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Cold-seep benthic communities in the Japan subduction zones: Geological control of community development

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ABSTRACT

A large number of *Calypptogena*-dominated benthic communities, apparently chemosynthetically-based, were discovered at methane-rich pore-water seeps in the Japan subduction zones (3850–6000 m depth). Photographic and video surveys from four submersible dives were analyzed to study the influence of faulting, topography and substratum on exploitation of cold seeps by megafauna. Pore-water seepage occurred in a variety of geological settings, including subduction-erosion and accretionary prism formation, always in association with major faults which likely facilitated upward migration of fluids from a deep high-pressure zone. Sediment cover and manganese crusts on the seafloor appeared to block pore-water discharge, except where interrupted by erosion, slumping or outcropping. Sediment or mudstone substrata may increase lateral diffusion of rising fluids, permitting more extensive biological exploitation than where fluids discharge directly from exposed rock. Cold seeps are ephemeral. Large long-lived "fields" of cold seeps may be important in the maintenance of regional populations of seep organisms and the transfer of cold-seep productivity to the surrounding deep-sea ecosystem.

1. Introduction

Most of the deep seafloor in the world ocean is populated by a sparse, food-limited assemblage of organisms dependent on trophic input from distant surface waters. A variety of localized seafloor emissions of reducing substances have been discovered recently that support chemosynthesis-based benthic communities. Emissions of this type include hydrothermal vents (Corliss *et al.*, 1979; see review by Grassle, 1985), brine seeps (Paull *et al.*, 1984; Hecker, 1985), oil/gas seeps (Kennicutt *et al.*, 1985) and subduction-zone cold seeps (Suess *et al.*, 1985; Kulm *et al.*, 1986). The global distribution of vent and seep communities appears to be significant, to the point where their influence on the ecology of the surrounding deep sea becomes of interest. Brooks *et al.* (1987) have recently described an integrated study of oil/gas seeps in the Gulf of Louisiana where physiological experimentation, submersible observation and seismic reflection data are being combined to assess seep distribution and seep-faunal associations over a large region of the seafloor. Such an approach is an essential first step in studying the impact these areas of intense productivity have on the adjacent

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deep-sea ecosystem, as well as being important in understanding the ecological functioning of vent and seep communities themselves. In this paper we examine the relationship between major geological features of the subduction zone environment and the occurrence of biological communities at "cold seeps" of methane-rich fluids. Data are from a 1985 Franco-Japanese submersible expedition to the Japanese subduction zones (Kaiko program) which used the French submersible *Nautilie*.

Subduction-zone cold seeps are thought to be fed by deep sediment pore waters that migrate to the seafloor surface during the subduction process, possibly as a result of compressional forces. Kulm *et al.* (1986) describe seafloor communities of bivalves, tube worms and other organisms from cold seeps on a sedimentary accretionary complex at the Oregon continental margin. They also report finding living clams, apparently species of *Calymene* in a dredge haul taken at 3600 m along the Peruvian continental margin in a subduction-erosion setting, where the oceanic plate descends beneath the continental plate without the formation of an accretionary prism of sediment.

The 1985 Kaiko diving program revealed cold seeps in a variety of geological settings, including zones of subduction-erosion, accretionary prism formation and the subduction of a seamount beneath the continental margin (Cadet *et al.*, 1985; Boulègue *et al.*, 1985; Le Pichon *et al.*, 1987a; Ohta and Laubier, 1987; Swinbanks, 1985a,b; Juniper and Sibuet, 1987). Colonies of the vesicomid clam *Calymene* and an associated deep-sea megafauna were seen in 10 of the 27 dives which explored accessible areas of the Nankai Trough, the Japan Trench and the Kuril Trench at depths of 3850 to near 6000 m (Fig. 1). The size and composition of the communities was highly variable, particularly in the deeper zones. Four geologically contrasting sites were selected for analysis of the distribution and composition of cold seep megafauna in relation to major faulting, topography and substratum.

2. Study areas

a. Tenryu Canyon (Dive 28). Tenryu Canyon cuts deeply (1 km depth) across the accretionary prism on the inner wall of the Eastern Nankai Trough (Fig. 1), which is the surface expression of the consuming plate boundary separating the Lower Miocene Shikoku Basin, to the south, from Japan. The trench is fed longitudinally from the northeast, along the meandering Nankai Deep, by detrital sediments which have been depositing at a high rate since the Early Pliocene. Trench fill is as thick as 4 km resulting in formation of a well-developed accretionary prism along the inner wall. The prism is left-laterally offset by about 30 km along a complex arrangement of N-S trending ridges and troughs that channel sediments through Tenryu Canyon. The canyon is a possible extension of a now inactive, left-lateral strike-slip fault (Le Pichon *et al.*, 1987b).

b. Kashima Seamount (Dive 43). At this site, a collapsed portion of Kashima Seamount has entered the Japan Trench prior to being subducted beneath the

