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THE DISTRIBUTION AND COMMUNITY STRUCTURE OF MEGAFAUNA AT THE GALAPAGOS RIFT HYDROTHERMAL VENTS

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ABSTRACT

The distributions of the twenty-two megafaunal species at the Galapagos Rift hydrothermal vents vary markedly with respect to the discharging warm water. Vent associated water temperature ranged to 14.72°C, substantially above the 2.01°C ambient temperature of the area. Because it is a conservative property, temperature is a general index of vent-water quality. Some animals (the vestimentiferan, limpets, clam, a shrimp, an anemone, and for the most part, the mussel) are limited to the mouths of vents, where the temperature is several degrees above ambient. Others (serpulid worm, a second anemone, galatheid crab, turid gastropod) are abundant around the vents, but avoid the vent openings and so never experience much more than a degree above ambient. A third group (the siphonophore, brachiopod, a third anemone, enteropneust, a shrimp, ophiuroid) remains at the periphery of the vent field where temperature is at most a few tenths of a degree above ambient. Some mobile species (vent fish, brachyuran crab, galatheid crab, amphipods) are most abundant at vent openings but range even into nonvent terrain. Among the taxa that are peripheral or at least avoid vent openings are species which also live in the vast nonvent milieu, but most vent field species are endemic. Conversely, most members of the nonvent environment are absent from vent fields. While vents are obviously a source of abundant nutrition, most deep-sea animals are probably not adapted to the elevated temperature and/or unusual chemistry. Some may be inhibited by interference competition. Those that are totally excluded must be especially sensitive because dilution at the periphery is high.

Chemoautotrophic bacteria form the base of the food chain. The largest portion of metazoan biomass thrives through symbiosis with an incorporated chemoautotrophic bacterial flora; these animals are most closely associated with vent openings. Others feed on suspended bacteria ejected from the vents, those that have settled out, or bacteria growing as a film on the substratum. Vent fields possess a well-developed plankton, but the extent to which they form an intermediate link is not known. Nor do we know the amount of photosynthetically derived plankton and detritus that is contributed via the thermally induced convection cell. The top of the food chain consists of scavengers, mostly malacostracan crustaceans, some of whom combine deposit feeding with carnivory. Oddly, fish are not important at this level.

INTRODUCTION

The Galapagos spreading center is the first place where deep-sea hydrothermal vents were investigated at close hand. The initial suspicion that they might be populated with a special fauna came from Deep Tow photographs made in 1976 (Lonsdale, 1977), but the full community, with its high standing crop and wonderous morphologies, was first seen in 1977 by geologists and chemists using Angus and Alvin (Corliss et al., 1979). News of the 1977 discovery resulted in a multi-investigator biological expedition to the site in 1979 (Grassle et al., 1979).

Hessler's role on this cruise was to characterize the megafauna (animals large enough to be recorded in photographs) and document its distribution. Such information supplies much basic data that is useful in biogeographic studies and analyses of vent aut- and synecology. It is therefore a natural complement to the studies of taxonomy, life histories, physiology and microbiology which took place at the same time.

The present paper provides a general description of nearly all the megafaunal taxa seen at the vent fields; a few rare ones are omitted. These distributions are summarized for each of the vent fields we visited, and the vent fauna is compared with the adjacent nonvent community. The reasons for these differences are discussed, and finally, distributional information is combined with what else is known about the biology of the animals to construct a food web for the community.

METHODS

All data were collected using the research submersible Alvin. Three cruise legs in January-February and November-December, 1979, allowed 23 dives of up to seven hours bottom time per dive. Each dive accommodated two scientific observers of varying interest. All dives had multiple tasks, but no individual programs had time allotted on every dive.

Distributional data for the megafauna were collected by direct observation and photography. Observations were recorded on voice tape. Photographs were taken either through view ports using 35mm, hand-held cameras (single lense reflex or stereo) by automatic external survey cameras, or our "arm-stereo" camera held by the starboard mechanical arm. The arm-stereo camera yielded especially clear close-up photographs which were taken with 28mm plane port corrected lenses one meter from the subject. The cameras of the stereo pair were 32.5mm apart. Distance was determined with a one-meter wand that incorporated a temperature sensor at its tip.

The temperature sensor provided information on the extent to which animals in the picture were exposed directly to vent water. If the temperature were ambient (2.01°C), vent water was not involved. Elevated temperatures need more careful interpretation because they should be related to the temperature of the vent water prior to exiting. For example, a temperature of 3°C results from much less dilution if the emerging vent water were at 8°C than at 15°C. About 400 arm-stereo photographs were taken, but unfortunately, the temperature sensor was not always working.

Hessler participated in seven dives, visiting all four vent sites. The observations in this paper are primarily his, although he profited from the observations of others where possible. In addition to the 400 arm-stereo photographs, 520 hand-held single lense reflex photographs (taken by many observers), 340 hand-held stereos, and nine 800 shot camera surveys constitute the photographic data base of this paper.

Some correlations for which there was insufficient data in the Galapagos study were clarified during our recent expedition to the vents on the East Pacific Rise at 21°N (Spiess et al., 1980). These will be utilized where necessary.

No maps of the vents we visited can be made. The terrain was too rough for surveys like that of Grassle et al. (1975), and Alvin's cameras and lighting were not oriented for higher altitude transects like the Angus surveys in Crane & Ballard (1980). Further, the navigation was too uncertain to map our wanderings while closer range photography was done. As a result, there exists only the most general idea about the interrelationship of various sections within any vent field. Finally, the photography is not unbiased. Arm-stereo photographs required the submarine to have settled, and the terrain limited where this was possible. Also, most photographs were taken of subjects of interest, usually biological, and not in a random way. For all these reasons, a calculation of total or average standing crop at a vent is impossible (Smithey & Hessler, in press). Arm-stereo photographs can be quantified, but the most they can give us is maximum densities that were photographed (Table 3).

Equipment and methods of photographic analysis are treated more fully in Smithey & Hessler (in press).

LOCATION

Three vent fields received several visits: Garden of Eden (4 dives), Musselbed (11 dives) and Rose Garden (7 dives) (Table 1). A fourth vent, here called Small Fry, was seen briefly once while searching for Musselbed. Garden of Eden was one of five vents visited by the physical scientists in 1977 and is described by Crane & Ballard (1980). Musselbed and Rose Garden were discovered on our 1979 expedition. Because vents are easily missed, there are probably more. The lineation of these nearly equatorial sites is essentially east-west, and approximately 20 km separates the extremes. Rose Garden is approximately 7,800 m from Musselbed, and the latter is 2,700 m from Garden of Eden.

The physical setting of the vents is described in van Andel & Ballard (1979), and Crane & Ballard (1980). The water chemistry is covered by Corliss et al. (1979), and Edmond et al. (1979a,b).

Table 1. Depth and coordinates of vents visited on the 1979 biological expedition.

Vent	Coordinates	Depth (approx. m)
Rose Garden	00°48.247'N; 86°13.478'W	2450
Musselbed	00°47.894'N; 86°09.210'W	2490
Small Fry	unknown, but near Musselbed	2495
Garden of Eden	00°47.692'N; 86°07.739'W	2485

DISTRIBUTIONS

Because the hydrothermal effluent is the driving force governing the existence of life at vents, the communities are characterized by a diffuse zonation centered on vent openings. Accordingly, the following descriptions of species distributions will begin with species found at the warmest vent openings and continue through those at cooler fissures, to intervening rock surfaces, and finish at the periphery of the vent field (Table 2). In reality, this zonation is not clear-cut; the untidy distribution of major and minor vent openings, combined with complexities in topography result in patchiness which is often difficult to explain. The vent megafauna is listed in Table 2. Undescribed species are identified to the lowest taxonomic level currently available. Additional photographs illustrating vent fauna distributions are found in Corliss & Ballard (1977), Grassle et al. (1979), and Ballard & Grassle (1979).

Vestimentifera

Riftia pachyptila (Jones, 1981) is only found at active vent openings, where it usually grows in clusters (Figs. 1,2,5,7). (Figures 1-6 will be found in the color insert following page 18.) Their density ranges from as few as one to dense stands of thousands. The largest thickets, seen at Rose Garden, stand two meters high and run many meters in length. The base of the tube is always hidden, either because it is attached down in the vent opening, or because of an overgrowth of other organisms. The tubes generally tend to parallel each other, but may form a more tangled pattern. For the most part, they are erect, but in cases where the density of individuals is sparse, they may be recumbent. The only part of the animal itself which emerges from the tube is the lamellate, red obturaculum, and the path and length of the tubes is such that the obturacula are usually exposed at the surface of the thicket where they are frequently clumped.

