

Estimated Population Densities of Megafauna in Two Chemosynthesis-based Communities: a Cold Seep in Sagami Bay and a Hydrothermal Vent in the Okinawa Trough

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Abstract: This study investigates the population density characteristics of the megafauna at two previously described chemosynthesis-based communities associated with cold seepage at the Off Hatsushima Island site (OHI) in Sagami Bay and hydrothermalism at the Minami-Ensei Knoll (MEK) in the Okinawa Trough. Quantitative sampling was conducted using a submersible, ROV and Deep Tow Camera array near each community. A total of 26 and 27 megafaunal species were recorded at OHI and MEK, respectively. The dominant organism with respect to population density was the provannid snail *Provanna glabra* at OHI. This species also occurred at MEK, but it had a lower density than at OHI. Instead, *Cantrainea jamsteci* was the dominant gastropod species at MEK. The community at MEK was dominated with respect to population density by the symbiont-containing mussel *Bathymodiolus japonicus*, but this species was not so common at OHI. The mean population densities of almost all megafaunal species, except for a few conspicuously predominant species at OHI and MEK, are similar to those for the dominant species in other deep-sea photosynthesis-based communities. Both sites were characterized by large populations of only a few dominant species (*Provanna glabra*, *Calypptogena okutanii*, and *C. soyoae* at OHI and *Bathymodiolus japonicus* at MEK). This pattern may be due to the extreme environments that occur near chemosynthesis-based communities.

Key words: cold-seep community, hydrothermal-vent community, megafauna, Minami-Ensei Knoll, Off Hatsushima Island site, population density

INTRODUCTION

The advent of submersible research in the deep sea has revealed the existence of deep-sea chemosynthesis-based communities (i.e., hydrothermal-vent and cold-seep communities) in various locations around the world, including along spreading axes, rift systems, plate convergence zones and hydrocarbon seep areas (see reviews by Sibuet & Olu 1998; Tunnicliffe et al. 1998; Van Dover 2000). To understand the community structure of

chemosynthesis-based communities, quantitative analyses have estimated the population density or biomass of the dominant megafauna, particularly symbiont-containing species. These analyses have been done for the Louisiana Slope (MacDonald et al. 1990), the Peruvian active margin (Olu et al. 1996a), the southern Barbados prism (Olu et al. 1996b, 1997) and the Juan de Fuca Ridge (Graham & Juniper 1996). Recently, the population density and biomass of non-symbiont-containing species, such as polychaetes, gastropods and crustaceans have been estimated at the Juan de Fuca (Sarrazin & Juniper 1999) and the Mid-Atlantic Ridges (Gebruk et al. 2000).

In Japanese waters, there are many cold-seep

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communities, including those in the Japan Trench, the Nankai Trough, Suruga Bay and Sagami Bay, and many hydrothermal-vent communities, including those in the Okinawa Trough and the Ogasawara (Bonin) Islands area (see reviews by Fujikura 1997; Kojima 2002). After the discovery of a cold-seep community at the Off Hatsushima Island site (OHI) in Sagami Bay (Okutani & Egawa 1985) and a hydrothermal-vent community at the Minami-Ensei Knoll (MEK) field in the Okinawa Trough (Hashimoto et al. 1995a), the taxonomy of megafaunal species (Miura 1988; Miura & Hashimoto 1991a, 1991b, 1993; Okutani & Fujikura 1992; Okutani et al. 1992, 1993; Hashimoto & Okutani 1994; Kojima & Ohta 1997; Machida & Hashimoto 1999; Kojima et al. 2000; Kikuchi & Hashimoto 2000) and the geochemistry of habitats (Sakai et al. 1987; Masuzawa et al. 1992; Hashimoto et al. 1995b; Tsunogai et al. 1996) at these two sites have been well studied. However there have been few quantitative analyses of chemosynthesis-based megafauna in Japan. Fujikura et al. (1995) reported preliminary estimates of the population densities at OHI and

MEK, but since the publication of that study, our knowledge of the taxonomy and ecology of these communities has progressed. The purpose of the present study is to present new estimates of population densities at OHI and MEK based on this new knowledge.