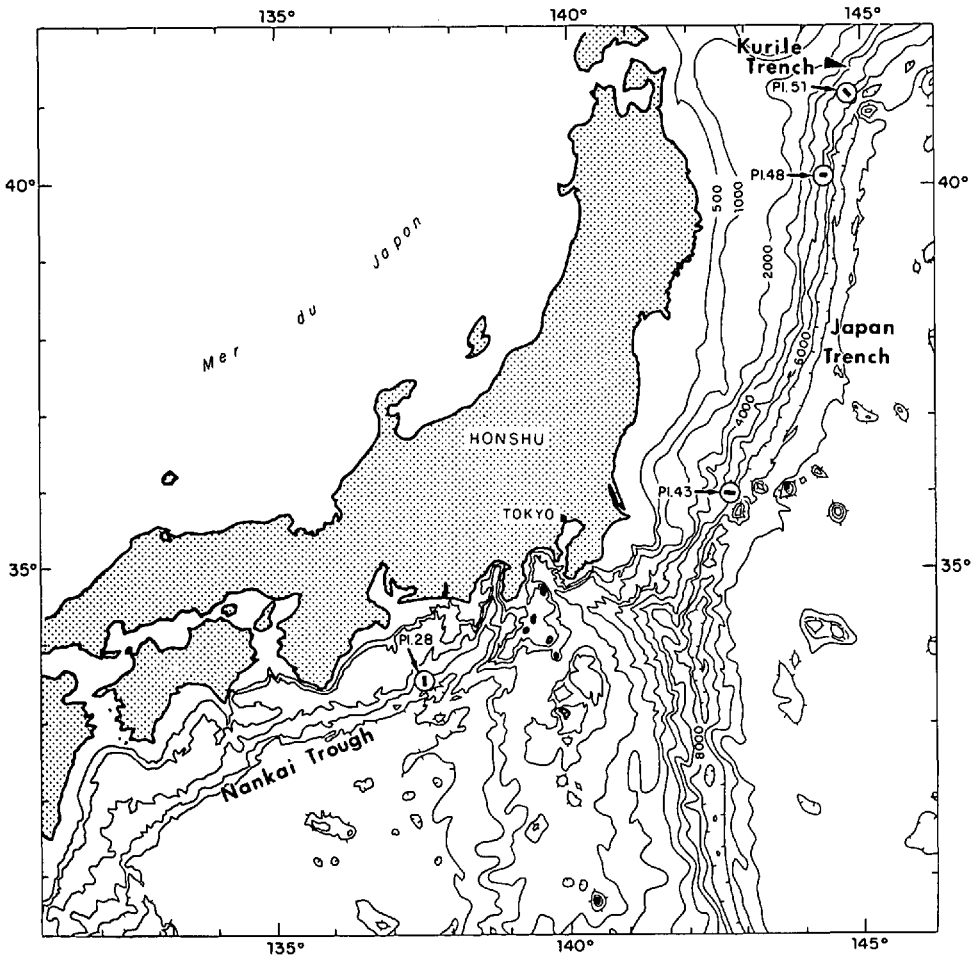


Figure 1. Bathymetry of the Pacific Ocean near Japan revealing the deep trenches of the subduction zones. Locations of the four studied dive sites are indicated: Pl. 28—Tenryu Canyon (Nankai Trough); Pl. 43—site of subduction of Kashima Seamount in the Japan Trench; Pl. 48—Japan Trench; Pl. 51—Kurile Trench.

continental margin. The presence of the seamount locally elevates the trench floor to a depth of 5890 m, from its usual depth of 7000–8000 m. The sedimentation rate is notably lower here than at the Tenryu Canyon site, and occasional ferro-manganese crusts can be seen. Frequent debris flows cover steep areas of the inner slope and small steps can be observed. Small valleys and aprons parallel the slope, showing an “en echelon” morphology. These valleys are carrying debris to the trench floor (Kobayashi *et al.*, 1987).

c. Japan Trench 40N (Dive 48). The landward wall of the Japan Trench at 40° 07' N (Fig. 1) can be divided into three main parts: the upper slope (shelf break down to

4,000 m depth) shows a very gentle gradient, the middle slope (4,000–6,000 m depth) forms an intermediate step bounded by two scarps, and the lower slope (6,000–7,500 m depth) constitutes the toe of the margin arriving in contact with the Japan Trench axis. The scarp separating the middle and lower slopes is the major scarp and was believed to be a panamean fault. The dive analyzed here explored the upper part of this scarp (above 6,000 m), an area characterized by a collapsed terrain with normal faults leading large-scale gravity sliding and avalanches (Cadet *et al.*, 1987a,b).

d. Kurile Trench (Dive 51). The inner wall of the Kurile Trench, near its junction with the Japan Trench (Fig. 1) shows a very steep relief. This site is also intersected by a major strike-slip fault (Fig. 1). In this complex geological setting the continental margin is being eroded rather than accumulating an accretionary prism. Dive 51 explored the upper part of the inner trench wall, between 5,785 m and 4,980 m depth, ascending the seaward face of the above mentioned major strike-slip fault. The slope consists of a succession of rock cliffs, with talus of gravels, sands and fallen rocks. Some of the cliffs are vertical, some with overhanging sections (Cadet *et al.*, 1987a,b).

3. Analytical methods

All video and photo documents from dives reporting the presence of *Calyptogena* were reviewed. In addition, photo records from several dives not reporting cold seeps were examined, as a reference to the general character of the abyssal fauna in the region. The above four dive sites were then selected for detailed study. *Calyptogena* colony location and approximate size, relative proportions of living and dead clams, and the occurrence of unusual macrofaunal aggregations were plotted on bathymetric profiles of the dive tracks (Figs. 5–8) along with indications of the nature of the substratum and direction of major geological faults and deformations as determined from *in situ* observations, bathymetry and multi-channel seismic reflection data. Where close-up video or photographs permitted, living and dead clams were distinguished by the presence/absence of visible mantle tissue. Otherwise, closed and vertically oriented valves were considered to be living clams, and open, horizontally-oriented valves and valve fragments were assumed to be the remains of dead clams. In order to illustrate the magnitude of cold seep exploitation by the clams, four categories of colony size are symbolically represented in the figured dive profiles. The most distinguishable groupings of clams were 1–5, 5–20, 20–50 and 50–100 individuals. A few colonies classified in the latter category (50–100 individuals) contained slightly more than 100 clams. Clams in the larger colonies were frequently packed very close together. Symbolic representation was also used to show the approximate proportions of living and dead clams in each colony (Figs. 5–8).