The growth form of thickets is easily interpreted in terms of nutritional needs. As an obligate chemoautotroph (Cavanaugh et al., 1981; Felbeck, 1981; Cavanaugh, 1983), a vestimentiferan requires exposure of its absorptive organ, the obturaculum, to H_2S coming from the vent and O_2 from ambient bottom water. The CO_2 which is also required could come from either source. To achieve this, the obturaculum must remain on the periphery of dense thickets, where ambient and vent waters mix. Within the thicket there may not be sufficient ambient water to allow survival of an animal whose obturaculum is placed there. Conversely, an obturaculum which protrudes too far may not be exposed to the vent water itself. The generally erect form of most thickets should be a response to the rising of the lighter vent water, and the clustering of obturacula could be in response to preferential channels of vent water flowing through the thicket. The reclined orientation seen in some sparse colonies is probably related to a weak flow of vent water which forces the animal to keep its obturaculum close to the vent crack in order to obtain a proper mixture.

Archaeogastropoda

Three limpets were visible in the photographs. Only one, Neomphalus fretterae (McLean, 1981), has been described. All three

Table 2. Megafaunal taxa of the Galapagos Rift hydrothermal vents. Abbreviations: Ca, carnivore; Ch, hemoautotroph; D, deposit feeder; indet., indeterminate; Ms, strongly mobile; Mw, weakly mobile; Nf, near part of vent field, but not in vent openings; Nv, nonvent; P, peripheral part of vent field; Sc, scavenger; Se, sessile; Su, suspension feeder; V, vent opening. Where capitals are not used in an abbreviation, it indicates lesser importance.

Major taxon	Name	Locality	Feeding type	Mobility	Common name
Vestimentifera	*Riftia pachyptila*	V	Ch	Se	Giant tube worm
Gastropoda	*Neomphalus fretterae*	V	Su,D	Se,mw	Limpet
Gastropoda	2 limpet species indet.	V	D	Ms	Limpet
Bivalvia	*Calyptogena magnifica*	V	Ch,Su?	Mw	Giant clam
Bivalvia	Mytilidae species indet.	V,nf	Ch,Su?	Mw	Mussel
Actinaria	Species indet.	V	Su	Se	Large, plumose, translucent anemone
Vertebrata	?*Diplacanthopoma* sp.	V,Nf,p	Ch?	Ms	Vent fish
Crustacea	*Bythograea thermydron*	V,Nf,p,nv	Sc,Ca	Ms	Brachyuran crab
Crustacea	*Alvinocaris lusca*	V	Sc	Ms	Vent shrimp
Annelida	Polynoidae species indet.	V	Ca,Sc?	Ms	Scale worm
Crustacea	Amphipoda, several kinds	V,Nf,p	Sc,Ca?	Ms	Amphipods
Actinaria	Species indet.	V,Nf,p	Su	Se	Small, translucent anemone
Annelida	Serpulidae species indet.	Nf,P	Su	Se	Featherduster worm
Crustacea	*Munidopsis* species indet.	Nf,p,nv	Sc	Ms	Galatheid crab, squat lobster
Crustacea	Natantia species indet.	Nf,P	Sc	Ms	Small, red shrimp
Gastropoda	Turidae species indet.	Nf,P	Ca	Ms	Whelk
Siphonophora	Species indet.	P	Su	Se,ms?	Dandelion; rhodaliid siphonophore
Brachiopoda	Inarticulata, species indet.	P,Nv?	Su	Se	Brachiopod
Actinaria	Species indet.	P,Nv?	Su	Se	Amber-scaled anemone
Enteropneusta	Species indet.	P,Nv	Su?	Mw	Spaghetti, acorn worm
Crustacea	?*Nematocarcinus* species indet.	P,Nv	Sc	Ms	Long-legged shrimp
Echinodermata	Ophiuroidea, species indet.	p,Nv	D	Ms	Thin, white ophiuroid; brittle star

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Crustacea	*Bythograea thermydron*	V,Nf,p,nv	Sc,Ca	Ms	Brachyuran crab
Crustacea	*Alvinocaris lusca*	V	Sc	Ms	Vent shrimp
Annelida	Polynoidae species indet.	V	Ca,Sc?	Ms	Scale worm
Crustacea	Amphipoda, several kinds	V,Nf,p	Sc,Ca?	Ms	Amphipods
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Siphonophora	Species indet.	P	Su	Se,ms?	Dandelion; rhodaliid siphonophore
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Enteropneusta	Species indet.	P,Nv	Su?	Mw	Spaghetti, acorn worm
Crustacea	?*Nematocarcinus* species indet.	P,Nv	Sc	Ms	Long-legged shrimp
Echinodermata	Ophiuroidea, species indet.	p,Nv	D	Ms	Thin, white ophiuroid; brittle star

species were limited to vent openings or their immediate proximity. They were seen on the rock walls of the vent opening, on mussels or the tubes of vestimentiferans. None were seen beyond the throat of the vent.

Neomphalus fretterae often forms aggregations so tightly packed on the walls of the vent that there is no space between individuals (Fig. 7). The largest specimens rested at the center, and individual size diminished toward the periphery. The white shell of this species is radially grooved and irregular. Its rim not only fits the irregular contour of the substrate, but conforms to that of adjacent individuals. The total effect is reminiscent of a chemical incrustation. Clearly, the animal does not move about much. Anatomical studies (Fretter et al., 1981) suggest some mobility and grazing activity, as well as the ability to suspension feed (McLean, 1981). It is likely that suspension feeding dominates in the clusters. *N. fretterae* occurs sparsely on vestimentiferan tubes, but was not found on other organisms.

The other two limpet species (Figs. 2,6) cannot be separated reliably in photographs; one is black, and the other translucent, but the latter may have either a dark oxide covering or transmit the color of the rock underneath. Both species occur on rock, vestimentiferan tubes and mussels. They may be abundant, but are always well separated from neighboring limpets, and their shell margin is regular. These observations suggest that the two species wander during their regular activities and are probably deposit feeders.

Calyptogena

The vesicomyid bivalve *Calyptogena magnifica* (Boss & Turner, 1980) easily catches the eye by virtue of its large, white shell (Figs. 1,3,4,8,9). It was seen at all vent areas, and concentrations of its shell were found even in areas where vents were not identified, indicating vent fields that had expired (Corliss & Ballard, 1977). Indeed, except at Rose Garden, most specimens were dead (Fig. 8). As a result, the animal appeared more common than was actually the case. This is in contrast to the large fields of living clams seen at 21°N on the East Pacific Rise (Ballard & Grassle, 1979; pers. obs.).

Both living animals and dead shells were concentrated in clefts between lava pillows or cracks in lava sheets. Rarely, a dead shell would be found lying on the unbroken rock surface, but never a living animal. The situations at Rose Garden and Musselbed encompass the range of conditions of *Calyptogena*'s distribution.

At Rose Garden (Fig. 1,3,4), the dominant environment for *Calyptogena* was a broad, flat, relatively unbroken expanse. There

Fig. 7. Garden of Eden. Vent opening encrusted with Neomphalus. A few Bythograea are concealed among the bases of the vestimentiferans, and one ?Diplacanthopoma hovers just beyond. (Photo by A. Giddings)

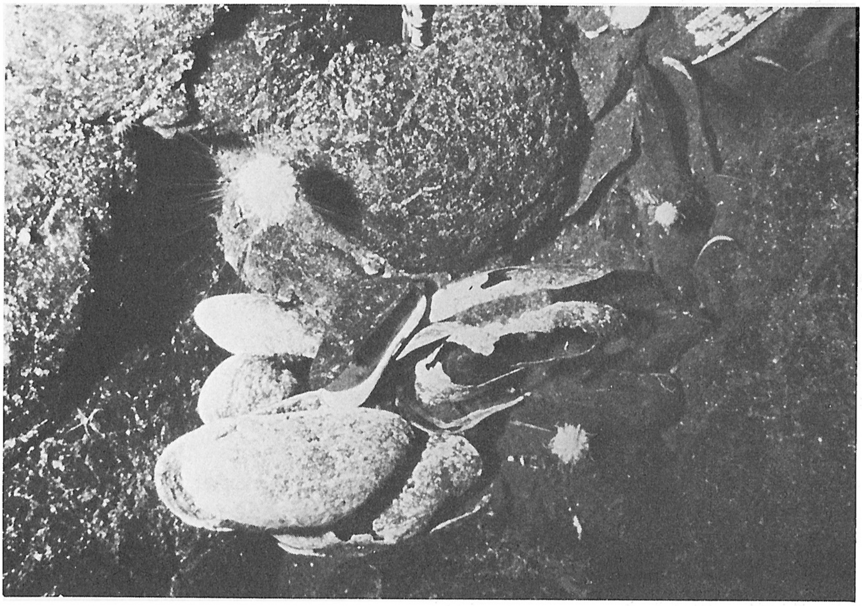

Fig. 8. Garden of Eden. Serpulids and translucent anemones, with a few Bythograea and Munidopsis. No vent openings can be seen in this view. (Photo by R. Hessler)

were no major fissures, but the surface was crossed by a number of straight cracks up to a few inches wide. Some ran into the main thicket of vestimentiferans and mussels, and disappeared under the clot of animals. Typically, these cracks were well populated with Calyptogena (Figs. 1,3). Often living individuals were oriented with the anterior end headed down into the crack. Some cracks were only wide enough to accommodate a single line of clams; others allowed two or more abreast. In places, gaps interrupted the line of clams.