MATERIALS AND METHODS

Survey fields and diving surveys

The locations and contour maps of the survey areas are shown in Fig. 1. The ocean floor of Sagami Bay is divided into two oceanic plates by a plate boundary. The western part is on the Philippine Sea Plate, and the eastern part is on the North American Plate. The cold-seep community at OHI is situated on the Philippine Sea Plate. The source of fluid seepage at OHI is thought to be a mixture of seawater, pore water and freshwater (Tsunogai et al. 1996). The hydrothermal vent community at MEK is situated on a back-arc basin in the northern part of the Okinawa Trough under extensional stress caused by tectonic activity (Kimura et al. 1988). Isotopic ratios of dissolved gasses (CO_2 and H_2S) in hydrothermal fluids imply a magmatic origin (Chiba et al. 1993).

The cold-seep community at OHI was concentrated near 1170 m depth, and the total community field area was 2146.5 m². The seafloor was covered mainly by mud and small clasts. Orange deposits covered approximately 100 m². Naganuma et al. (1999) suggested these orange deposits have high bacterial activity, and Tsunogai et al. (1996) showed that temperatures are more than 10°C higher below the orange seabed than in ambient water. Black layers in the sediment indicative of a reducing environment were attributed to anaerobic bacterial activity.

At MEK, the observed field was 546 m² in area and ranged from 600–740 m in depth. The MEK was a typical hydrothermal-vent field covered by volcanic rocks and slabs of hydrothermal precipitates. Some chimneys were distributed over the seafloor. Water temperature from the vent chimneys was over 270°C. Coarse volcanic sand and debris surrounded the chimneys. One previous report on the faunal composition and micro-scale distributions at MEK by Hashimoto et al. (1995a) supplements this analysis.

Biological surveys were conducted from 1989 to 1992 at OHI (34°59.3–35°00.8'N, 139°12.6–14.1'E) using the crewed submersible *Shinkai 2000*, the ROV *Dolphin-3K*, and a Deep Tow Camera array (see www.jamstec.go.jp), and from 1988 to 1992 at MEK (28°23.2–24.3'N, 127°38–38.8'E) using only the

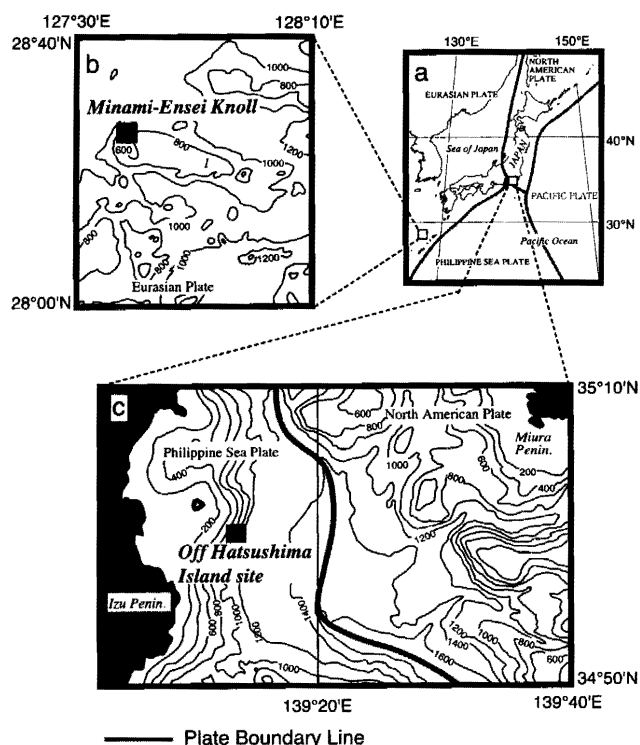


Fig. 1. (a) Map of Japan showing locations of Sagami Bay and the Okinawa Trough. (b) Detailed map showing the location of the hydrothermal-vent community at the Minami-Ensei Knoll (MEK) in the Okinawa Trough. (c) Detailed map showing the location of the cold-seep community at the Off Hatsushima Island site (OHI) in Sagami Bay. Depths are in meters.

Shinkai 2000 (Table 1). When chemosynthesis-based communities were observed during the surveys, we took 35mm photographs of the communities using the following cameras: the QI DSC2050A camera of the *Shinkai 2000*, the PHOTOSEA PS1000A camera of the *Dolphin-3K* and the BENTHOS MODEL 372A camera of the Deep Tow array. Vehicle positioning was recorded by the Super Short Base Line (SSBL) method using the GPS or LORAN-C.

