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Benthic Communities on Lō'ihi Submarine Volcano Reflect High-Disturbance Environment[1]

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ABSTRACT: Bottom surveys and collections on Lō'ihi Seamount, Hawai'i, revealed two distinct and recurrent benthic communities. One comprises bacterial mats and is closely associated with hydrothermal vents. The other consists of dense aggregations of megabenthos—octocorals, sponges, hydroids, and black corals—all normal inhabitants of nonvolcanic hard-bottom habitats at comparable depths in the Hawaiian Islands. The bacterial mats are devoid of specialized megafauna and are found in summit areas or rift peaks where diffuse low-temperature hydrothermal vents are common. The absence of megafauna there may be due to extreme environmental conditions produced by vent waters that contain no oxygen and extraordinarily high concentrations of CO_2 (pH = 5.5) and trace metals. At greater depths, from 200–300 to 1,000 m below the summit, dense aggregations of gorgonians and other megafauna exist but are uncommon. Aggregations are restricted to stable outcrops of pillow basalts (kīpukas). Surrounding areas are covered by talus and are virtually devoid of benthic organisms. Their rarity may be due to instability of the substratum caused by frequent slumping and debris avalanching (mass wasting). Both bacterial mat and deep flank megabenthic communities reflect a high-disturbance environment.

LŌ'IHI VOLCANO IS an emerging submarine volcano currently situated over the Hawaiian hot spot and likely the site of the next Hawaiian Island (Klein 1982, Malahoff 1987). In this paper, the results of bottom camera surveys, dredge hauls, and bottom submersible transects conducted in 1986 and 1987 to map benthic communities on the summit and deep flanks of Lō'ihi are described. While extensive hydrothermal vents are known to exist at the summit at 960 m (Pele's Vents) and all along the south rift to 4800 m (Malahoff 1993), biological communities associated with vent systems are limited to dense bacterial mats (Grigg 1987, Karl et al. 1988, Moyer et al. 1995). Specialized megafauna common at other hydrothermal vent sites in the world (Tunnicliffe 1991), such as vestimentiferan tube worms (*Riftia pachyptila* Jones, 1980) and giant clams (*Calyptogena magnifica* Boss & Turner, 1980), are conspicuously absent. A combination of factors associated with fluid chemistry of hydrothermal vents along the rifts and at the summit appears to limit the abundance and diversity of benthos in this habitat.

On the flanks of Lō'ihi Seamount, deep-water benthos common at equivalent depths at many sites elsewhere in Hawai'i, such as large octocorals and hexacorals, are extremely sparse except on infrequent outcrops. Such areas support clusters of large (old) octocorals including *Corallium* sp. (pink coral) and several species of primnoid gorgonians (gold corals). They occur in areas of unusual stability analogous to kīpukas (isolated patches or islands of high ground that support older stand forests that escape coverage or burning caused by recent lava flows [Stearns 1966]) on subaerial lava flows. Most of the flank area on Lō'ihi is covered by talus. In this habitat, frequent submarine landslides (mass wasting) appear to severely impede the buildup and succession of otherwise common deep-sea benthic communities.

Geological Setting of Lō'ihi Volcano and Hydrothermal Activity

Lō'ihi Volcano is situated 30 km east of the island of Hawai'i (Figure 1). It is the youngest