For the most part, living individuals dominated the cracks. Dead shells were more abundant on the rock adjacent to the cracks. Calyptogena has a long, flexible foot and can adjust its position actively. As animals oriented themselves in the cracks, it would be natural for dead shells to be knocked out of the way.

Nearer to the main vestimentiferan/mussel thicket, mussels become more abundant. Where the two species were in direct contact, the clam would tend to be below, often lying on its side (Fig. 1). Clams were in direct contact with the main thicket, tucked under the mass of mussels that often made the thicket's fringe.

At Musselbed, living Calyptogena were far less abundant, but dead shells were numerous (Fig. 8). Typically a crevasse between pillows would be covered with shells lying in a jumble or lying flat and packed more closely. Among these might be a few living individuals poked down into the substrate. Here, mussels were commonly associated with the clams, either singly or in clumps; again, Calyptogena would be underneath.

We saw several beds where all the clams were dead. The general distribution of shells with respect to general topography was the same as with living animals. The relative age of the bed could be discerned from whether the valves were still articulated, whether any organic structures remained, degree of breakage, or dissolution and amount of associated sediment. At one extreme were fresh, articulated shells loosely packed and in a variety of orientations. Such relatively recent situations were common in portions of the vent field. The oldest dead clam field, to the best of our knowledge, was not in the immediate vicinity of any active vent. There were no living vent organisms in the area. All shells were disarticulated and broken or with their thin, central areas dissolved away. They were lying flat, mostly convex side up and closely packed down. There was a heavy dusting of sediment over the whole area. Killingley et al. (1980) estimate a whole shell will dissolve in approximately 25 years.

An impression gained by all who dove on the site was that individuals of Calyptogena were smaller at Rose Garden. Elsewhere,

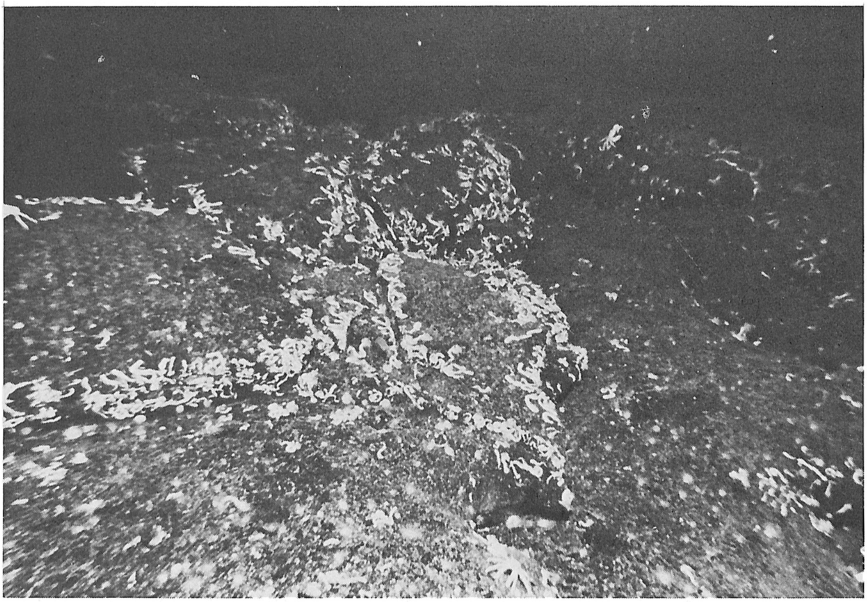

Fig. 9. Musselbed. Siphonophores in the peripheral zone. The dead clams and mussels suggest this is an extinguished vent. Temperature 2.15°C. (Photo by R. Hessler)

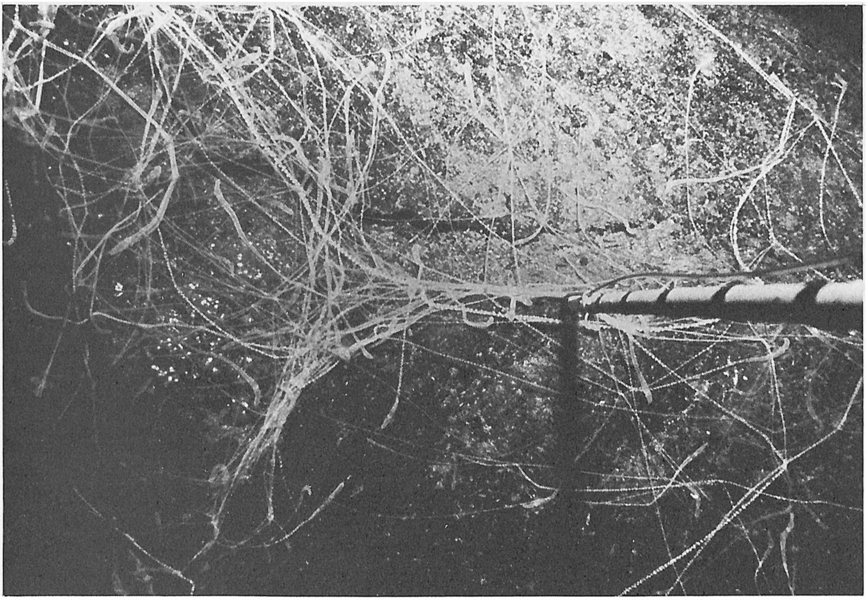

Fig. 10. Garden of Eden. Enteropneusts on peripheral pillow basalt. Temperature 2.08°C. (Photo by R. Hessler)

living and dead tended to be of a relatively uniform, large size. Our experience at 21°N tells us smaller individuals probably resided underneath. Therefore, the hypothesis that clam populations are the result of a single pulse of colonization (Corliss et al., 1979) may not be correct.

Mytilidae

The distribution of this undescribed mussel is a result of its apparent preference for vent water together with its ability to exist where not much is present, and its facility for attaching to steep surfaces through use of byssal threads. Musselbed, the vent area where mussels were the dominant life form, shows their range of distribution clearly (Figs. 5,6,9).

Here, the main source of exiting water was a complex cluster of openings in a nearly vertical surface of jumbled pillow basalt. The mussels occurred in dense clumps, often many individuals thick, with animals attached to each other. We estimate densities as high as 312 ind./m^2, with a biomass of approximately 10.1 kg/m^2. Smoky vent water could be seen emerging around these clumps. Here and there small clusters of vestimentiferans were interspersed. Often the mussel shells or vestimentiferan tubes had numerous byssal thread bases attached to them, giving evidence of the mussels' mobility. Nearby, other clumps were lying in the bottom of declivities between pillows or stuffed tightly into cracks. In this situation, they were often interspersed among living and dead Calyptogena (Fig. 8); whether the mussels were clumped or single, they rested on top. Finally, in this region (never far from vent cracks) individual mussels might be lying on top of unbroken pillows.

While vestimentiferans attracted most notice at Rose Garden, mussels probably had an equivalent standing crop (Figs. 1-3). The interstices of the lower half or third of each vestimentiferan thicket was completely filled with mussels, so that this region of the thicket was truly a solid mound of life (Table 3). Many mussels were attached to the higher, free-standing portion of vestimentiferan tubes (Fig. 2). At the bottom of the thickets, there was often a densely packed fringe of mussels. Cracks near the thickets were dominated by mussel clumps rather than clams (Fig. 1). In some places a few twisted vestimentiferans protruded from large mussel clumps, and clams fringed the clump below. Even in the region somewhat further away, clusters of mussels might dominate a crack. Wherever mussels occurred at cracks, a few scattered individuals might be seen on the adjacent unbroken lava among the anemones (Fig. 3).

Table 3. Maximum numerical density of selected species as seen with the arm-stereo camera. This is not necessarily the highest density the animals achieve.