Table 1. Summary of survey data from the chemosynthesis-based communities at the Off Hatsushima Island site (OHI) and the Minami-Ensei Knoll (MEK).

Community	No. of observations	Community area (m ²)	Depth (m)
	15 (<i>Shinkai 2000</i>)		
OHI	8 (<i>Dolphin-3K</i>)	2146.5	830–1230
	14 (Deep Tow Camera)		
MEK	15 (<i>Shinkai 2000</i>)	546	600–740

Analytical methods

Biological samples were collected either directly using manipulators or with scoop samplers attached to the manipulators of the submersible. These samples were partially sorted and fixed in 10% buffered formaldehyde-seawater solution onboard ship. Megafaunal species were identified both from samples and photographs.

Mean population density was estimated for the dominant species. We assumed that the population density of each species did not fluctuate during the study period. Total numbers of individuals were directly counted from photographs. *Calyptogena soyoae* and *C. okutanii* could not be reliably identified to species level using only photographs. This was also true for *Bathymodiolus japonicus*, *B. platifrons* and *B. aduloides*. When cold-seep communities were first discovered at OHI, *Calyptogena* was treated as a single species, *C. soyoae* (Okutani & Egawa 1985; Ohta et al. 1987; Hashimoto et al. 1989). However, molecular and detailed morphological analyses have also identified a sibling species, *C. okutanii* (Kojima & Ohta 1997). The mean surface area covered by each photograph was estimated to be approximately 1.5 m² based on the dimensions of known objects such as the manipulators and sample baskets of the submersibles, and the chain of the Deep Tow Camera array. The field area of the chemosynthesis-based community at each field was determined using photographs

of species observed in every frame. The number of photographs that contained species in the frame was 1,431 at OHI and 364 at MEK. Mean population density (D) was roughly estimated by the following formula:

$$D \text{ (inds./m}^2\text{)} = \sum_{i=1}^n x_i / 1.5n$$

where n and x_i are the photograph number and the number of individuals in the frame, respectively. The maximum population density of species was calculated from the photograph with the highest number of specimens. In the case of small, parasitic or deeply buried animals, population densities could not be estimated because these animals could not be counted from photographs.

RESULTS

Off Hatsushima Island site (OHI)

Twenty-six megafaunal species occurred at this site (Table 2). The provannid snail *Provanna glabra* was the most abundant megafaunal species with respect to mean population density. Relatively high densities of two vesicomid clams, *Calyptogena okutanii* and *C. soyoae*, and a conid whelk, *Oenopota sagamiana*, were also observed (Table 2). *P. glabra* was distributed most widely and crept over hard substrata including the shell surfaces of *Calyptogena* and *Bathymodiolus* bivalves, rock outcrops, and sediments (Fig. 2a, c). The maximum population density of *P. glabra* recorded was 1073 inds./m². Live *Calyptogena* clams formed densely clustered beds among thick sediments, and these clusters ranged in size from a few to over 100 m² (Fig. 2a). Beds of empty clam shells were also observed in and around the live-clam beds. *Calyptogena* clams occurred sparsely over the orange areas of the seabed. Locally, the maximum population density of the integrated *Calyptogena* species (*C. soyoae* and *C. okutanii*) recorded was 352 inds./m².

A high population density of the conid whelk *Oenopota sagamiana* was observed concentrated over the orange areas of the seabed (Fig. 2b). No specimens were observed in any other habitat. Another conid whelk, *Phymorhynchus buccinoides*, was also limited in its distribution, aggregating on the shell surfaces of *Bathymodiolus* mussels and on outcrops over the orange areas (Fig. 2c). Locally, the maximum population densities of *O. sagamiana* and *P. buccinoides* were 219 inds./m² and 63 inds./m², respectively. The limpet *Bathymacra nipponica* and the trochid snail *Margarites shinkai* were representative faunal constituents at this field and crept mainly on the shell surfaces of

Table 2. Faunal list of species and their population densities at the cold-seep community at the Off Hatsushima Island site (OHI) and at the hydrothermal-vent community at the Minami-Ensei Knoll (MEK). +: present, but population density not estimated, -: not present.