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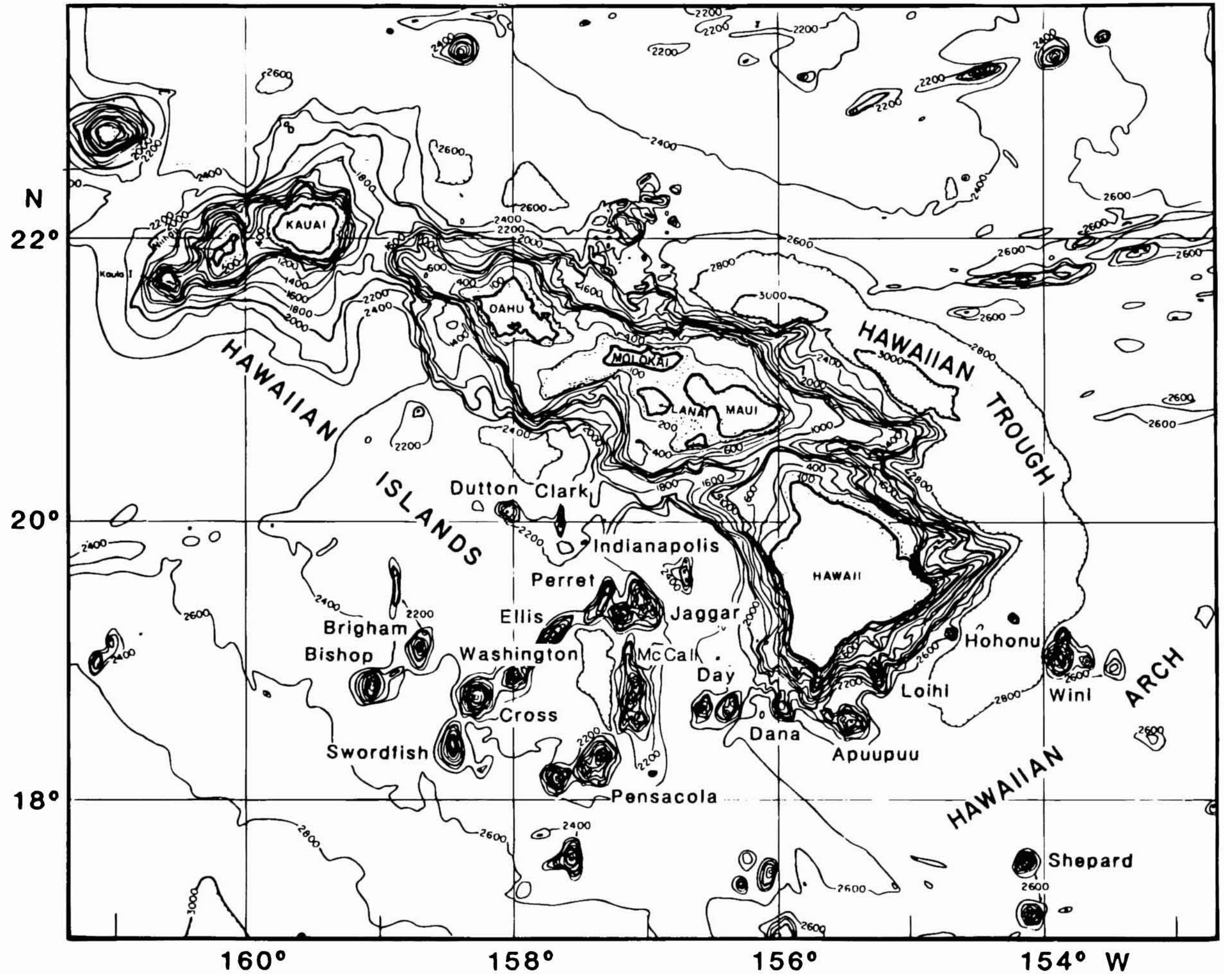

FIGURE 1. Map of major Hawaiian Islands showing location of Lō'ihi Seamount.

volcano in the Hawaiian chain, situated at the southeastern end of the Kaho'olawe–Hualālai–Moana Loa volcanic line (Jackson et al. 1982). Frequent seismic activity and abundant fresh lavas indicate continuing volcanic activity (Moore et al. 1982, Cooper and Duennebier 1988, Karl et al. 1988; F. Duennebier and F. Sansone, unpublished data, 1996). A deep zone of earthquakes, at a depth of 60 km between Kīlauea, Lō'ihi, and Moana Loa, suggests that the three volcanoes share a common source of magma from the Hawaiian hot spot (Malahoff 1987). Although the elongate edifice rises approximately 4 km from the bottom, its summit depth is still 960 m from the surface.

Moore (1979) showed that many of the rocks from the summit area are highly volatile, containing 30 to 50% vesicles. Vesicularity is highest in the shallowest basalts, suggesting the possibility of mild explosive activity near the summit (Moore et al. 1982). In an earlier paper, Moore (1979) showed that 95% of the gas in the vesicles of spreading center basalts (MORBs) is CO_2.