Taxon	Site	Density .125 m^2 (measured)	 1.0 m^2 (extrapolated)
Riftia	Rose Garden	22	176
Mytilid	Musselbed/Rose Garden	39	312
Serpulid	Garden of Eden	135	1080
Neomphalus	Garden of Eden	68	544
Other limpets	Garden of Eden	77	616
Small, translucent anemone	Garden of Eden	57	456
Alvinocaris	Rose Garden	14	112
Brachiopod	Rose Garden	21	168
Enteropneust	Garden of Eden	34	272

Actinarians

Describing the distribution of anemones is complicated because, as with the archaeogastropod limpets, there are more than one species that cannot be discriminated reliably from photographs. Unlike the limpets, however, the different anemone species may have differing distributions. In the present discussion, we limit ourselves to types that are common in the vent area. There are others, usually quite large, that were seen individually only a few times and were too poorly documented to discuss. One of these is memorable because a large individual was videotaped with its long tentacles streaming in the current of a vent. Its tolerance of higher temperatures suggests that it probably does not occur away from vents, making it a unique example of a rare vent species.

The common anemones are all of modest size. They appear in elevated concentrations from the margin of the vent field to the vent openings themselves. One is characterized by amber-colored papillae in rows on its column and elongate form, even when contracted. The others are more translucent and when contracted are much shorter than broad. Some are pigmentless, while others are light pink. Papillae, if present, are scattered. Of the colorless anemones, one type is larger and has more numerous tentacles.

The larger, pigmentless, more numerously tentacled anemone is seen frequently at vent openings, growing on vestimentiferan tubes or on rock. Often they are tucked tightly into crevasses, much as with mussels, with which they may be associated. *Neomphalus* sometimes encrusts the vent wall above them.

The smaller translucent anemones may be seen anywhere in the vent area (Figs. 1,3,4,9,11). Sometimes they occur peripherally, but most typically, they are found in intermediate environments. The largest display is at Rose Garden, where they dominate the rock flats adjacent to the main thickets (Figs. 1,3,4). Individuals of every size are mixed together in densities as high as 456 ind/m^2. These concentrations extend undiminished up to the edge of the vestimentiferans or the clams and mussels in the cracks that crossed the flats. These anemones are also abundant at Garden of Eden, where the topography was much more irregular (Fig. 9). Here, individuals showed especially clearly a general tendency to occupy topographic lows as well as flats. Unlike serpulids, they seem to avoid ridges and crests. Anemones and serpulids (below) are frequently mixed, but tend to display inverse abundances.

The elongate anemones with rows of papillae are found mainly in peripheral locations and never in high densities. They are associated with enteropneusts, siphonophores, brachiopods and low densities of serpulids (Fig. 11). They have also been seen with the nonvent holothurians and xenophyophorians.

Vertebrata

The only fish commonly seen at vent fields has been tentatively identified as the bythitid ?*Diplacanthopoma* (Cohen & Haedrich, in press). This is uncertain because it has never been caught.

?*Diplacanthopoma* might be seen throughout the vent area, but is clearly concentrated at the most active vent openings, such as with vestimentiferan thickets (Fig. 7), or the main area of Musselbed (Fig. 5) . Here, they would swim down into the vent, to the extent allowed by other associated organisms. In the vents, they would hover, heads angled downward, with their tails undulating slowly. Often, several would be next to each other so that their movement appeared to be in unison. Otherwise, ?*Diplacanthopoma* swam slowly about. They were never seen purposefully in contact with the bottom, even in vents, except when stationary in clumps of organisms.

Bythograea

The brachyuran crab *Bythograea thermydron* (Williams, 1980) occurs throughout the vent area and even beyond, but their peak abundance is unquestionably on animal clumps in the vent openings themselves, particularly vestimentiferan thickets (Figs. 2,5-7,9). Here they usually nestle down among the tubes (Fig. 2), often in the throat of the vent, but also climb up individual tubes. Where mussels are mixed among the vestimentiferans, as at Rose Garden, *Bythograea* is equally abundant on the mussels, except at the

Fig. 11. Garden of Eden. Detail of pillow lava. Numerous unknown tubes, anemones, and brachiopods (particularly lower center) are shown. Temperature 2.14°C. (Photo by R. Hessler)

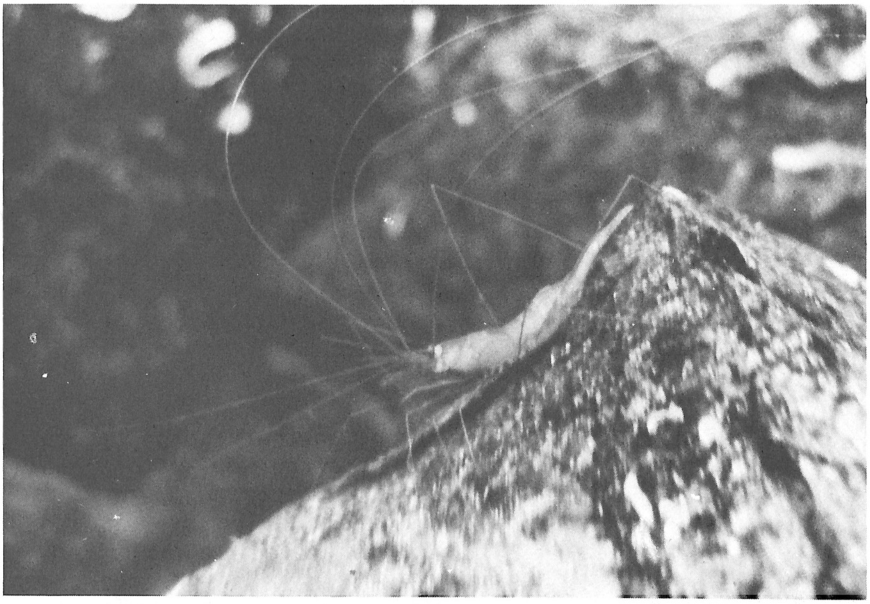

Fig. 12. Peripheral to Musselbed. ?<u>Nematocarcinus</u> on pillow basalt.

margins, where fewer crabs are sitting upon the pure bivalve fringe.

Bythograea also is present in elevated abundance at vents where species other than vestimentiferans dominate. At Musselbed they clambered among the mussels and into the cavities between them (Figs. 5,6). In the rare instances of vents dominated by limpets, _Bythograea_ might be seen in the vent opening. In all of these cases, crabs would frequently be sitting on the rock adjacent to the vents.

Specimens in ones and twos occur elsewhere in the vent field: on bare rocks or rocks dominated by serpulids and anemones. They are found occasionally in peripheral areas where siphonophores or brachiopods may be abundant, or where nonvent taxa might be found. Rarely, they are even seen in barren terrain away from vent fields.

Alvinocaris

The bresiliid caridean shrimp _Alvinocaris_ _lusca_ (Williams & Chace, 1982) is present for the most part only at vent openings, usually residing on the larger sessile organisms (Figs. 2,6). Its highest densities were seen in the large vestimentiferan/mussel thickets at Rose Garden (Fig. 2), where closeup photographs usually show numbers of them on either kind of sessile animal. Here an occasional individual might also be seen on the adjacent rock, in one case on neighboring ledges with serpulids and anemones.

Alvinocaris was also found on vestimentiferans at Garden of Eden, but at Musselbed they were found in mussel encrustations, even where vestimentiferans were not present (Fig. 6). Here, small numbers of shrimp were sometimes seen on mussel clumps away from the main bed, even under conditions where dead clams were present. Rarely, an individual was present where vent conditions were barely detectable.

Polynoidae

A pink polynoid polychaete is abundant at vent openings, in association with vestimentiferans, mussels, clams, limpets and the usual other vent organisms. It crawls on the rock walls, mussel shells or less commonly, vestimentiferan tubes.

Amphipoda

Some amphipods are marginally large enough to be seen and photographed. They were noticed throughout the vent field, sometimes swimming, but because they are usually cryptic, their real abundance is much greater than what was seen in undisturbed circumstances; while sampling clumps of mussels or vestimentiferans, many might swim out. No patterns can be deduced because several species are involved.

Serpulidae

These abundant tubicolous polychaetes have not yet been identified. Their distribution is difficult to describe because they are found in so many situations, and while some patterns seem apparent, we are aware of exceptions to most of them.

From some approaches upon entering a vent field, serpulids are the first animals seen in any concentration. At Garden of Eden (Fig. 9), they are abundant in the same region as the generally peripheral siphonophores (below). They are also found in close proximity to vent openings. At Musselbed, patches of them live on the vertical wall amongst the clumps of mussels at the main vent opening (Fig. 5). For all practical purposes, they are not found directly in the vent opening, but even this occurs rarely; at Garden of Eden, a concentration of them extended down into a cleft where they were finally replaced by limpets. In another case at an apparently peripheral region, serpulids were concentrated at the bottom of a cleft, much as a vent species would be. No temperatures were taken in such situations to verify the amount of vent activity.