4. Results and discussion

a. Abyssal fauna and evidence of pore-water venting. Away from the localized cold-seep communities, video and photo records of the explored sectors revealed a

typical sparse abyssal fauna. Rock outcrops were occasionally colonized by sessile organisms such as sponges, deep-sea corals (gorgonians, pennatulids, actinarians), stalked crinoids and serpulid polychaetes. Often rock surfaces and even entire cliff faces were devoid of fauna. Areas of soft bottom were also poorly populated by visible organisms. As usual for sediments at these oligotrophic depths, echinoderms were the best represented group, with asteroids, holothurians and echinoids occurring in most regions. Among the swimming fauna, paeneid prawns were occasionally seen, while fish were rarely encountered. Lebensspurren (Young *et al.*, 1985), either from echurians or enteropneusts, testified to the presence of a sediment infauna. Branching, agglutinating foraminifera (Komokiacea?), typical of hadal trenches (Tendal and Hessler, 1977) were also visible in photographs.

The most visible indicators of cold seeps were colonies of *Calyptogena*. Temperature anomalies and elevated CH₄ concentrations in seawater within the clam colonies verified the presence of discharging pore-waters (Boulègue *et al.*, 1987a,b). All four species of *Calyptogena* identified from this region (Métivier *et al.*, 1986; Okutani and Métivier, 1986) were associated with confirmed active cold seeps and had high haem protein levels in their blood. One species, *Calyptogena fascioliformis*, was found to harbor endosymbiotic bacteria in its gill tissue (Boulègue *et al.*, 1987a). Tissue samples from this species had very negative $\delta^{13}\text{C}$ values (-37 to -40), indicating that its major carbon source was chemosynthesis (Boulègue *et al.*, 1987a). Ultrastructural and tissue $\delta^{13}\text{C}$ information was not available for the other three *Calyptogena* species identified from this region.

Clam distribution was sporadic, with colony size ranging from a few individuals to densely-packed colonies of over 100 clams. Larger colonies were usually circular in shape. Occasionally many clam colonies were found in close proximity, suggesting the presence of a "field" of multiple seep exits. The megafauna associated with the clams was clearly distinguishable from that of the surrounding region, in terms of both its unusual composition and greater density (Juniper and Sibuet, 1987). A direct relationship between megafauna and clam abundances was apparent and three clam-associated faunas were distinguishable:

(1) Large circular colonies containing up to three species of *Calyptogena* (*C. nautilei*, *C. laubieri*, and *C. kaïko*) (Okutani and Métivier, 1986) on soft sediment along with a small number of accompanying organisms, mainly suspension feeders and omnivores (Fig. 2). This typifies the Tenryu Canyon site. Serpulid polychaetes were the most abundant accompanying organism, occurring on the shells of dead clams and on nearby boulders. Other accompanying megafauna included large holothurians, galatheid crabs and actinarians.

(2) Large circular or elongate colonies composed of *Calyptogena phaseoliformis* only (Métivier *et al.*, 1986), accompanied by dense aggregations of deposit-feeding and omnivorous organisms (Fig. 3). This type of colony occurred at the Kashima and Japan Trench sites. Deposit feeders, swimming holothurians (*Peniagone*) and/or large tubicolous polychaetes, were very abundant, covering large areas of the seafloor