Approximately 90% of the summit is covered by talus or ash fields (Malahoff 1992*a*). Talus is the dominant rock type to depths of 2500 m. Malahoff (1987) also mapped 10 new lava flows between 1978 and 1981 near the summit. Talus flows were present everywhere along their edges, apparently forming from the fracturing of new pillows shortly after their formation. Moore et al. (1973) observed a similar process on an active submarine flow off the shoreline of Kealakomo, Hawai'i, in 1971. During that flow, talus slopes consisting of angular, well-sorted blocks (fragments of cylindrical pillow lavas) built up slope angles of 30–45 degrees before slumping or avalanching into deeper water. On Lō'ihi, similar processes appear to have shaped the summit edifice. The presence of armchairlike indentations in the edifice and the dominance of talus flows to 2500 m suggest that slumps and debris avalanching (mass wasting) are contemporaneous with the growth of the volcano (Malahoff 1987). These processes are responsible for the porous structure of the summit notwithstanding the plumbing (dikes and conduits) associated with the reservoir of magma deep within the pile (Malahoff 1987).

Hydrothermal activity along the summit and downrift vents is relatively diffuse (Karl et al. 1988). All vents that have been studied to date are low temperature in character, generally 30°C or less. Only one small plume with a higher temperature (80°C) has been found at the base of a pit crater (Malahoff 1993). High-temperature vents (≈350°C) and black smokers so common at spreading centers are absent on Lō'ihi. The relatively high porosity of the summit edifice may be responsible for both the diffuse nature of the vents and the lack of more concentrated and hotter hydrothermal fluids.

MATERIALS AND METHODS

Data collection was conducted over the course of three cruises to Lō'ihi Volcano in 1986 and 1987. During the first cruise, on board the *Moana Wave* in 1986, nine dredge hauls at depths ranging between 985 and 1875 m were carried out. Six were conducted with tangle nets designed to collect benthic organisms (Grigg et al. 1973). The nature of the substratum (loose talus, rock, sand, etc.) was interpreted by observing the strain gauge on the winch cable over the course of each dredge haul. Three dredge hauls were conducted with a standard rock dredge.

Five bottom camera transects were run at depths ranging between 1025 and 2000 m covering 6 km of linear bottom. The camera system was "flown" at a height of about 5–10 m off the bottom. Almost 500 photographs of the bottom were obtained. The camera system, the ALX - 1, was designed and built by personnel of the Hawaii Undersea Research Laboratory (HURL), at the Makai Pier, Waimānalo, Hawai'i (Kelly 1988). The system consists of two deep-sea cameras (Benthos model 377) and 200-watt second strobe lights (Benthos model 383), mounted on a steel frame such that stereo images are obtained (80% overlap at 10 m off the bottom). The system is powered by six 6-volt 50 amp hour, lead-acid jell-cell batteries mounted in an oil-filled pressure compensation bladder. Each camera contains a 122-m roll of film (Kodak Ektachrome ASA 400) capable of recording 3200 exposures. The camera lenses are 28-mm Nikonos lenses. At a setting of f-8, this produces a depth of field of 0.9 m to infinity. Camera strobe synchronization (Benthos model 1391) was set for a 12-sec interval between images. During the

Lō'ihi cruise, an altimeter on the camera sled recorded the height of the camera off the bottom and encoded this information on each photographic image. The scale of each photograph was calculated from lens focal length and height off the bottom. The same scale was used to estimate the size of objects (megabenthos) in the photographs. The exposed film for all 5 transects is archived at HURL at the University of Hawai'i.

Two submersible dives were conducted in 1987. The first, on 15 February, in the *Alvin* submersible, was a reconnaissance of the summit area at Pele's Vents (Craig 1987, Karl et al. 1988, 1989). Four transects covering 630 m of bottom at depths between 970 and 1075 m were completed. The second dive to Lō'ihi was on 5 September 1987 in the University of Hawai'i submersible *Pisces V.* That dive was a linear transect of 1500 m between 1220 and 1700 m depth designed to count and measure megabenthos.