The densest concentrations of serpulids are found on steeper surfaces. Often, but by no means invariably, the slopes of a pillow will be heavily encrusted while the top is barren or only lightly populated (Fig. 9). As a result, they are mostly found in irregular topography; they are abundant in a pillow region adjacent to the large thickets at Rose Garden, but are nearly absent from the extensive flats. In many places, the concentration of individuals also decreases going down into nonvent clefts. On complex surfaces with ridges separated by narrow clefts, the serpulids tend to be concentrated on the ridges and absent from the intervening troughs.

A striking pattern that is frequently seen is an abruptly dense concentration along the edge of a rock, such as a sharp crest or the broken edge of a collapse structure (Fig. 9). A small ridge on an otherwise flat surface may bear numerous serpulids, which are abruptly absent from the adjacent plane.

Individuals of a cluster tend to be the same size, but frequently smaller individuals occupy the edges. Areas where all the individuals are dead are not uncommon, particularly near patches of dead Calyptogena. Where a serpulid patch butts against a cluster of mussels, there is frequently a border of unoccupied rock. Perhaps interference from the movement of the mussels keeps serpulids from settling. Serpulids are usually found in pure stands, but also occur in reduced numbers mixed with translucent anemones.

Galatheidae

An unidentified species of the galatheid crab Munidopsis is as broadly distributed as the brachyuran crab Bythograea, with one important difference--it is virtually absent from vent openings or on clumps of sessile animals living in vent openings. Its greatest concentrations are on pillows with a healthy growth of serpulids (Fig. 9), and rock surfaces adjacent to animal-occluded vent openings. The rocks around the main mussel-filled vent at Musselbed are a good example (Fig. 5). Generally, Munidopsis is less common on surfaces dominated by anemones; at Rose Garden, it was relatively uncommon on the anemone flats adjacent to the main vent system, compared to pillows with serpulids.

Munidopsis also lives in more peripheral portions of vent areas. They are found in small numbers near small vents with moderate or small clumps of mussels and living clams, or where dead clam shells are abundant. They appear where serpulids are sparsely present, along with siphonophores and brachiopods. Finally, they are seen occasionally in nonvent regions in association with the sparse nonvent fauna.

Natantia indet.

A very small shrimp (not yet identified) with red viscera occurs broadly, but sporatically through the vent field. It is most common on rocks with serpulids near secondary vent cracks occupied by mussels, but it was also seen as peripherally as with elongate anemones and dead Calyptogena shells, and as centrally as on rock by a major mussel vent.

Turidae

The distribution of whelks is opposite that of the limpets. They are never in the vent throat itself, although they come close to it (Fig. 3). At Rose Garden, they were not uncommon on the flat basalt area that was rich in anemones right up to the margin of the vestimentiferan/mussel thicket. At Musselbed, whelks were seen one-third meter or less from a vent crack with mussels in it. They also occur at the periphery of a vent, in the vicinity of siphonophores and even enteropneusts. Throughout their range, they are associated with serpulids and anemones. The strong development of the foot suggests that individuals move about actively.

Siphonophora

The rhodaliid siphonophore (Pugh, in press) may be found in abundance, and even dominates the macrofauna locally (Fig. 8). They are most abundant toward the periphery of a vent field, but not so far out as with the center of concentration of enterpneusts (below). Unlike other sessile taxa, even at the height of concentration, they are always well separated from each other.

The majority of individuals are attached in low areas--general topographic lows, the clefts between lava pillows, or in collapse chambers. This may well be caused by their mode of attachment. Siphonophores are positioned in the water column a few centimeters above the bottom. They are held there by many long, radiating attachment filaments. These are fragile (only a little current stirred up by Alvin would break them loose), so that exposed individuals might be in danger of detachment. Occasionally, however, individuals are seen near the tops of rocks.

Siphonophores may be found some distance from vent outflows, in areas where the nonvent fauna begins to dominate--with holothurians and xenophyophorians (large, mud agglutinating protozoans), for example. They may rarely come close to a vent opening. One individual was seen in a cleft next to a crack with a concentration of healthy mussels. Most commonly this species is associated with brachiopods, serpulids or anemones, although the last two usually occupy rocks above the attachment sites of the siphonophores.

Brachiopoda

No brachiopods were collected, so that detailed identification is not possible. They appear to be Inarticulata of the family Discinidae or Craniidae and are easily recognized by their translucent nacreous luster, somewhat irregular discoid shape, subcentral umbo, and recumbent orientation (Fig. 11).

None was seen near vent openings. Indeed, they were always found in areas remote from direct influence, on horizontal or steeply sloping surfaces, even in the clefts between lava pillows. The most typical associates are anemones and an unidentified agglutinated tube builder. Occasional enteropneusts, siphonophores and isolated mussels are also associates. Brachiopods are not not found with living serpulids, but can be found in conjunction with dead ones or near dead Calyptogena.

Enteropneusta

A still undescribed species of enteropneust, aptly called "spaghetti" by those who first saw it, attracts immediate attention because of the characteristic aggregations in which it lives. Typically they lie draped over the tops of rocks in dense profusion (Fig. 10). Concentrations may be so great that the rock is completely hidden, and the covering is many animals deep. The general impression is somewhat like that of cobwebs because along the vertical and lower undercutting portions of the rock, the animals dangle freely in the water or arc over to other surfaces. Often it is the anterior end of the animal that is dangling freely.

Unquestionably, the animals prefer high, exposed surfaces. In places where a slab of lava has tilted and cracked, the enteropneusts upon it are concentrated along the ridge formed by the broken edge. These animals also occur at low densities and even as isolated individuals, where they are occasionally seen on open upper surfaces that are not necessarily topographic highs, but never in depressions.

Enteropneusts only appear towards the periphery of vent areas. Indeed, at vents where they are present, they are the last indication of the presence of a vent before entering the adjacent nonvent terrain. Water temperature is always ambient. Various members of the nonvent or peripheral vent fauna may be nearby, but are never found on the same rocks where enteropneusts are aggregated in abundance.

No pattern is perfect. One photograph at Musselbed shows three small individuals on a dead mussel shell in a peripheral crevasse. Other mussels are in the clump, and most are dead. It was not possible to tell whether any were living. As will be discussed, enteropneusts are also found in nonvent regions.

?Nematocarcinus

Of all the mobile animals that were seen commonly in vent areas, this long-legged, red caridean shrimp is the only one that showed greatest abundance at the margins of the vent region (Fig. 12). Indeed, it does not occur anywhere near the vents themselves. Typical associates among the vent fauna are the siphonophore, enteropneust, brachiopod and amber-scaled anemone. They also associate with dead Calyptogena and sparse mussels or serpulids. ?Nematocarcinus was not uncommon in nonvent terrain, associated with nonvent organisms. Usually they occurred in ones or twos, but occasionally in higher densities. Approximately 10 were seen once in a small collapse pit that also contained siphonophores.

Ophiuroidea

A thin, white ophiuroid was seen at peripheral portions of the vent field, sometimes in concentrations above that of the nonvent region. It was associated with siphonophores, *Calyptogena* shells or solitary mussels.

Vent Field Temperatures and Faunal Overview

At the hydrothermal vents, temperature is both a critical environmental parameter and an index of a complicated interplay of the 2.01°C ambient bottom water with the chemically unique and nutrient-rich vent water. It is clear that some of the fauna live preferentially in areas of less diluted vent water, while others prefer water with only a very minor vent-originated component.

Water exiting from a Galapagos vent is estimated to have been heated to 350° in its journey through the earth's crust, yet the warmest temperature actually recorded at the vents was 17°C (Corliss et al., 1979). We recorded a range of elevated temperatures from slightly above ambient to 14.72°C.

The mixing process resulting in the cooling of the 350°C water to ambient has several components. The largest drop occurs within the plumbing of the vents. Our high of 14.72°C was reached by plunging a temperature probe at least 30 cm into a vent choked with *Riftia*, so that the temperature was unlikely to have been influenced by surface mixing. The decrease is a result of subsurface mixing within the "leaky" plumbing of the vent combined with cooling to surrounding rocks.

After leaving the mouth of a vent, mixing is rapid. In cases where water flow is unimpeded by organisms, the temperature is reduced to a few tenths of a degree above ambient within a meter of the vent opening. Dense aggregations of fauna can modify the mixing process. Temperatures within a clump of *Riftia* are definitely higher than would be the case at the same elevation were the thicket not there, because the aggregation of tubes acts as a porous chimney. Mussels clogging the main vent at Musselbed experienced temperatures several degrees above ambient (once as high as 12°C) on the vent-facing (upstream) side, while the surface that faced away from the vent was exposed to water as low as a few tenths of a degree above ambient.

