the landward wall of the Japan Trench (FUJIOKA and MURAYAMA, 1992). A location map of vent and seep sites found to date around Japan is shown in Fig. 7. Analysis of organisms and results obtained from these new environments, when coupled with genetic studies of the retrieved organisms, should greatly increase our understanding of the biogeography of hydrothermal vent and cold seep organisms.

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