RESULTS

Hydrothermal Vent Communities

Submersible observations revealed that hydrothermal vents on Lō'ihi are restricted to the summit and south rift zones of the volcano. Clusters of vents are associated with topographic highs along the ridges (Figure 2). Karl et al. (1988, 1989) described Pele's Vents at the summit in 1987 as an area covering 250 m^2 at depths between 960 and 980 m. On my dive, in the *Alvin* submersible in February 1987, I found this area to be covered by dense bacterial mats ranging in thickness between <1 cm and 10 cm. The mats were smooth but covered with many small hummocks and pocked by a profusion of individual vent orifices about 2–10 per square meter (Figure 3). Each orifice was lined with white elemental sulfur. The mats were rusty orange, consisting of nontronite (ferric oxides, silica, and iron-rich smectite) and matrices of bacterial filaments (Karl et al. 1989). Measures of temperature within vent orifices during the *Alvin* 1987 dives showed the exiting fluid to be 31°C. Vent fluids were also collected in situ with the use of pressure-sealed titanium samplers. Control samples were also collected using Niskin bottles lowered from the surface. Chemical components most enriched in the vent fluid were CO_2, trace metals, and methane. Carbon dioxide was 140 times more concentrated than normal, and iron, manganese, and methane were 10^6, 10^5, and 10^5 times above ambient, respectively (Karl et al. 1988). The pH of the water was exceeding low (5.3–5.5) as well as totally lacking in dissolved oxygen (Craig 1987). Subsequent dives to sample vent waters produced similar values for these variables (Sedwick et al. 1992).

All areas where active vents were found were characterized by shimmering water (Figure 2). The shimmering appearance of the water is caused by the lights of the submersible refracting through plume waters of differing temperature and density. Numerous small particles of bacterial floc were observed entrained in the vent plumes. Plume water initially rose several meters above the bottom but then spread laterally and slowly descended over the summit flanks. The high concentrations of particulate material and dissolved CO_2 may have served to increase the density of the plume water such that it gradually began sinking after a brief inertial rise from the vents (Craig 1987). Along the flanks of both sides of the summit out to depths of at least 1075 m, the entire landscape was covered by various amounts of bacterial floc accumulating in pits and depressions like a "light snow" (Figure 2). This zone was completely devoid of life other than the bacteria. Numerous carcasses of dead caridean shrimp were observed in the area of the vents, suggesting that bacteria are the only organisms that can tolerate the fluid water chemistry surrounding the summit. A new species of caridean shrimp, *Opaepele loihi* (Williams & Dobbs, 1995), was recently described from baited traps set and recovered from the summit area of Lō'ihi (Williams and Dobbs 1995). This species was not seen on my dive in February 1987 to the vents. Moreover, because it was collected in a baited trap, it may not be a normal resident of this habitat.

Distribution and Abundance of Megabenthos on the Flanks of Lō'ihi

Ninety percent of the bottom photographs taken at depths below the summit to 2000 m contained no visible megafauna. Even fish and mac-