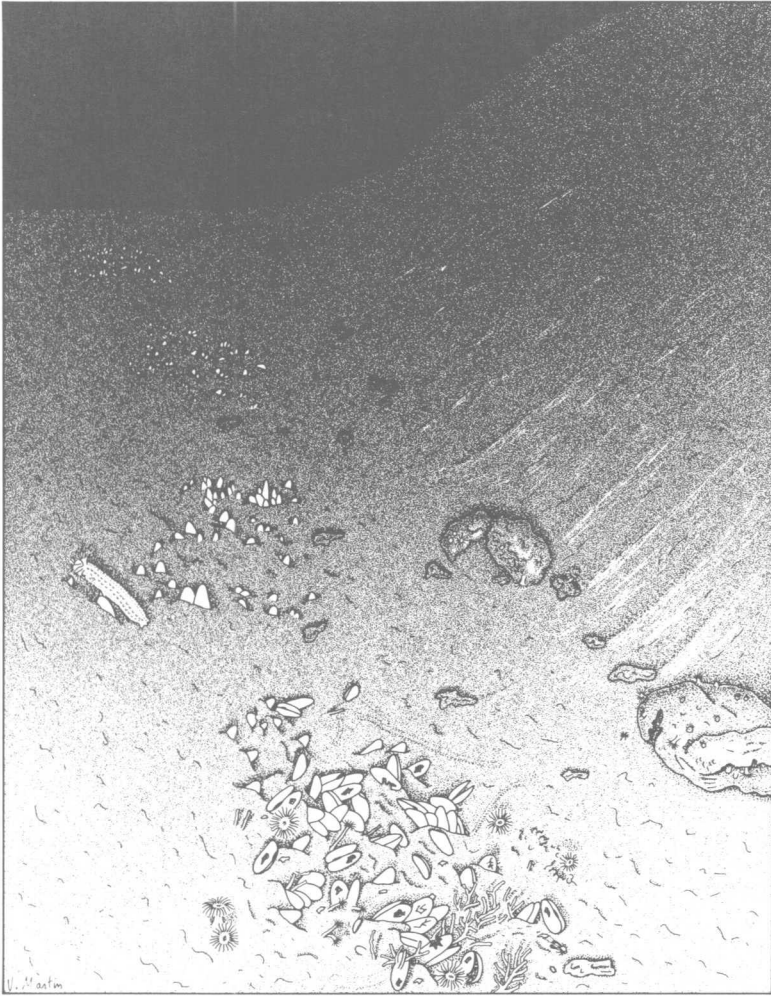


Figure 2. Artist's conception of the alignment of clam colonies in a cold seep field in Tenryu Canyon. Figure drawn from a photomosaic of clam field A in Figure 6. Colonies contain up to three species of *Calyptogena* (*C. nautilei*, *C. laubieri* and *C. kaiko*). Other organisms clearly associated with the clams are serpulid polychaetes, galatheid crabs and large holothurians.

around the clam colonies. Caprellid amphipods were very numerous within and outside of the clam colonies. Actinarians and a buccinid gastropod were common members of this assemblage.

(3) Small clam colonies or scattered individual clams without visible accompanying fauna (Fig. 4). This third type of community was encountered on all dives on all types of substrata but was most common on rocky or gravely surfaces.

One exception to the generally impoverished condition of the nonseep megafauna

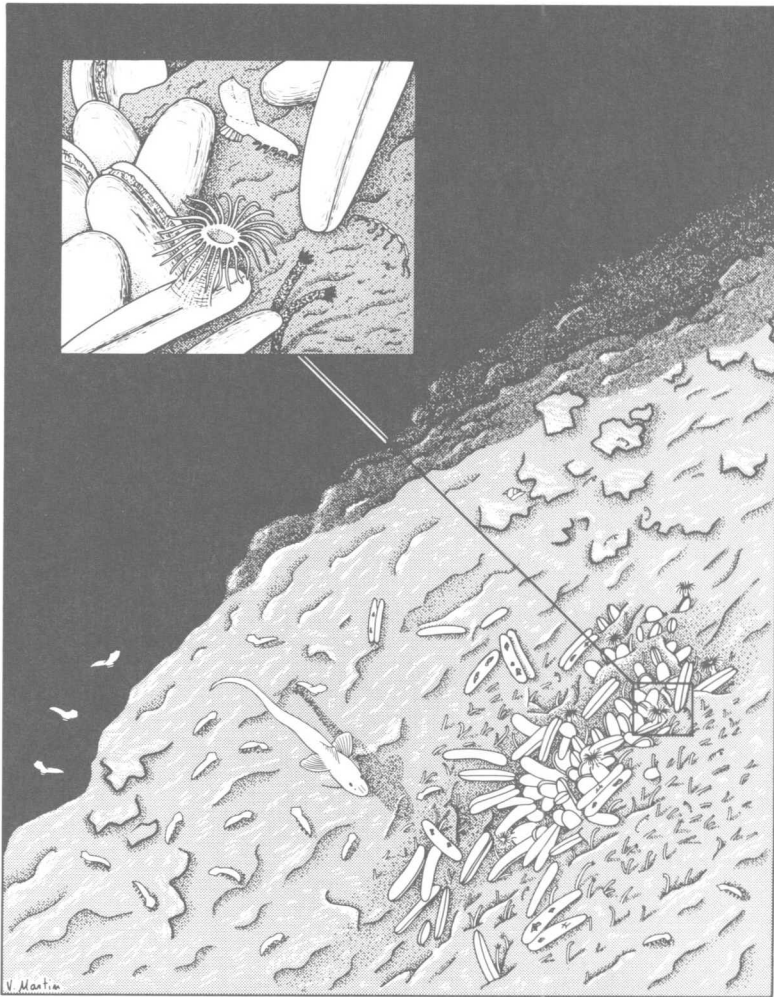


Figure 3. Artist's conception of the second type of large clam colony seen during the Kaiko diving program. Figure corresponds to the single active seep found during Dive 43 on Kashima Seamount (Fig. 5). Colony is aligned along a sediment slide scar. Clams are all *Calyptogena phaseoliformis*. Caprellid amphipods are abundant within and outside of the clam colony. Sediments surrounding the clam colony are heavily populated by detritivores, in this case both swimming holothurians (*Peniagone*) and unidentified tube-dwelling polychaetes. The polychaetes were the only deposit feeder found at most other sites of this type.

was an unusual enrichment of echinoderms at the Kashima Seamount site. A large deposit-feeding holothurian (*Scotoplanes* sp.) was very abundant on the seaward slope of the Japan Trench at this site. Where the bottom was clearly visible, the animals were enumerated (Fig. 6). For this size category of holothurian, estimated density was nearly 5 times greater than is usually seen at these depths (Sibuet, 1985; Sibuet,