Species	Community		Species	Community	
	OHI (inds./m ²)	MEK (inds./m ²)		OHI (inds./m ²)	MEK (inds./m ²)
Polychaeta			Bivalvia		
<i>Brachipolynoe pettiboneae</i>	—	+	<i>Bathymodiolus platifrons</i>	2.4	—
<i>Protomystides hatsushimaensis</i>	+	—	<i>Bathymodiolus japonicus</i>		53.0
<i>Nicomache ohtai</i>	+	—	<i>Bathymodiolus aduloides</i>		
<i>Shinkai sagamiensis</i>	+	—	<i>Bathymodiolus</i> sp.	0.1	
<i>Shinkai</i> n. sp.	—	+	<i>Lucinoma yoshidai</i>	—	
<i>Natsushima bifurcata</i>	+	—	<i>Conchocele disjuncta</i>	+	—
<i>Mytilidiphila enseiensis</i>	—	+	<i>Calyptogena soyoae</i>	127.6	—
<i>Mytilidiphila okinawaensis</i>	—	+	<i>Calyptogena okutanii</i>		—
unidentified Nautiliniellidae species	+	—	<i>Calyptogena solidissima</i>	—	0.2
<i>Paralinella hessleri</i>	—	+	Cirripedia		
Obturata			<i>Neolepas</i> sp.1	+	—
<i>Lamellibrachia</i> sp.	0.3	—	<i>Neolepas</i> sp.2	—	+
<i>Alysia</i> -like vestimentiferan	0.2	—	Decapoda		
unidentified species 1	—	1.4	<i>Alvinocaris longirostris</i>	0.1	—
unidentified species 2	—	0.5	<i>Alvinocaris brevitelsonis</i>	—	0.4
Gastropoda			<i>Alvinocaris leurokolos</i>	—	2.8
<i>Puncturella parvinobilis</i>	—	+	<i>Lebbeus washingtonianus</i>	—	1.4
<i>Serradonta vestimentifericola</i>	+	—	<i>Lebbeus</i> sp.	+	—
<i>Bathyacmaea nipponica</i>	4.1	—	<i>Paracrangon</i> sp.	—	0.1
<i>Bathyacmaea secunda</i>	—	0.4	unidentified Bythograeidae species	—	+
<i>Lepetodrilus jaopnicus</i>	—	0.8	<i>Paralomis jamsteci</i>	—	0.3
<i>Margarites shinkai</i>	4.2	—	<i>Paralomis</i> sp.	—	>0.1
<i>Cantrainea jamsteci</i>	—	5.3	<i>Shinkata crosnieri</i>	—	0.3
<i>Provanna glabra</i>	309.9	0.1	Vertebrate		
<i>Oenopota sagamiana</i>	8.2	—	<i>Lycodes</i> sp.1	+	—
<i>Phymorhynchus buccinoides</i>	0.3	—	<i>Lycodes</i> sp.2	+	—
Bivalvia			unidentified Zoarcidae species 1	+	—
<i>Acharax johnsoni</i>	+	—	unidentified Zoarcidae species 2	—	0.1
			<i>Symphurus</i> cf. <i>orientalis</i>	—	>0.1

Calyptogena clams. Lower population densities of two *Bathymodiolus* species, *B. platifrons* and *B. japonicus*, were found attached via their byssi to rock outcrops. Live mussels formed densely clustered beds of a few square meters in area. These mussels were confined to only three rock outcrops in the field. The maximum integrated population density of the two *Bathymodiolus* species, *B. platifrons* and *B. japonicus*, reached 366 inds./m². Sprawling tangles of tubes of pogonophorans, *Lamellibrachia* sp. and an *Alaysia*-like vestimentiferan, occurred over the muddy sediments, with their posterior ends buried in the sediment or under rocks. Sometimes both species were found at the same microhabitat. The maximum population densities of *Lamellibrachia* sp. and the *Alaysia*-like vestimentiferan recorded were 20 inds./m² and 101 inds./m², respectively.