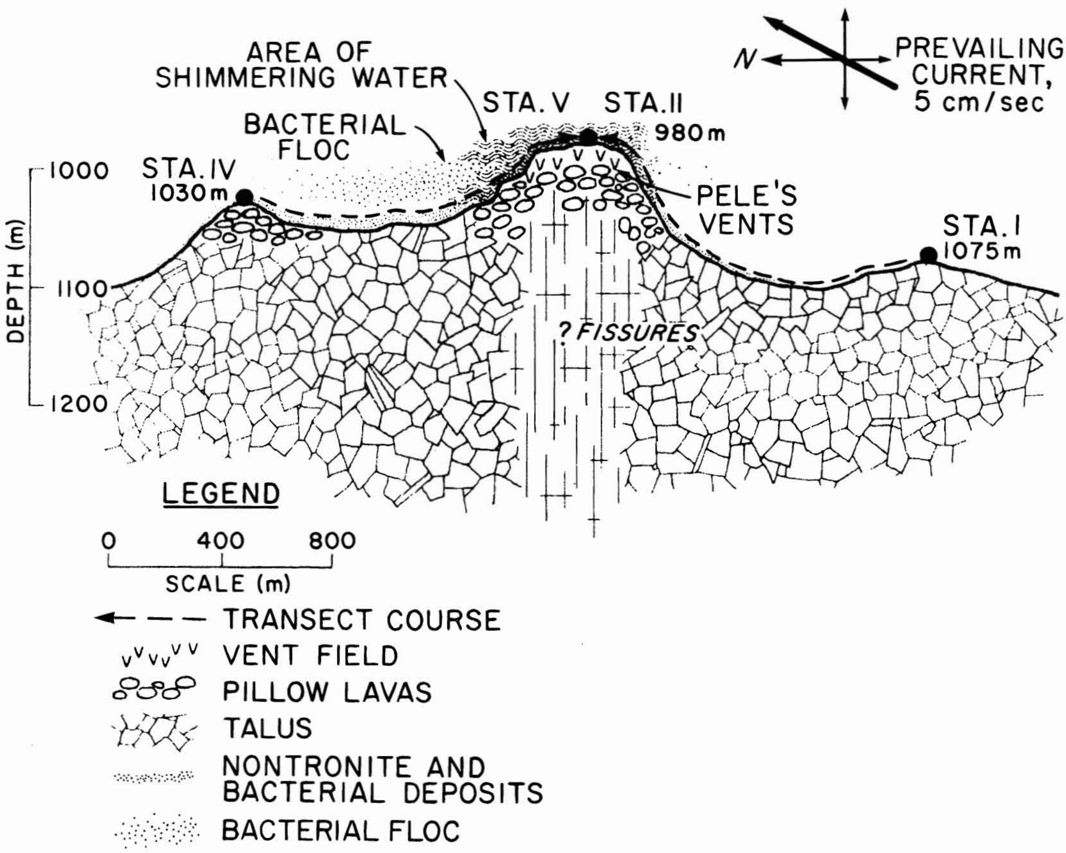

FIGURE 2. Schematic figure of the summit of Lō'ihi Volcano at 960 m in 1987. Hydrothermal vents are concentrated along topographic highs where escaping fluids produce a zone of shimmering water.

roplankton such as medusae were extremely rare. The only patches of substratum where any benthic organisms existed were elevated outcrops consisting of consolidated lobate flows (Figure 4). The bottom otherwise was dominated by fragmental talus and debris flows (Figures 5 and 6). The lack of organisms on the talus fields suggests that these areas are highly unstable. The surfaces of the substratum may be constantly renewed by slippage or slumping into deeper water or by burial from fresh landslides originating upslope. The lack of iron oxides or nontronite surface deposits between talus debris suggests that the release of hydrothermal fluids is not taking place within talus fields and is not an inhibiting factor for potential species of megafauna.

Areas of high-density aggregations of benthic organisms were only found in elevated areas on outcropping consolidated pillow flows (Figure 4). the dominant organisms were large octocorals. Colonies of *Corallium* spp. and *Paragorgia* sp. up to about 50 cm in height were found in five isolated patches (Figure 4). The area of the high-density aggregations of benthic organisms observed during the *Pisces V* dive were on the average about 5000 m^2 (Tables 1 and 2). Highest-density aggregations occurred in the smallest areas. The density of organisms within aggregations on Lō'ihi was higher than, or comparable with, densities of megabenthos encountered elsewhere at similar depths in nonvolcanic rocky habitats in Hawai'i (see Grigg et al. [1987]:fig. 4*A* and Grigg [1988]:table 1). Such habitats in nonvolcanic areas can be viewed as "controls" for the interpretation of abundance patterns on Lō'ihi Seamount.

Measurement of the growth rate of a related species of *Corallium* at 400 m depth off O'ahu