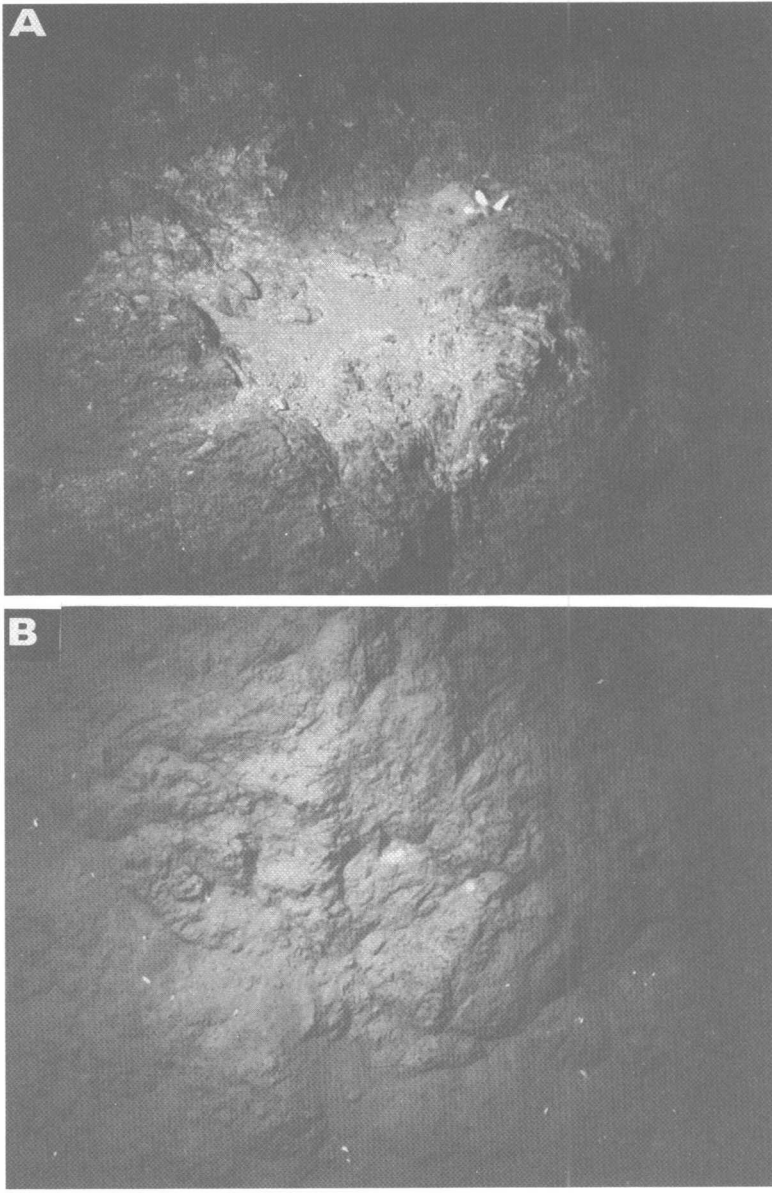


Figure 4. Photos of the third type of clam colony, which occurred mainly on rugged gravely or rocky terrain. (A) Small isolated colony perched on a lightly-sedimented ledge on a steep, near-vertical cliff (Dive 48, Japan Trench). (B) Near-vertical cliff face colonized by scattered clams (Dive 51, Kurile Trench). (Photos—IFREMER Nautille).

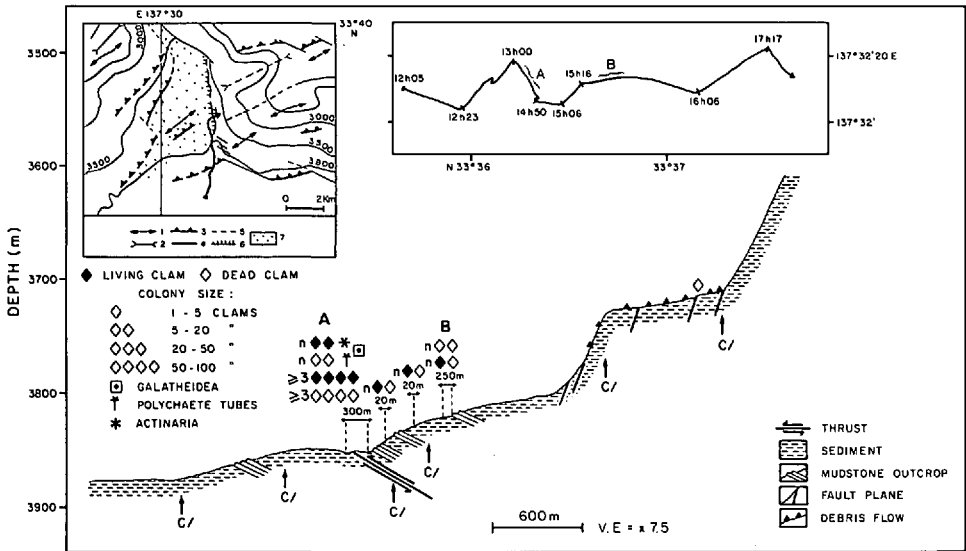


Figure 5. Profile of Dive 28 in Tenryu Canyon. Main figure shows topography, substratum, faulting and cold seep communities encountered during the dive. Insets indicate location of dive track in relation to local bathymetry (upper left inset) and course changes during submersible transit (upper right inset). Key to upper left inset: 1—anticline axis, 2—syncline axis, 3—thrust fault, 4—strike-slip fault, 5—canyon erosional boundary, 6—panamanean fault, 7—canyon bed.