Some shells of the bivalves *Acharax johnsoni*, *Lucinoma yoshidai* and *Conchocele disjuncta* were present among the *Calyptogena* beds. Live clams were

usually buried approximately 20 cm below the sediment surface. The commensal polychaete worm *Shinkai sagamiensis* was collected from within the mantle cavity of *C. soyoae* and *C. okutanii*. Another commensal polychaete, *Natsushima bifurcata*, was collected from within *A. johnsoni*. An unidentified nautiliniellid species was found from within the mantle cavity of *Conchocele disjuncta* (T. Miura, personal communication). Two species of polychaetes, *Protomystides hatsushimaensis* and *Nicomache ohtai*, were occasionally collected from sediments in the *Calyptogena* beds. Three crustacean species (an unidentified *Neolepas* barnacle, *Alvinocaris longirostris* and *Lebbeus* sp.) occurred on one rock outcrop surface covered with grayish-white deposits. The population densities of these deep-buried clams, polychaete worms and crustaceans could not be estimated.

Buccinid whelks, *Buccinum soyomaruae* and *Neptunea acutispiralis*, and an anomuran crab,

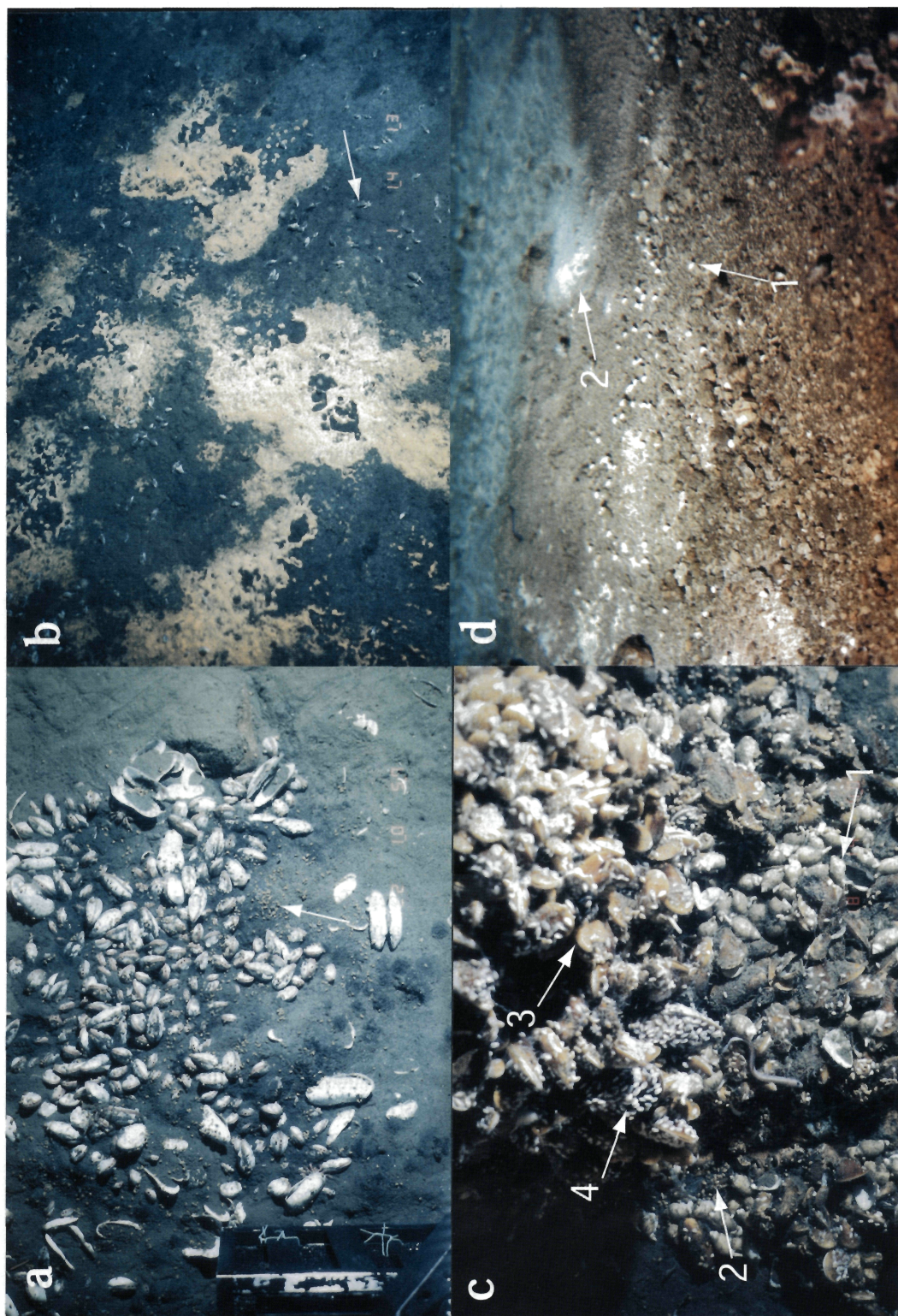


Fig. 2. Chemosynthesis-based communities at the Off Hatsushima Island site (OHI) and the Minami-Ensei Knoll (MEK). The mean surface area in each photograph was approximately 1.5 m². All photos taken by the *Shinkai 2000*. (a) Distribution of live provannid gastropods, *Provanella glabra* (arrow), and two species of vesicomyid clams, *Calyptogena soyoae* and *C. okutanii*, at the cold-seep site at the Off Hatsushima Island site (OHI) in Sagami Bay. *Provanella glabra* aggregated on the sediments and shell surfaces of *Calyptogena soyoae* or *C. okutanii*. (b) The orange seabed near *Calyptogena* aggregations at the Off Hatsushima Island site (OHI) in Sagami Bay. Note the large aggregation of turrid gastropods, *Oenopota sagamiensis* (arrow). (c) A dense biological community composed of the turrid gastropod *Phymorhynchus buccinoides* (arrow 1), small brown provannid gastropod *Provanella glabra* (arrow 2), and mytilid bivalve *Bathymodiolus japonicus* (arrow 3) on rock outcrops