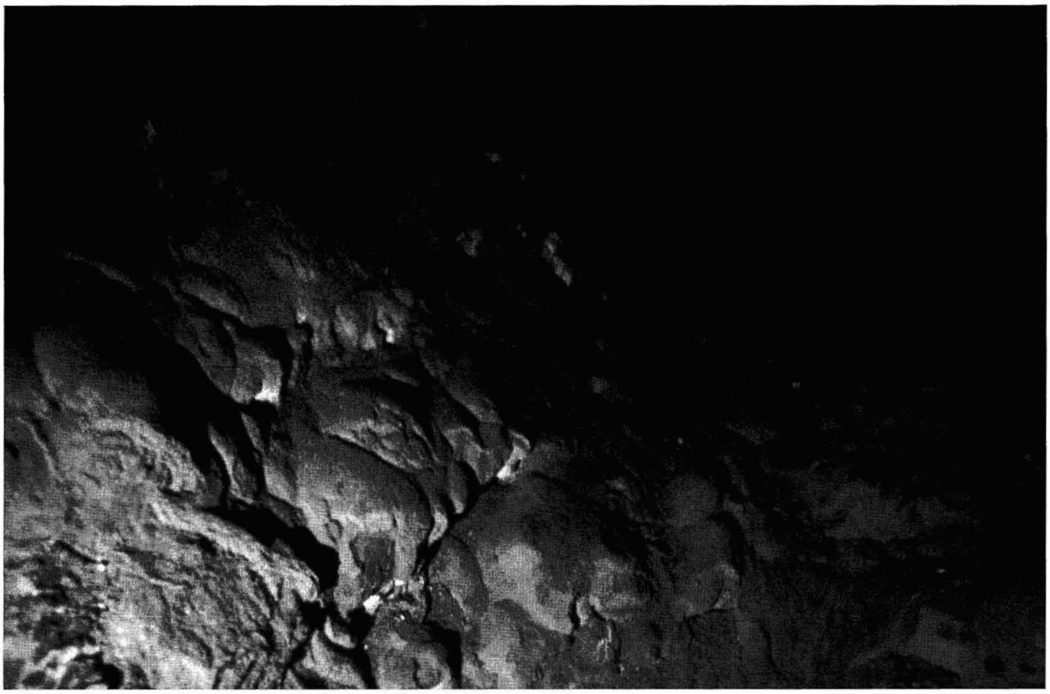

FIGURE 3. Bacterial mats mixed with deposits of nontronite coat the surface rocks in close proximity to the vents. Individual vents are lined with elemental sulfur and appear as white pockets in the photograph.

showed it to have a linear growth rate on the order of 0.9 cm/yr (Grigg 1976). If a similar rate of growth can be applied to deeper colonies of *Corallium* found on Lō'ihi, the age frequency distribution of this species may serve as an estimate of the minimum temporal stability of the substrata, which would therefore be about 50 or 60 yr.

Areas containing high-density aggregations of benthic organisms were invariably surrounded by talus flows on which megabenthic communities were virtually absent. The only difference between the patches rich in benthic species and barren areas was the apparent stability of the substrate. Stable areas where large numbers of benthic organisms were found resemble biological oases, analogous to kīpukas in terrestrial lava flow environments. On the flanks of Lō'ihi, kīpukas supporting benthic communities only occur on stable outcrops where they apparently escape burial from talus debris flows and slumps (Figure 4). After aggregations have become established, gregarious larval behavior could increase the density of some species capable of settling in the presence of adult colonies (Grigg et al. 1987). The presence of species capable of asexual reproduction would also increase density within aggregations.

Other megabenthic organisms commonly found in high-density aggregations include the gorgonians *Paragorgia* sp., *Calyptrophora wyvilli* (Wright & Studer, 1889), *Iridogorgia* sp., *Chrysogorgia* cf. *japonica, Swiftia* sp., *Acanella* sp., large white vasiform hexactinellid sponges, hydroids (family Syntheciidae), black corals *Parantipathes* sp. and *Stichopathes* sp., galatheid crabs, and the shrimp *Heterocarpus* sp.

DISCUSSION

The abundance, distribution, and diversity of benthic communities in both hydrothermal areas and on the deeper slopes of Lō'ihi are limited by high levels of disturbance associated with volcanic processes (hydrothermal fluids, eruptions, slumping, and debris avalanches). The effects of these processes and events are inte-

