Uiblein, F., Ott, J., Stachowtisch, M. (Eds), 1996: Deep-sea and extreme shallow-water habitats:
affinities and adaptations. - Biosystematics and Ecology Series 11: 313-336.

Ecophysiology of primary production at deep-sea vents and seeps

Ch. R. FISHER

Abstract: Symbiotic associations with chemolithotrophic or methanotrophic symbionts have been suggested for eleven phyla of marine invertebrates. The polyphyletic origin of these symbioses implies significant benefits to the hosts of the associations, which seem to be largely nutritional benefits. In order to reap the nutritional benefits of autotrophic symbionts, the hosts must supply the symbionts with oxygen, a carbon source, and an energy source. In large metazoans the symbiont-containing tissues are often hypertrophied and packed with high densities of symbionts. The resultant large biomass of symbionts is necessary to supply a significant portion of the hosts nutritional needs, but also results in substantial demands for the substrates required by the symbionts for chemosynthesis. A variety of physiological, anatomical, and behavioral mechanisms have evolved in the various host groups to facilitate the supply of the substrates required by their symbionts. These adaptations are reviewed along with sometimes similar adaptations in species of free-living bacteria. One result of very efficient symbioses and free-living bacteria living in the energy-rich vent and seep environments is that these communities are extremely productive. This is in stark contrast to the surrounding ambient deep-sea communities which are often nutrient-limited. The literature using stable carbon and nitrogen isotopes to examine nutritional relations in vent communities is reviewed and additional information on the Gulf of Mexico seep communities is presented. Evidence and arguments that deep-sea vent and seep community primary production may be important to the nutrition of the surrounding ambient deep-sea fauna are considered, and a case is made that this is likely for large regions of the Gulf of Mexico.

Introduction

Symbioses between chemoautotrophic bacteria and metazoans were first discovered in some of the dominant fauna of Pacific deep-sea hydrothermal vents. Since that discovery numerous other associations have been described in eleven different phyla. One unifying feature of these symbioses is that the hosts are found in microhabitats where reduced inorganic chemicals are present, at least some of the time. Beyond that, chemoautotrophic symbioses are extremely diverse with respect to virtually all aspects of the symbiotic association. At one extreme, the occurrence of a few epibiotic symbionts on the surface of an animal living in reduced sediments may be basically coincidental, while at the other extreme there are tightly evolved associations with a high biomass of intracellular symbionts in specialized tissues. In between these extremes are a wide variety of symbioses where the nature of the interactions between host and symbiont are often obscure. The biology of hydrothermal vents and chemoautotrophic symbioses have been reviewed in depth from several different perspectives in recent years. In this paper, review articles are referenced extensively and the reader is referred to those reviews for more details and the original literature on the subjects.

Tab. 1 lists 11 phyla for which symbioses with chemoautotrophic or methanotrophic symbionts have been reported. The weight of literature available on the different associations ranges greatly. In some cases, it is not clear that the reported occurrence of bacteria, in or on the host, represents a stable chemoautotrophic symbiosis. Nonetheless, even if one considers only the phyla for which the occurrence of chemoautotrophic symbionts is well accepted, it is clear that chemoautotrophic symbioses have arisen numerous times in diverse phyla. In fact, in some groups such as the mollusks, chemoautotrophic symbiotic associations have arisen polyphyletically in several different families (of two classes), with significant differences between the different associations (REID and BRAND 1986, FISHER 1990).

Tab. 1: Phyla of animals containing at least a single species with reported chemoautotrophic or methanotrophic symbionts.

Phylum	Symbiont type	Symbiont location	Symbiont abundance	References
Arthropoda	Chem.	Surface	Moderate	1
Annelida	Chem.	Surface/intracellular	Abundant - Spare	2
Ciliata	Chem.	Surface	Abundant	3
Echinodermata	Chem.	Gut	Spare	4
Molluska	Chem. and/or Meth.	Intracellular	Abundant-Spare	5
Nematoda	Chem.	Surface	Abundant	6
Platyhelminthes	Chem.	Intracellular	Moderate	7
Pogonophora	Chem. or Meth	Intracellular	Moderate	8
Porifera	Meth.	Intra-/Extracellular	Moderate	9
Priapulida	Chem.	Surface	Spare	10
Vestimentifera	Chem.	Intracellular	Abundant	5

References: 1. VAN DOVER 1995; 2. GIERE 1981, GAILL et al. 1987; 3. BAUER-NEBELSICK et al. in 1996; 4. TEMARA et al., 1993; 5 FISHER 1990; 6. OTT et al. 1991; 7. OTT et al. 1982; 8. SOUTHWARD 1982; 9. VACELET et al. 1995; 10. OESCHGER & SCHMALJOHANN 1988.