within the orange seabed at the Off Hatsushima Island site (OHI) in Sagami Bay. Numerous whitish egg cases (arrow 4) of *Phymorhynchus buccinoides* were found attached to the surface of *Bathymodiolus japonicus*. (d) Distribution of live turrid gastropods, *Caminaria jamstecti* (arrow 1), near the filamentous bacterial mat (arrow 2) areas on sediments associated with hydrothermal vents at the Minami-Ensei Knoll (MEK) in the Okinawa Trough.

Paralomis multispina, were encountered frequently in and around the *Calyptogena* beds.

Minami-Ensei Knoll (MEK)

A total of 27 benthic species were recorded here (Table 2). The integrated population density of two *Bathymodiolus* mussel species, *B. japonicus* and *B. aduloides*, was very high (Table 2). Locally, the maximum population density values for these mussels reached 644 inds./m². These mussels formed dense aggregations and were found attached via their byssi to rock outcrops in the vicinity of the vents. The population density of *B. japonicus* was probably larger than that of *B. aduloides*, because the ratio between *B. japonicus* and *B. aduloides* from collected specimens was 13:2. The turbinid snail *Cantrainea jamsteci* also occurred at relatively high densities. *C. jamsteci* crawled over the shell surfaces of *Bathymodiolus* mussels and was especially concentrated near filamentous bacterial mat areas on the sediments (Fig. 2d). The maximum population density of *C. jamsteci* was 127 inds./m².

Two species of limpets, *Bathyaemaea secunda* and *Lepetodorilus japonicus*, and four species of crustaceans, *Alvinocaris leurokolos*, *Lebbeus washingtonianus*, *Paralomis jamsteci* and *Shinkaia crosnieri*, were commonly found on and within the *Bathymodiolus* aggregations, and these population densities ranged from 0.3 to 2.8 inds./m² (Table 2). Two species of bivalve, *Calyptogena solidissima* and *Bathymodiolus* sp., formed aggregates in the coarse sediments. *Provanna glabra*, which was the dominant species at OHI, was present at much lower population densities, approximately 1/3000 of those at OHI. *P. glabra* crawled over the shell surfaces of *Bathymodiolus* mussels.