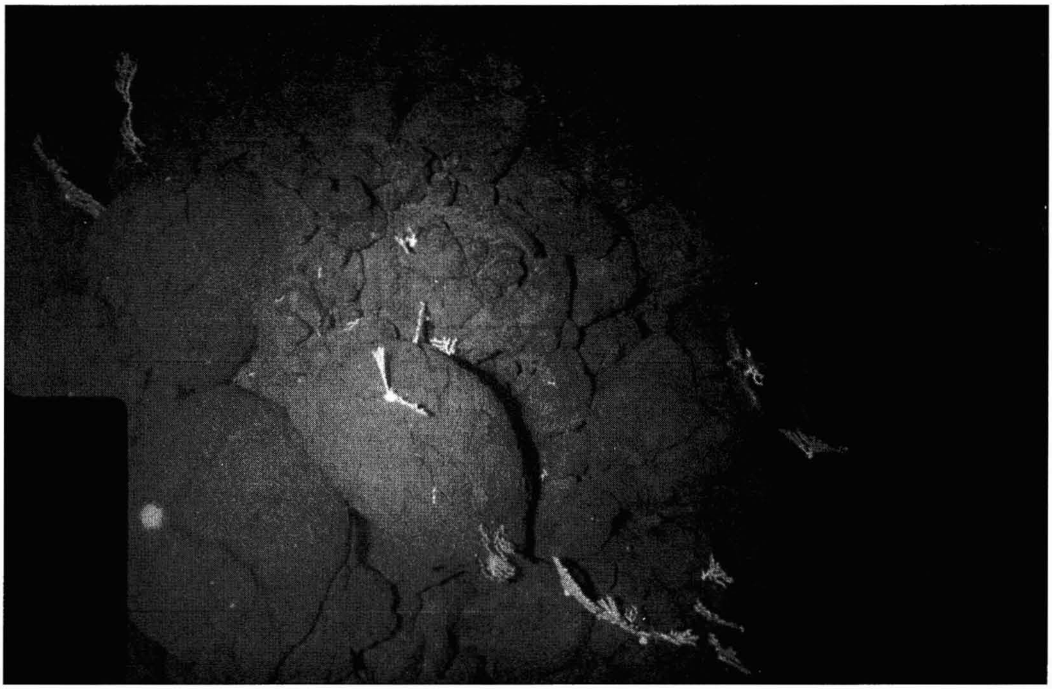

FIGURE 4. High-density aggregations consisting of large (old) octocoral colonies of *Corallium* spp. and *Paragorgia* sp. exist in areas of high stability analogous to kīpukas on subaerial lava flows. Depth of photograph is 1600 m.

grated such that the species composition and size frequency of benthic communities may serve as an indicator of specific types of disturbance.

At the summit, the major source of disturbance is the presence of hydrothermal fluids containing no oxygen but high levels of CO_2, methane, and trace metals. The lack of oxygen alone may be sufficient to exclude aerobic organisms from this environment, although the corrosivity caused by low pH water and/or toxicity due to high concentrations of trace metals may further narrow the diversity of organisms that are able to tolerate this environment.

The abundance of the bacterial mats in the presence of potential predators suggests that vent habitats may be an environmental refuge in which the toxicity of vent waters exceeds the tolerance of most predators. Alternatively, the bacterial mats may not be an attractive source of organic carbon. Karl et al. (1989) found that only 1–2% of the bacterial filaments contained recognizable cellular material. He concluded that the mats may be "fossil" communities.

Along the flanks of Lō'ihi Volcano, the major source of disturbance appears to be debris avalanching. This is reflected in the widespread occurrence of talus, which drapes all sides of the volcano. Moore et al. (1994) found that large, undersea landslides are extremely common in the Hawaiian Archipelago. They mapped a total of 68 giant slides occurring on average once every 32 km along the chain. The largest slides apparently occur late in the period of shield growth when volcanoes are close to their maximum size and when seismic activity is still high. Giant landslide events may in part be associated with the high production of talus during the shallow-water phase of edifice building (Malahoff 1992*b*). Layers of talus, overlain by consolidated flows, may produce inherent instability in the underlying foundation. Talus production is enhanced by high vesicularity, which in turn depends both on basalt CO_2 content and depth (Moore 1979). The vesicularity of Lō'ihi summit basalts ranges up to 50% (Moore et al. 1982).

Although the nature of the disturbance at the summit and flank areas is different (hydrothermal fluids versus mass wasting), the cause of

FIGURE 5. Pillow lavas on the summit appear to fracture immediately after eruption, producing large quantities of talus.

both may have a common source, the structural porosity and instability of the summit. Because of the high porosity of the summit basalts and the magma reservoir in the pile serving as a heat source, a thermal-driven convection system is produced (Malahoff 1992*b*). The diffuse distribution of the vents may explain their low temperature. High-temperature vents (hot smokers) are probably lacking because the flow through the hydrothermal system is insufficiently concentrated. So, too, nutrients necessary to support a richer hydrothermal community may be insufficiently concentrated. The summit is an environment that appears to be tolerant only to iron-oxidizing bacteria (Karl et al. 1989). The high levels of CO_2 and trace metals that characterize mid-plate volcanoes versus spreading-center hydrothermal vents may be a serious limiting factor. Primitive magmas associated with hot spots originate deep within the mantle of the earth and are typically higher in CO_2 than more-depleted MORBs at spreading centers (Seyfried and Mottl 1995). The lack of megafauna on the flanks of Lō'ihi also appears to be related to the high porosity and instability of summit basalts. As noted above, the high frequency of debris flows on Lō'ihi is likely a function of high talus production near the summit (Figure 7).

The unique properties of Lō'ihi Volcano may be typical of emerging hot-spot volcanoes in shallow water. If so, every Hawaiian Island may have passed through this stage. Conditions necessary for the buildup of more complex and diverse hydrothermal vent communities may never have existed in the Hawaiian Islands.