unpublished data). *Scotoplanes* were less numerous on the trench floor and absent on the landward slope where swimming holothurians (*Peniagone* sp.) and large asteroids (Porcellanasteridae) were unusually abundant (Fig. 6). None of the other seven dives on Kashima Seamount encountered similar concentrations of echinoderms. Unusual aggregations of echinoderms are known from deep sea-photographs (Billet and Hansen, 1982), but the responsible environmental factors remain unidentified.

b. Tectonics and pore-water migration. All cold-seep communities in the study areas occurred in association with one of several types of major faults, indicating the importance of faults as a pathway for the upward migration of deep pore waters. The largest clam field (A in Fig. 5) was found at the Tenryu Canyon site where colonies were discontinuously distributed along a line coinciding with the deformation front (Fig. 2). Discharging pore-waters at the Tenryu Canyon site likely originate in a deep high-pressure zone and seep up along the thrust plane (Fig. 5) which extends here to at least 3 km depth, emerging near the foot of the sedimentary prism. When arriving at the level of the actively deformed zone, the fluids ascend along deformation fractures to the surface. An essential element, however, seems to be the active erosion at this point in Tenryu Canyon, as no bivalve communities were found during another dive (Dive 27) along the well-developed frontal zone of deformation to the east.

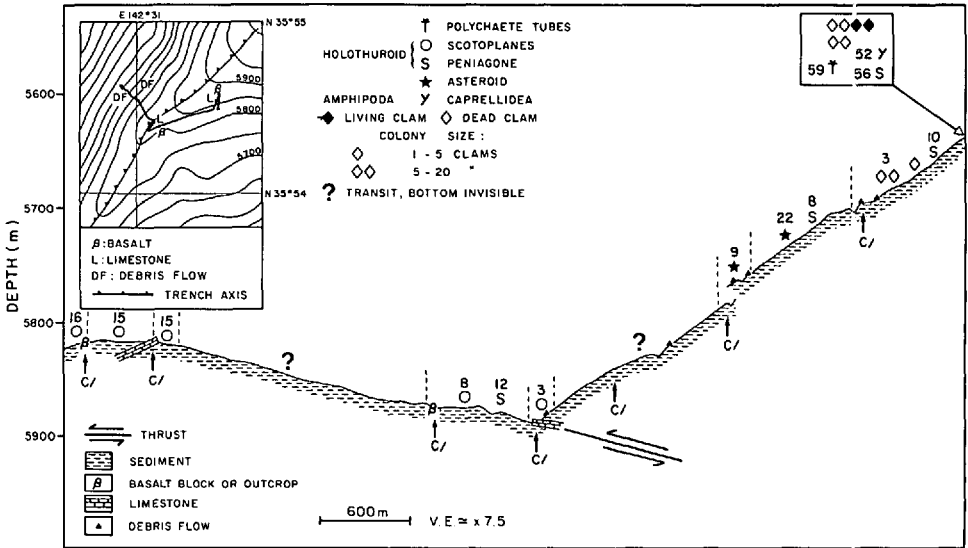


Figure 6. Profile of Dive 43 on Kashima Seamount. Main figure illustrates topography, substratum, major faulting, cold seep communities, and unusual echinoderm densities. Inset shows location of dive track in relation to local bathymetry. The dive began on the seaward slope of the trench (left of figure), descended to the trench floor and climbed the inner trench wall.

At the Kashima Seamount site, multi-channel seismic reflection profiles show the subduction plane deepening below the Japanese continental margin. No clear reflectors are apparent in the toe of the inner wall. The presence of a reduced accretionary prism is probable in this area and the observed steps on the lower slope (Fig. 6) could correspond to moderate thrust planes. Nevertheless, no clear compressional tectonic features were observed on the lower slope. The dominant process is erosional, with transit and accumulation of debris-flows possibly masking the underlying thrust planes. A single active seep occurred in association with the toe of the inner wall, near the main thrust plane in a complex landscape with minor accretion and dominant erosion (Fig. 6). Alignment of the clams at this site indicated that seeping was concentrated in a sediment slide scar on a small terrace (Fig. 3). The absence of seeping and clams on the mid-slope where both folding and land-slides are seen could be due to obstruction of pore-water migration.

Bivalve colonies were encountered intermittently along the scarp explored in Dive 48 (Fig. 7). The panamean fault which the scarp represents is likely the major conduit for upward migration of fluids. Overpressure fluids migrate up to 4 km along the landward sedimentary strata if they are coming from the subduction plane. The intensity of the erosive process allows the fluids to seep high on the continental margin by way of fractured strata. The abundance of both clam colonies and their accompanying fauna