The maximum temperature recorded varied little among vents, with Rose Garden registering 14.72°C, Garden of Eden 13.00°C and Musselbed around 12.00°C. Perhaps more telling than this was the amount that the vent water warmed the ambient water in the area of the site. This effect is a combined function of both the maximum temperature and the volume of water spewed out at each vent. With the temperature probe at a height of 1.5 to 2.5 meters above the bottom, a transect over Rose Garden recorded a high of 2.32°C, Garden of Eden, 2.35°C and Musselbed, 2.10°C. The extent and shape of this regional anomaly must be influenced by several factors. Local currents and tidal flux undoubtedly have an effect. Also, as evidenced at Musselbed, the extent, type and density of fauna may influence the rapidity of mixing. We know nothing of the variation in temperature with time or volume of the vent emissions.

Because of convection lifting most of the diluted vent water upward, vent influence degrades quickly from areas directly bathed by warm water to those lateral to the source (Fig. 13). The distribution pattern of each species with respect to the exiting vent water is much the same at the four vents, as seen from the treatment of individual taxa. In some cases the species closely reflect the abrupt changes in water quality while other species distributions may transcend them.

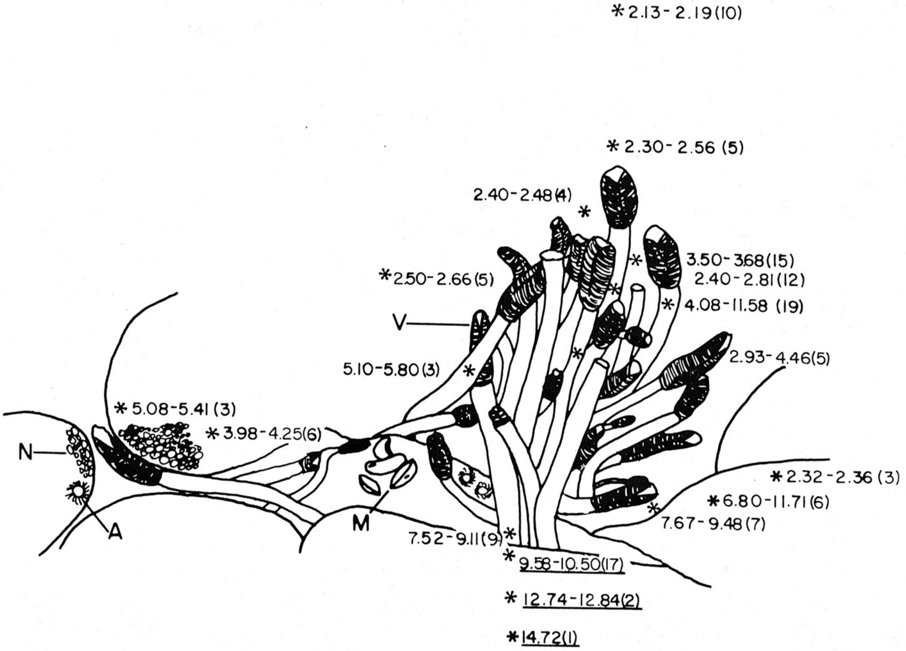

Fig. 13. Diagram of the temperature field around a vent dominated by vestimentiferans. This is a composite of many observations. Temperature (°C) is given as a range; number of observations is indicated parenthetically. Underlined numbers indicate measurements down in the vent opening. Symbols: A, plumose anemone; M, mytilid, some with limpets; N, Neomphalus; V, vestimentiferan.

Most easily categorized are those animals found at vent openings, in water of 4-15°C. Riftia, Alvinocaris and the large, plumose anemone are limited to this situation. The mytilid, Bythograea, ?Diplacanthopoma, Neomphalus and the other limpets for the most part are found in these conditions. While Calyptogena is occasionally found at such temperatures, it is more numerous lining cracks with exiting water a few tenths of a degree above ambient. Within vestimentiferan thickets, the temperature grades from above 12°C at the base to around 3.5°C at the obturacula. Mussels clogging vents at Musselbed were bathed in water in excess of 8°C on the surface facing the flow. This fell to around 3°C on the side away from the flow.

Other animals live lateral to vents, but close enough to be within the influence of vent waters, where the temperature is just a few tenths to a full degree above ambient. Dominant are serpulids (up to 2.94°C) and small, translucent anemones (up to 2.68°C). Living among them are the whelk and the small red shrimp. Mussels are found in this area in temperatures up to 2.72°C. The galatheid crab is most often in these areas.

The siphonophore, enteropneust, brachiopod and ?Nematocarcinus are found in areas sufficiently peripheral that the temperature is usually ambient, but occasionally slightly above. The maximum temperature was 2.24°C for the siphonophore, 2.11°C for the enteropneust, 2.10°C for the brachiopod and 2.15°C for ?Nematocarcinus. All these values are within 0.2°C of ambient.

Animals we have classified as nonvent are those that were never observed in water of elevated temperature. These will be discussed shortly.

Vents as a Whole

While the distribution pattern of species remains consistent between vent fields, the relative abundance may vary.

Rose Garden (Figs. 1-4). This vent field displays the highest standing crop that has been found in the Galapagos system, primarily due to the huge thickets of vestimentiferans and mussels. The largest thickets are confined to a single fissure which is manifested by the smoky water percolating out through the animals. Other, smaller thickets are abundant; they are dominated more by mussels with decreasing size. Clams are a minor component by comparison, forming a fringe of the mussel clumps, but gradually coming to dominate smaller fissures away from the main thickets. Brachyuran crabs and vent shrimp are abundant in the larger thickets. The two mobile limpets and the large translucent anemone are not uncommon.

Much of the area surrounding the main vents, particularly to the south, is flat and unbroken, except for occasional cracks clogged with bivalves. These surfaces are dominated by dense concentration of the small translucent anemone, but with brachiopods locally abundant toward the outer edges. Further away from the central thickets, this gives way to dense stands of serpulids.

The more jumbled pillow basalts that abutt on the central thickets, especially to the northwest have anemones closest to the thickets, but these are shortly replaced by serpulids, which extend nearly to the margin of the vent field. Galatheids are particularly abundant on these pillows.

At the limits of the vent field occur a few patches of siphonophores which are not extensive and many small clumps of enteropneusts.

?Diplacanthopoma and Neomphalus are uncommon here, perhaps because of the domination by vestimentiferans and mussels leaving few open surfaces or spaces exposed to vent water.

Musselbed (Figs. 5,6,8,12). This vent field contrasts strongly with Rose Garden, both topographically and in relative positions of its fauna. It is located in a very jumbled terrain of pillow basalt. The main vent openings are on a steep slope. Here dense beds of mussels dominate, but tufts of vestimentiferans poke out here and there. Immediately adjacent rocks have high concentrations of serpulids.

?Diplacanthopoma is abundant in the smoky vent water. Crabs are common--Bythograea more on the vent organisms, Munidopsis on the adjacent serpulids. As elsewhere, they also occur in more peripheral areas.

At least one small vent is dominated by Neomphalus.

Surrounding the incline bearing the main vents are flatter areas with numerous beds of dead clams in varying states of decalcification, with an intermixture of a few living clams and mussels, many of them dead. Serpulids cover the intervening pillows in moderate densities. Here and there in peripheral regions are modest patches of siphonophores, and a few patches of enteropneusts occur at the limits of the vent field. At least one of these was spectacularly large.

Garden of Eden (Figs. 7,9,10,11). The terrain of this vent field is entirely pillow basalt. Vent water flow seemed less than at Rose Garden or Musselbed, as indicated by the amount of vent-opening faunal clusters. Only a few modest tufts of vestimentiferans were seen. Well-developed rock encrustations of Neomphalus were associated with each of these, interspersed with openings having Neomphalus alone. ?Diplacanthopoma was abundant. Mussels were not common, mainly appearing in small numbers in a few feeble vent cracks. Small clam shells were seen, but no living individuals.

Extensive fields of serpulids, including many very dense concentrations butted directly up to the vents. There were also healthy patches of small, translucent anemones, some of the patches being quite large. More peripherally were dense concentrations of siphonophores.

The crabs Munidopsis and Bythograea were both common throughout the area, the former particularly so, with aggregations even peripheral to the concentrations of sessile suspension feeders.

Small Fry. This small site (radius 10 m or less) was covered with pillow basalt. No discrete vent was seen, yet ?Diplacanthopoma was common, particularly swimming out of a deep, crater-like depression. The dominant sessile organisms were siphonophores, with a sparse admixture of serpulids. Galatheids were common, and a few Bythograea were present. Enteropneusts covered some pillows in the vicinity. None of the usual sessile vent-opening organisms were seen. It is possible that we missed the main vent, but that does not explain why ?Diplacanthopoma was so common where we saw it.

General

Clearly, while the participants are the same, the communities differ distinctly in dominance at different vents. For example, the importance of mussels varies strikingly between Rose Garden and Garden of Eden, and living Calyptogena appeared to be missing from the latter locality. Crane & Ballard (1979) give other examples involving different vents.