Population densities of the primitive barnacle *Neolepas* sp., the limpet *Puncturella parvinobilis*, and four commensal polychaete species, *Mytilidiphila okinawaensis*, *M. enseiensis*, *Brachipolynoe pettiboneae* and *Shinkai* sp., could not be determined because the number of individuals could not be counted in the photographs. Only six specimens of *Neolepas* sp. were collected from the shell surfaces of *C. solidissima* and only four specimens of *P. parvinobilis* occurred on the shell surfaces of *Bathymodiolus* mussels. The commensal polychaetes *Mytilidiphila okinawaensis* and *Brachipolynoe pettiboneae* were collected from within the mantle cavities of *Bathymodiolus japonicus* and/or *B. aduloides*. Another commensal polychaete, *Mytilidiphila enseiensis*, was found within the mantle cavity of an undescribed *Bathymodiolus* species buried in sediments.

Thirty-seven specimens of *M. enseiensis* were found in 3 specimens of the undescribed *Bathymodiolus* species. The nautiliniellid polychaete *Shinkai* sp. has been observed in the mantle cavity of *Calyptogena solidissima* (T. Miura, personal communication).

DISCUSSION

Deep-sea chemosynthesis-based communities are considered widely to have richer concentrations of biomass and higher densities of megafauna than other deep-sea areas (Gage & Tyler 1991). The mean population densities of *Provanna glabra*, *Calyptogena soyoae* and *C. okutanii* at OHI, and of *Bathymodiolus japonicus* at MEK were very high, with values greater than 10 inds./m² (Table 2). However, other megafaunal species occurred at densities from 0.1 to 8.2 inds./m². Ohta (1983) estimated the mean population densities of benthic animals from photosynthetically-based communities between 950 and 1340 m depth in Suruga Bay based on photographs taken by an underwater camera unit. Mean population densities of the holothurian *Peniagone japonica* were conspicuously higher (7.9 inds./m²) than those of other benthic megafauna (less than 0.1 inds./m²). According to data from the U.S. crewed submersible *Alvin* during surveys of the continental slope south of New England from 500 to 1800 m depth, almost all megafaunal species occurred at low population densities of less than 0.02 inds./m². However, three megafaunal species (the sea urchin *Echinus affinis*, a cerianthid sea anemone, and the brittle star *Ophiomusium lymani*) were present at high density values of 0.3, 0.8 and 2.4 inds./m², respectively (Grassle et al. 1975). Except for a few predominant species at OHI and MEK, almost all of the megafaunal species at these two chemosynthesis-based communities had similar population density values to the dominant species in deep-sea photosynthetically-based communities at similar depth.

The most dominant animal with respect to population density was *Provanna glabra* at OHI (Table 2). At MEK, *P. glabra* was not abundant, however, the gastropod *Cantrainea jamsteci* was present at relatively high population densities. *P. glabra* has a taenioglossate radula (Okutani et al. 1992) indicative of omnivory and/or scavenging. In contrast with *P. glabra*, *C. jamsteci* is a so-called "specialist" grazer based on its rhipidoglossate radula (Okutani & Fujikura 1990). Bacterial mats and films are formed on the surfaces of substrata such as debris, rocks and the shells of *Bathymodiolus* mussels. *C. jamsteci* was concentrated

Table 3. Population densities of different species at other chemosynthesis-based communities.

Species	Community field	Type	Population density (inds./m ²)	Source
Gastropoda				
<i>Provanna variabilis</i>	Endeavour Segment, Juan de Fuca Ridge	Vent	32–4259	Sarrazin & Juniper, 1999
<i>Leptodrilus fucensis</i>	Endeavour Segment, Juan de Fuca Ridge	Vent	305–108226	Sarrazin & Juniper, 1999
Bivalvia				
<i>Calyptogena</i> sp.	Peruvian active margin	Seep	39.5	Olu et al., 1996a
<i>Calyptogena</i> sp.	Barbados accretionary prism	Seep	0.007–0.105	Olu et al., 1997
Vesicomylid clam A	Middle Valley, Juan de Fuca Ridge	Vent	5	Grahan & Juniper, 1996
Vesicomylid clam B	Logatchev area, Mid-Atlantic Ridge	Vent	3–4	Gebruk et al., 2000
<i>Bathymodiolus</i> sp. A	Southern Barbados prism	Seep	139.5	Olu et al., 1996b
<i>Bathymodiolus</i> sp. B	Southern Barbados prism	Seep	175–370	Olu et al., 1996b
<i>Bathymodiolus</i> sp. C	Louisiana Slope	Seep	467–829	MacDonald et al., 1990
Crustacea				
<i>Alvinocaris</i> sp.	Logatchev area, Mid-Atlantic Ridge	Vent	1–5	Gebruk et al., 2000