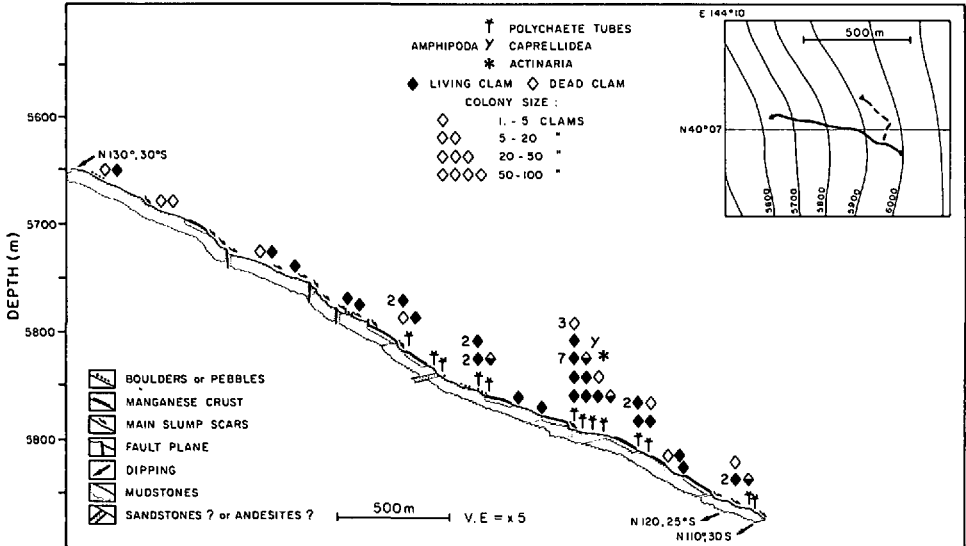


Figure 7. Profile of Dive 48 in the Japan Trench. Main figure illustrates topography, substratum, major faulting and cold seep communities. Note interruption of manganese crust in areas of slumping. Inset shows dive track on local bathymetry. Dashed line in inset marks transit out-of-site of bottom at beginning of dive.

decreased with distance upward from the subduction plane at this site (Fig. 7), suggesting a corresponding weakening or chemical alteration of pore-water discharge.

In the complicated geological setting of the Kurile Trench site it is difficult to relate pore-water discharge to any particular surface feature. Small groups of clams were observed throughout the dive. Frequently, extensive areas of vertical cliff face were colonized by individual clams or small groups lodged in ledges (Fig. 8). The major strike-slip fault present at this site may provide a very direct pathway for upward migration of deep pore waters along an extensive zone. Heavy erosion and faulting of the inner trench wall (Fig. 8) likely provide a multitude of points where rising fluids could escape from rock strata.

The proportions of living clams and empty valves within colonies were highly variable. We interpret this as a reflection of the ephemeral nature of individual cold seeps. Assuming a vital dependence of the clams on pore-water seepage, Juniper and Sibuet (1987) argue that colonies consisting only of the empty valves of dead clams mark sites where cold seeps are no longer active, that colonies composed entirely of living clams likely indicate recently colonized sites and possibly newly-activated cold seeps, and that similar proportions of living clams and empty valves within a colony reveal longer-lived cold seeps where empty valves have accumulated by natural mortality. Although this demographic aspect of the clam colonies showed no apparent correlation with tectonic features, the larger cold-seep fields contained both relict and

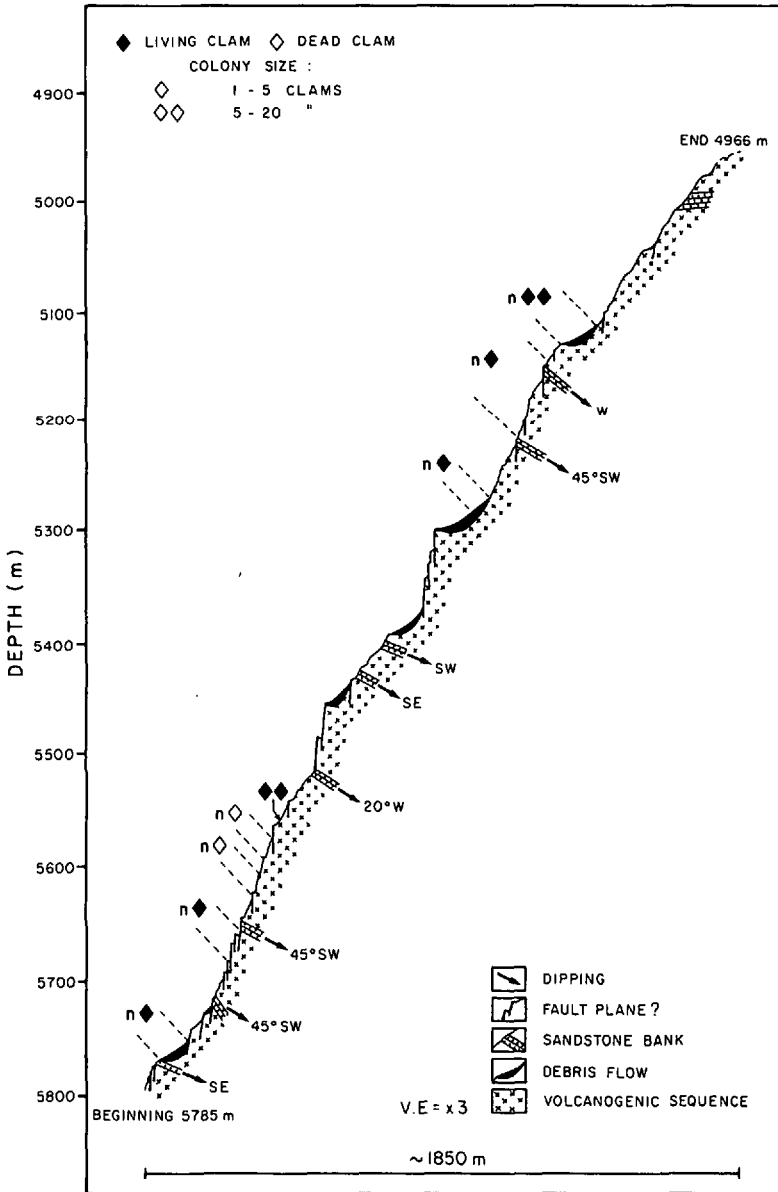


Figure 8. Profile of Dive 51 in the Kurile Trench. The steep topography, substrate, complex faulting and clam locations are illustrated. The cliffs are built by two main families of subvertical faults, the major one striking 330N and the other striking 60N.