We have insufficient knowledge of the natural history of the animals and physical conditions at the vents to be able to identify the causes, but some reasonable possibilities may be suggested. Exiting vent water chemistry is known to vary in proportion to the amount of subsurface mixing (Corliss et al., 1979; Edmond et al., 1979a,b), so that waters of different temperatures represent different chemical milieus. To a minor extent, different vent fields can display variation in abundance of some chemicals, presumably because of differing rock regimes (Corliss et al., 1979). These differences in chemistry and temperature should affect the conditions for growth of the microflora, both free-living and symbiotic, as well as affecting the animals directly. The rate of vent water flow and bacterial production will vary, and differences in topography, which affect currents, will influence the path, residence time and diffusion of the plume. The size and abundance of particles emitted from the vent varies, as is visually obvious; vent water may be clear or smoky, and with or without large particulates. The bacterial content of the particulates is not likely to be constant. All these variables could influence metazoan distribution, but there are still no concrete data for testing whether correlations exist.

At the Galapagos site in general, vestimentiferans experienced higher temperatures than those recorded for clams or mussels. However, at Clam Acres at the 21°N site on the East Pacific Rise, tufts of vestimentiferans grow in the same cracks as clams (a combination not seen at the Galapagos), and both experience 15°C. It may mean that volume of flow is equally important. Vestimentiferans may require higher flow to bathe their generally elevated obturacula, while bivalves can make do with lesser flow because they can nestle down into the water more effectively. Growing in a reclined position is only a limited solution for vestimentiferans because physical interference by bivalves must offer problems. Thus, inadequate flow at any one spot may explain low abundance of vestimentiferans at Musselbed and Garden of Eden.

If ?Diplacanthopoma needs access to vent openings, its low abundance at Rose Garden may result from the generally clogged condition of vents there.

The success of sessile animals in the vent field away from vents must be related to the volume and quality of vent water of the field as a whole. The general ambient temperature anomaly is a measure of total vent flow and is lowest at Musselbed, where this sessile fauna is least well developed.

These are examples of possible causes for variation in the vent community. The reasons for most differences await clarification. Indeed, the distribution of many species is puzzlingly patchy within a vent field; for example, the reason for the presence of serpulids on one pillow and absence on the adjacent one remains to be revealed.

Dispersal does not seem to be a factor in this issue. Except for the apparent absence of Neomphalus at Rose Garden, all species were seen at all three of the well-studied vent fields; Small Fry was not explored well enough to be sure of its fauna. Living clams were absent from Garden of Eden, but shells prove they had been there. This shows that at Galapagos, distances of a kilometer more or less are not a discernable barrier to the vent fauna. Therefore, if the faunas vary, ecological causes are more likely.

Corliss et al. (1979) have suggested the vent faunas vary in a successional sequence that reflects the aging process of the vent itself. Crane & Ballard (1980) propose the cycle propagates from east to west. That is, the western vent fields are youngest. In some ways, the fauna supports the Crane & Ballard hypothesis. The western-most vent Rose Garden seems to have the strongest flow of warm water, as documented by the luxuriance of the vent-opening fauna, and the generally smaller size of *Calyptogena* there might be construed as an indication of recent colonization. However, Garden of Eden (eastern-most) did not have the large fields of dead clams to indicate it had ever been more active. Perhaps it was always a more modest vent system. In general, local peculiarities of the physical setting dominate over the influence of vent age.

Relation to Nonvent Fauna

So far, we have devoted attention to distributions within vent fields. There remains the question of the extent to which the vent fauna is endemic. Answering this is difficult because of the paucity of observations away from vents. At those times when we did visit nonvent areas, we cruised, which could result in overlooking smaller organisms. Thus, with many taxa, the possibility of vent endemism must be viewed cautiously.

Taxa which are most clearly limited to vent areas are those which live at discharge openings: *Riftia*, *Calyptogena*, the mytilid, the limpets, the large plumose anemone and ?*Diplacanthopoma*. None of these were observed away from vent fields, and except for the mytilid and fish, they were always directly at vent openings. Exceptional is the crab *Bythograea*, which was seen rarely completely away from vents (Mickel & Childress, 1982a; pers. obs.); these occurrences seem best interpreted as expatriates--animals that accidentally wandered from the vent area and are perishing or living so marginally that reproduction is impossible. The absence of deep bathyal records of brachyurans prior to the discovery of the vents (Balss, 1955; Zarenkov, 1969; Hessler & Wilson, in press) shows we have little reason to expect *Bythograea* to be a regular part of the rocky deep-sea fauna.

Routine members of the general vent-field fauna that were not seen away from vents include the serpulid, the most common translucent anemone, the siphonophore, brachiopod and whelk. The serpulid, whelk and siphonophore are so noticeable that their presence would probably have been detected. Thus, they are likely to be vent endemics. The anemone and brachiopod easily could have been missed. Inarticulate brachiopods of that sort are typical of hard bottoms in the deep sea (Zezina, 1965, 1969). It could well be an example of higher standing crop resulting from the enhanced vent nutrition.

As already mentioned, the enteropneust and ophiuroid are successful inhabitants of the nonvent bottom. ?*Nematocarcinus* and

Munidopsis were seen several times away from the vent field. The abundant records of these two crustacean genera in the deep sea (Zarenkov, 1969), and their aversion for situations with elevated temperatures at the vents suggest they are nonvent taxa profiting from vent productivity.

Only two species of nonvent fish (both of the macrourid genus Coryphaenoides) showed somewhat elevated abundance near the vent field (Cohen & Haedrick, in press). But taking the fish fauna as a whole, species diversity is lower near vents than away from them (ibid.).

The rest of the nonvent fauna does not even penetrate the vent field, that is, the region near vents where species show elevated abundance. Principal among these are the holothurians and many kinds of typical deep-sea anthozoan coelenterates including gorgonians, antipatharians, hydroids, hydrocorallines and actinarians. Other invertebrates with this distribution were asteroids, hexactinellid sponges, xenophyophorians (rhizopod protozoans) and other animals we were not able to identify.

The dominant pattern, then, of the distribution of animals which thrive on hard bottoms away from vents is absence from the vent field. The importance of this pattern is accentuated by the high taxonomic level at which it operates (nearly all echinoderms, most coelenterates, sponges). At this stage of investigation, one can only speculate about causes.

The most reasonable possibility is that most nonvent taxa are intolerant of physical conditions engendered by the vents. Perhaps they cannot survive elevated temperatures or aspects of the water chemistry. In both cases, unusual sensitivity is suggested because the thermally driven convection cell lifts vent water away from the bottom (Corliss et al., 1979; Lipton et al., 1980), so that except in the immediate vicinity of vent openings, vent field temperatures are at most a few tenths of a degree above ambient, indicating considerable dilution of vent-water chemicals. Hydrogen sulfide levels should be even lower than what would result from dilution because of oxidation on contact with oxygen-rich ambient water. Temperature has not been recorded in such places over time, and it is possible that occasionally, warmer boluses would impinge. (Oxygen isotope ratios in Calyptogena [Killingley et al., 1980; Fatton et al., 1981] suggest variation in vent discharge, but do not take into account the possibility of movement of the clam.) Still, because of the efficiency of mixing, it is unlikely that the temperature would be elevated by even a degree. The concentration of potentially toxic substances has not been measured at the bottom away from vent openings. We lack more than anecdotal information on the tolerance of typical deep-sea organisms to temperature fluctuation. Deep-sea organisms in nonvent regions live under thermally unvarying circumstances and therefore have been under no selective pressure for tolerance to temperature change. How much variation is acceptable in such cases, and for how much time? It is not simply a question of the latitude of single metabolic pathways, which tend to react more coarsely, but the synergistically complex functioning of the whole organism.

The Food Web

A reasonable approximation of the food web (Fig. 14) at hydrothermal vents can be derived from consideration of behavior of living animals, their physiology, biochemistry, anatomy and distribution, as well as knowledge of the functional morphology and natural history of related taxa. The primary source of nutrition is surely the vent water, with chemoautotrophic bacteria using its chemically reduced constituents as an energy source to synthesize protoplasm (Jannasch & Wirsen, 1979, 1981; Rau & Hedges, 1979; Karl et al., 1980; Felbeck, 1981; Cavanaugh et al., 1981; Rau, 1981a,b; Felbeck & Somero, 1982). The intense concentration of metazoans in the mouth of vent openings is a good indication of this. The bacteria are utilized by the community in three major ways.

They may grow symbiotically in close conjunction with the animal, as best seen with Riftia, which brings the essential inorganic constituents of vent and ambient water to the bacterial culture within it (Felbeck, 1981; Cavanaugh et al., 1981). Calyptogena and the mytilid also have associated bacteria, in this case in their gills (Felbeck & Somero, 1982). All three taxa show stable isotope ratios that indicate a local food source (Rau & Hedges, 1979; Rau, 1981a,b).