near the filamentous bacterial mat areas on sediments and along the shell surfaces of *Bathymodiolus* mussels where filamentous bacteria also occur. This suggests that chemosynthetic bacteria provide an important food source for *C. jamsteci*. The conid whelk *Oenopota sagamiana* had a relatively high population density at OHI and was concentrated over the orange areas of the seabed. The radula of *O. sagamiana* is toxoglossate (Okutani & Fujikura 1992). Generally, the feeding habits of gastropods with this radula type are carnivorous. Based on observation of the gill tissue of this whelk, however, Endow et al. (1992) suggested that it performs intracellular digestion of material filtered from ambient water. We have no data on the relationship between feeding habits and the orange-colored deposits.

Bathymodiolus japonicus contains symbionts that are associated with methanotrophic bacteria, and thus the distribution of *B. japonicus* is strongly influenced by the methane concentration in vent and seep areas (Fujiwara et al. 2000). The community at MEK was dominated by *B. japonicus* with respect to population density, but this mussel was not as common at OHI. The methane concentration ranged from 0.029 to 2.5 mmol/kg above the seabed at OHI (Tsunogai et al. 1996), and from 2.63 to 7.0 mmoles/kg at MEK (Chiba et al. 1993). The higher methane levels at MEK may support the higher population densities of *B. japonicus*.

Megafaunal population densities at other chemosynthesis-based communities are listed in Table 3. The maximum density recorded for *Provanna variabilis* is 4259 inds./m² at the Endeavour Segment on the Juan de Fuca Ridge (Sarrazin & Juniper 1999), which is

approximately 4 times the maximum value of *P. glabra* at OHI. The population densities of vesicomylid clams varied from 0.007 to 39.5 inds./m² among different community fields. The ratio between *C. okutanii* and *C. soyoae* in the OHI community is approximately 2.87:1 (K. Ito, unpublished data). To calculate the mean population densities of the two *Calyptogena* species at OHI, we applied this ratio, and the resulting densities for *C. okutanii* and *C. soyoae* were 94.6 and 33.0 inds./m², respectively. These values are higher than those from other community fields, such as at the Peruvian active margin, the Barbados accretionary prism, the Middle Valley in the Juan de Fuca Ridge and the Logatchev area in the Mid-Atlantic Ridge. Henry et al. (1992), Lallemand et al. (1994) and Sibuet & Olu (1998) suggested that biological production at cold seeps is related to the intensity of the fluid flux from the sea bottom. *Calyptogena* clams contain intracellular symbiotic chemoautotrophic sulfur-oxidizing bacteria in their gills (Nelson & Fisher 1995). At cold-seep fields, hydrogen sulfide in the pore water of sediments is produced by sulfate reducers (bacteria) using the sulfate from overlying bottom water and methane (presumably of microbial origin) (Masuzawa et al. 1992). Concentrations of hydrogen sulfide ranging from 0.05 to 0.6 mmol/kg are suitable for *C. soyoae*, and concentrations over 1 mmol/kg are detrimental (Hashimoto et al. 1995b). Methane flux of fluid seepage was estimated at less than 10^{12±1} mol/year at OHI by geochemical analysis (Tsunogai et al. 1996). To understand the factors controlling population densities of *C. soyoae*, it is important to accumulate data on the methane flux and production of hydrogen sulfide by sulfate reducers.

A few species conspicuously predominated in abundance during the present study; they involved *Provanna glabra*, *Calyptogena okutani*, and *C. soyoae* at OHI, and *Bathymodiolus japonicus* at MEK. Whittaker (1975) suggested that conspicuously large populations of only a few species are characteristics of biological communities under severe environmental conditions. This is the case for chemosynthesis-based communities, since these are sites where hydrogen sulfide, methane, heavy metal concentrations, and extreme fluctuations in water temperature (particularly at hydrothermal-vent fields) occur (Lalou & Bricet 1982; Juniper & Sibuet 1987; Tunnicliffe et al. 1990; Lutz & Kennish, 1993; Massoth et al. 1994). The conspicuousness of only a few megafaunal species may reflect the severe environment at chemosynthesis-based community fields.

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