The fact that this type of symbiosis has evolved and persisted so many times over evolutionary history is strong evidence for significant evolutionary advantages to these associations. There are two attributes of chemoautotrophic bacteria which could confer significant advantages to receptive hosts. (Although hosts can also confer significant advantages to their symbionts, these advantages will only indirectly affect the fitness of the host, which is the major focus of evolutionary selection on the intact association). The first potential advantage stems from the fact that these bacteria are autotrophic; they are able to synthesize organic carbon from inorganic sources. Simply put, the symbionts are a potential source of nutrition for their host. Although direct evidence for nutritional transfer from symbiont to host is actually very rare in the literature, there is abundant indirect evidence of this in a wide variety of hosts. This includes hosts whose normal feeding and/or digestive apparatus is either reduced or absent, hosts whose distribution and health is tightly tied to reduced environments, stable isotope data implicating chemoautotrophic or methanotrophic origin of host organic carbon, nitrogen, and/or sulfur, and ultrastructural or histochemical evidence of symbiont digestion. This topic was recently reviewed by NELSON and FISHER (1995) and the reader is referred there for references to earlier reviews and the original literature on this subject.

The second potential advantage to a host of chemoautotrophic symbionts living in reducing habitats is the fact that these symbionts can oxidize sulfide, which is toxic to most metazoans (SOMERO et al. 1989) . This is an even more difficult advantage to quantify because of the diversity of mechanisms which may be operable, and because many animals without chemoautotrophic symbionts can effectively detoxify sulfide and live in sulfidic environments. Life with sulfide was the topic of two recent symposia (American Society of Zoologists Annual Meeting in December 1993 and the Fourth International Congress of Comparative Physiology and Biochemistry in August 1995), and the invited papers from the 1993 symposia are contained in Volume 35 of the American Zoologist (1995). This subject is also reviewed by SOMERO et al. (1989) and CHILDRESS and FISHER (1992) and will not be reviewed here. Rather, in the following section I will accept the thesis that the symbionts and their chemoautotrophic activities are beneficial to their host and explore some of the strategies available to a metazoan exploiting the "chemoautotrophic life- style".

Constraints and approaches for chemoautotrophy

Whether the symbionts are functionally a sulfide detoxification mechanism or a source of nutrition for their host, they (like free-living chemoautotrophs) require access to both reduced inorganic chemicals (usually sulfide) and an oxidant (usually oxygen) in order to grow chemoautotrophically. This can be somewhat problematic as sulfide and oxygen do not coexist for significant times or in significant amounts due to spontaneous oxidation of sulfide by oxygen. In the case of symbiotic associations where the symbionts are likely to provide a significant portion of the nutritional needs of moderately sized animals, quite substantial amounts of both oxygen and sulfide must be available to the symbionts in order to provide sufficient energy for the level of carbon fixation necessary to sustain the association.

There are two types of marine environments where both oxygen and sulfide are found in close proximity and in significant quantities. One is in areas of active mixing of reduced fluids from one source with oxic water from another. The best known of these are hydrothermal vent environments, where the reduced hydrothermal fluids are mixing with ambient oxic bottom water at or near the sea floor. Some active seeps, such as those in the Gulf of Mexico, are also sites of active mixing of reduced fluids and ambient bottom water at the sea floor. The second type of marine environments where both sulfide and oxygen co-occur are interface environments between reduced sediments and overlying oxic waters. It should be noted that these environments are in fact sites of mixing of the two fluids; however, the motive force is diffusion and not water motion and the extent of the habitat where both oxygen and sulfide are simultaneously present is normally less than one mm wide (JØRGENSEN and REVSBECH 1983). There are, of course, examples of environments intermediate between these two, such as areas of very slow seepage or venting of pore fluids.

With few exceptions, significant numbers of free-living chemoautotrophic bacteria are only found in the very narrow interface environments between reduced and oxic pools of water. NELSON et al. (1983, 1986) used gel-stabilized gradient cultures to demonstrate chemoautotrophic growth of a bacterium with sulfide as the sole energy source. In these experiments the motile *Beggiatoa* migrated to and grew in a tight horizontal band less than 1 mm wide between the sulfide plug in the bottom of the tube and the surface of the gel, which was exposed to air. Both sulfide and oxygen were present in this band, with only sulfide present below, and only oxygen above. In nature this environment is most often at or near the water/soil interface, where the soil provides a surface for the bacteria to proliferate, allowing them to remain in the interface. In some well-stratified water bodies, however, veils of bacteria may form at the chemocline between reduced and oxic waters.