Their distribution correlates nicely with this life style. Because dilution of vent water is so complete at the bottom, the concentration of reduced ions will be too low except in the vent openings. Accordingly, Riftia and Calyptogena are limited to vents, and that is the only place the mytilid is abundant. Further, mytilids growing away from vents are less well nourished (Hiatt, 1980 quoting K. L. Smith).

That mussels can live away from directly outwelling vent water at all points toward an ability to nourish themselves in another way. Both the mussel and Calyptogena have a well-developed digestive tract (unlike Riftia), and it is possible that a portion of their diet is based on suspension feeding (see below). To date, gut-content studies have not been adequate to clarify this point.

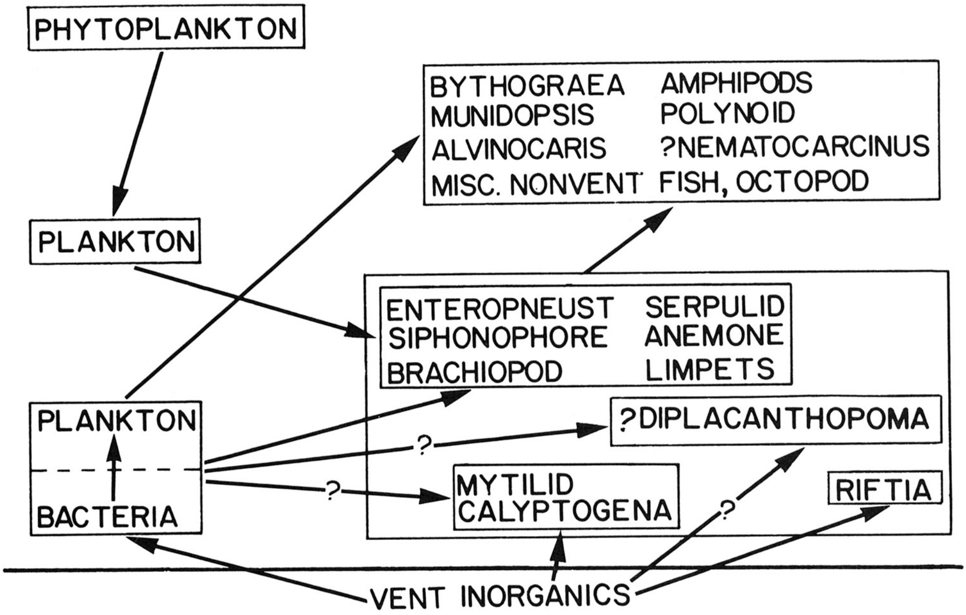

Fig. 14. Food web of vent megafauna. Linkages that are likely to be minor are not included.

?Diplacanthopoma also may be a chemoautotroph, as shown by its behavior. Its unwillingness to approach bait suggests it is not a scavenger. Nor was it ever seen to feed (Cohen & Haedrich, in press). Its frequent hovering in the vent throat without touching the rock walls and without any apparent movements of its mouth implies some significant purpose. Chemoautotrophy is quite possible. In this connection, it is important to note that we have seen the hovering behavior even when the vent water appeared quite clear, implying a paucity of particles of filterable size. The growing list of animals that independently evolved the ability to utilize chemoautotrophic bacteria demonstrates that this may not be a difficult ability to acquire.

While it has never been rigorously quantified, it is obvious that the greatest portion of vent biomass (75%) is made up of these symbiotically chemoautotrophic taxa.

A second source of nutrition is encrusting bacteria (Jannasch & Wirsen, 1979, 1981). Because the most flourishing bacterial growth depends on vent water, this food source is developed primarily at vent openings, either on rock or organisms. The two limpet species that move about on rocks, bivalves and vestimentiferans likely feed on this resource. The vent-water adapted crustaceans (*Alvinocaris*, *Bythograea*) also partake; *Bythograea* has been observed to sweep surfaces with its maxillipeds, and at 21°N we saw *Munidopsis* feed on bacterial overgrowth.

Finally, bacteria grow suspended in the subsurface vent water and also surely break loose from surfaces and are washed out. High concentrations of bacteria have been measured in vent water, and much of it is in aggregations that are large enough to be filtered by suspension feeders (Karl et al., 1980). Those suspension feeding animals that live in the vent throat (*Neomphalus*, anemones) may well live primarily off this food source.

The greatest cause of uncertainty about the precise nature of food for suspension feeders is our scant understanding of the vent plankton assemblage. Observers at vents on the East Pacific Rise at 21°N noted plankters living in the vent throat. Subsequently we saw the same thing in photographs from the Galapagos vents. Vent-mouth suspension feeders may also be feeding on these.

The plume of vent water rises away from the bottom because of its lower specific gravity, carrying living and nonliving particulates. This was observed on several occasions a number of meters up. These particles slowly rain down on the adjacent terrain. Thus, vent bacteria are even available to suspension and deposit feeders living in the immediate vicinity. An observable plankton fauna also occupies this plume and associated water. Amphipods are not uncommon swimming here, and one could see many plankters too small to identify. Once again, there is no certainty about the extent to which the benthic fauna away from a vent opening is feeding directly on bacteria or indirectly by eating plankton and plankton byproducts.

Further, some portion of the plankton is likely to be derived from the outlying nonvent region, having been carried in by the centripetal flow of the thermal convection cell (Enright et al., 1981). These provide a nutritional resource whose ultimate origin is derived from the normal, sunlight-powered photosynthetic food chain.

Serpulids, anemones, brachiopods, the siphonophore and the enteropneust are the obvious megafaunal suspension feeders relying on this whole complex, suspended and settling resource, while *Munidopsis*, ?*Nematocarcinus*, amphipods and wandering *Bythograea* are the dominant deposit feeders. Enteropneusts are normally considered deposit feeders (Hyman, 1959), but their intensely aggregated draping over elevated surfaces, often with their anterior ends hanging freely, makes suspension feeding more likely. Utilization of dissolved organics was suggested by one anonymous reviewer.

The distribution of the siphonophore, brachiopod, enteropneust, elongate anemone and ?Nematocarcinus are not fully explained by this senario because it would predict that their concentration should be highest toward the vent openings. Instead, their highest concentrations are more peripheral. The siphonophore may be inhibited by the fragileness of its attachment to the bottom (Pugh, in press). This would exclude it from regions of higher current or concentrations of larger mobile organisms, such as the galatheid. Its preference for sheltered low spots is consistent with the suggestion.

Interference by other organisms may limit the other taxa to peripheral areas, but this does not seem likely for any but the enteropneust. As already suggested, they are possibly more sensitive to elevated temperatures or vent-water chemistry. Finally, it may indicate a shift in food preferences. The enteropneust is not totally limited to vent sites. Dive 985 cruised extensively over nonvent terrain where more than once enteropneusts were sighted, and in each case they were concentrated on the crest of irregular ridges, once at the lip of a deep gorge. We interpret this as indicating a preference for places where current intensification exists. If this is so, the presence of enteropneusts at vents may be stimulated by the convection cell drawing food in from the outlying nonvent region (Enright et al., 1981). But need for current does not explain why they are not closer to the vents, where current would be stronger. It would be helpful to emplace sedimentation traps in the vicinity of peripherally concentrated taxa to see what kinds of food are available there.

So far, we have emphasized primary consumer activities and plankton feeding. Higher in the food chain are scavengers--those omnivorous animals that feed on deposited animal byproducts (carcasses, exuveae, feces, etc.), smaller living animals, and even pieces of much larger animals in addition to benthic microflora. At the Galapagos vents, crustaceans dominate this category: Munidopsis, Bythograea, Alvinocaris, ?Nematocarcinus and amphipods. The polynoid polychaete also probably belongs here. A few nonvent fish which appear in the vent region at somewhat higher concentrations (Cohen & Haedrich, in press) also fall in this category, but are not significant factors. Of all these, only Bythograea actually has been documented as a carnivore (Mickel & Childress, 1982b; pers. obs.). Carnivory has been attributed to Alvinocaris (Jones, 1981; Williams & Chase, 1982), but Childress was cited erroneously on this point (Childress, pers. comm.).

This food web suffers from neglecting the macrofauna (Sanders, in prep.) and smaller taxa. These surely play a major role in detritus feeding. A further weakness is that this scheme is based more on knowledge of the activities of homologous taxa than is desirable, but concrete data on most of the vent fauna have not yet been accumulated. While gut contents are difficult to analyze, they might be useful in specific instances; inspection of potential chemoautotrophs would be especially valuable. Particularly vexing is the void in information on plankton. Settling trap deployments would do much to reveal the kinds of particulates available in different parts of the vent field. The plankton fauna must be analyzed before we can hope to have a balanced picture of trophic structure of vent communities.

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