recently established (living clams only) clam colonies (Figs. 5, 6 and 7), suggesting some long-term localization of pore-water seepage within large fields. Such areas would be of greater importance in the long-term maintenance of regional populations of cold-seep organisms than would more ephemeral seeps or seep fields. Larger seep fields also had extensively developed accompanying faunas, perhaps as a result of their long duration. This is important in energy transfer between cold seeps and the surrounding deep-sea ecosystem, since the development of an accompanying fauna marks the integration of cold-seep productivity into the deep-sea food web. Observations are too few to permit consideration of the duration of cold-seep fields in different subduction settings.

c. Topography and substratum. The occurrence of clam colonies on all types of terrain from gentle, sedimented slopes to vertical rock cliffs indicates that there is no major topographic control of the exploitation of cold seeps by clams. However the clam distribution data do suggest that the nature of the seafloor substratum affects the final release of pore waters migrating along fault planes. A cover of sediment or a heavy manganese crust appears to restrict the escape of fluids from underlying strata. Sedimentation and sediment cover were heavy in Tenryu Canyon, more moderate at Kashima Seamount, and extremely light or nonexistent at the other two sites. At the two sedimented sites, bivalve colonies were clearly limited to locations where erosion of the sediment cover permitted fluids to exit. The heavy manganese crust on the slope at the Japan Trench site (Dive 48) also appeared to block pore-water seepage. There, clam colonies were limited to areas of the slope where recent slumping or outcropping had interrupted the manganese crust (Fig. 7). The absence of sediment cover or manganese crust at the Kurile Trench site (Dive 51), together with the heavy erosion of the slope, likely accounts for the observed abundance of small clam colonies along the dive track in this area (Fig. 8).

Substratum also appeared to influence the size and composition of these cold-seep communities. While clam colonies occurred on sediment and mudstone surfaces, gravel talus and even on ledges on vertical rock cliffs, large colonies and an accompanying fauna were limited to sediment or mudstone substrata. No large colonies were seen on rock or gravel surfaces, which were the domains of isolated clams and colonies of fewer than six individuals. This substratum effect was consistently observed at the more than 50 cold seep sites discovered during the Kaiko diving program, including those sites not presented here. It does not appear to be related to any need of the clams to burrow into the substratum. While clams on soft sediment were usually partially buried, some of the largest colonies were epibenthic on mudstone surfaces. A more likely explanation is that sediment or mudstone substrata cause rising pore waters to diffuse laterally, resulting in cold seeps of greater surficial area than if fluids discharged directly from rock fractures. Where fluid flow was sufficient this effect could produce seeps extensive enough to be exploited by colonies of over 100 clams. The close packing of

clams within colonies suggests that the surficial extent of fluid discharge is an important limiting factor in colony development. Whether sediments block discharge of upwardly migrating pore waters or act as a diffuser may depend on the relationship between sediment cover thickness and the strength of pore water flow. For example, heavy sediment cover would tend to diffuse weaker flows to the point where discharge would be negligible in terms of exploitability by clams and other organisms.

Lateral diffusion of fluids may explain the abundance of deposit-feeding organisms around the large clam colonies. If emissions of methane-rich pore water extend to sediments outside of the clam colonies, they could possibly enhance organic matter production by free-living bacteria. Such a local enrichment of sediments could be the food source of the swimming holothurians and large tubicolous polychaetes found at the Japan Trench and Kashima Seamount cold seep sites. Limitation of other accompanying species to large clam colonies may, in part, be related to their dependence on organic debris produced within the clam colonies (Juniper and Sibuet, 1987). Production of such debris by small colonies may not be sufficient enough to support scavenging and suspension-feeding organisms such as caprellid amphipods, galatheid crabs, serpulid polychaetes and actinarians. The direct and indirect utilization of methane by the clams and other cold-seep organisms are examined elsewhere (Juniper and Sibuet, 1987).

5. Conclusions

The Kaiko diving program has greatly enlarged observational records of subduction zone cold-seep communities. Our analysis of four contrasting dive sites leads us to several conclusions regarding the basic geological circumstances controlling development of these communities:

(1) Cold seeps and cold-seep communities can occur in both subduction-accretion and subduction-erosion settings, wherever there are major faults permitting upward migration of deep pore waters. Thus they have the potential to occur in subduction zones worldwide.

(2) Passage of migrating pore waters through sediment or mudstone substrata may cause lateral diffusion, thereby enlarging the surficial area of fluid emissions, allowing large cold seep communities to develop.

(3) Heavy accumulations of sediment or thick manganese crusts may block the discharge of pore-waters ascending along faults in underlying rock strata, limiting cold seeps to sites where erosion, slumping or outcropping reduce or interrupt these coverings.

(4) Large cold-seep fields may represent sites of long-term localization of pore water emissions and, since cold seeps appear to be ephemeral, they may be important in the maintenance of regional populations of seep organisms and in the transfer of cold-seep productivity to the ecosystem of the surrounding deep sea.

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