In conclusion, vent fluid chemistry at the summit (high CO_2, trace metals, and lack of oxygen) appears to limit the development of benthic communities to highly tolerant species

FIGURE 6. Large quantities of talus produced by fracture of pillow lavas on the summit, which contribute to debris avalanching. Ninety percent of the flanks of Lō'ihi are draped by debris flows.

TABLE 1

SIZE AND DENSITY OF BENTHIC MEGAFAUNA AGGREGATIONS ON THE DEEP FLANKS OF LŌ'IHI

AGGREGATION	DEPTH (m)	WIDTH AND LENGTH (m)	TOTAL AREA (m^2)	DENSITY OF ALL SPECIES (m^2)
I	1,250	10 by 40	400	0.10
II	1,500	30 by 50	1,500	0.05
III	1,600	10 by 10	100	0.50
IV	1,700	100 by 200	20,000	0.10
V	1,900	30 by 100	3,000	0.05

of hydrothermal vent bacteria. Along the flanks, isolated patches of widely distributed species of usual deep-sea megabenthos are found but only on stable high ground or outcrops (kīpukas) where their abundance approximates densities at comparable depths in nonvolcanic areas in Hawai'i. Kīpukas appear to be less subject to burial by debris avalanching. The rarity of deep flank species on talus flows may not be due to isolation or lack of recruitment (Karl et al. 1989, Tunnicliffe and Fowler 1996), but rather to frequent disturbance from debris avalanches.

Addendum

In response to a seismic swarm of approximately 4000 earthquakes detected near the summit of Lō'ihi Volcano in early August 1996, a cruise to the site was organized by a rapid-response team headed by Fred Duennebier of the University of Hawai'i. The cruise departed Honolulu on 5 August and returned on 9 August after spending 4 days over the volcano. During

TABLE 2

MEGAFAUNA COLLECTED IN TANGLE NET DREDGES FROM OFF-SUMMIT ZONES OF LŌI'HI SEAMOUNT, AUGUST 1986, ON THE *MOANA WAVE*

DREDGE HAUL	DEPTH (m)	LOCATION	BOTTOM TYPE	SPECIES
CD 1	1,040–1,100	18°55.4′N 155°15.5′W	Broken talus	Shrimp, *Heterocarpus* sp.; gorgonian, *Swiftia* sp.
CD 2	985–1,225	18°55.0′N 155°15.5′W	Broken talus	Empty
CD 3	1,200–1,400	18°54.8′N 155°14.9′W	Broken talus	Hydroids, family Syntheciidae
CD 4	1,425–1,800	18°57.8′N 155°15.9′W	Rocky	Gorgonians, *Calyptrophora wyvilli* (Wright & Studer, 1889), *Iridogorgia* sp., *Chrysogorgia* cf. *japonica;* ophiuroid; sponges, hexactinellids
CD 5	1,500–1,875	18°59.7′N 155°15.3′W	Rocky	Gorgonians, *Acanella* sp., *Chrysogorgia* cf. *delicata;* black corals, *Parantipathes* sp., *Stichopathes* sp.; galatheid crab; sponges, hexactinellids
CD 6	1,355–1,600	18°52.9′N 155°16.5′W	Rocky	Sponges, hexactinellids

FIGURE 7. Highly fractured pillow flows are common on the summit of Lō'ihi and are the source of large quantities of talus.

the cruise, two dives in the *Pisces V* submersible were conducted. Multiple seabeam acoustic surveys and three hydrographic (CTD and Two-Yo) sections were also completed. Press releases from the scientific team reported major changes in the summit geomorphology (F. Duennebier and F. Sansone, unpubl. data, 1996). Former high points such as Pele's Vents (formerly 960 m depth) were reported to have been replaced by a new pit crater 550 m in diameter and 300 m deep, roughly the same size as the crater at Kīlauea, on the island of Hawai'i. Several former pits near the summit appeared to have collapsed and coalesced into a larger summit caldera, which may be in the process of formation. These results underscore the dynamic nature of Lō'ihi Volcano and the magnitude of changes in geomorphology that occur there because of mass wasting, including crater collapse and debris avalanching. Clearly, the results reported in this paper refer to conditions that existed at Lō'ihi Seamount before the latest episode of seismic activity.

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