Multicellular animals, due to their larger size, increased motility, and organ level of development, have several options available to acquire both sulfide and oxygen, which are largely unavailable to bacteria. These options are listed in Tab. 2 and addressed individually below.

Tab. 2: Options for the acquisition of sulfide and oxygen by chemoautotrophic symbioses.

1) Animals can acquire sulfide and oxygen from areas of active mixing of two fluids, even when the area of active mixing is not in immediate contact with a surface (such as centimeters to meters above the ocean floor).

2) Animals can spatially separate the acquisition of sulfide and oxygen by physically bridging the interface between the two environments and obtaining oxygen from one environment and sulfide from the other.

3) Animals can temporally separate the acquisition of the sulfide and oxygen by accumulating the substrates one at a time in either a variable environment or by moving between microhabitats.

A. Animals can acquire sulfide and oxygen from areas of active mixing of two fluids, even when the area of active mixing is not in immediate contact with a surface (such as centimeters to meters above the ocean floor).

This habitat is essentially a scaled-up version of the interface habitat discussed above, where turbulent mixing has expanded the area where both sulfide and oxygen are present together. Free-living bacteria can persist in this environment if the area of active mixing is adjacent to a surface to which the bacteria can attach and grow. If such areas are more that a few mm above the substrate, the size and limited locomotory capabilities of free-living bacteria will preclude their persistence in that environment. In many cases, however, well illustrated by hydrothermal vent examples, free-living bacteria can flourish on the surfaces of organisms which either grow or move into areas of active mixing of reduced and oxic water. Although usually not visible on the tubes of vestimentiferans on the East Pacific Rise, thick bacterial growth is often found associated with the tubes of *Ridgeia piscesae* at vents in the North-East Pacific (Fig. 1), and on the shells of mussels such as a bathymodiolid (SMII) from the Alaminos Canyon seep in the Gulf of Mexico (Fig. 2). Other examples include the thick bacterial mats often present on the scales of the polychaete *Lepidonotopodium piscesae* and on the shells of the limpet *Lepetodrilus fucensis*, both of which are often associated with *Ridgeia pisce-*

sae in some environments on the Juan de Fuca Ridge (DE ANGELIS et al. 1991) . In fact, this type of external fouling growth may be the rule, rather than the exception, on hard surfaces of hydrothermal vent fauna.

The line between free-living bacteria fouling a biological surface and a symbiosis can be hard to draw. On the one extreme are associations like those described in the previous paragraph; the other extreme includes associations like those between specific external bacteria and alvinellid polychaetes (GAILL et al. 1987) or some nematodes (OTT et al. 1991) (although the relations between hosts and symbionts are often less well understood). Somewhere between these extremes are many other associations of unclear affinities. One in particular is relevant to this discussion because the host shrimp are one of the dominant animals associated with many Mid Atlantic Ridge vents and their preferred habitat is zones of active mixing of vent and ambient waters around hydrothermal chimneys, where they "swarm". Epibiotic bacteria are found on all species of bresiliid shrimp so far collected from the Mid-Atlantic vents, and thick mats of chemoautotrophs are associated with the ventral surface of the cephalothorax of some species. The physiological importance of these external symbionts to their host is still being debated; however, the fact that the epibionts flourish as a result of the shrimps' swarming behavior in shimmering mixtures of vent and ambient water is unquestioned. The evidence for and against the presence of internal symbionts as well as a detailed discussion of the trophic ecology of these shrimp can be found in VAN DOVER (1995) and the references therein.

Habitats where the two fluids are actively and turbulently mixed are relatively limited and usually occur above the rock/water interface. The unrivaled exploiters of this habitat are the hydrothermal vent tube worms. These large worms thrive in areas with substantial flow of diffuse vent fluid and are thus exposed to large pools of both sulfide and oxygen. Their physiological adaptations are reviewed in detail by CHILDRESS and FISHER (1992) and NELSON and FISHER (1995) and are briefly summarized here: Hydrothermal vestimentiferan tube worms grow such that their plume, which is a highly vascularized gas exchange organ, is positioned in areas of shimmering water where warm, reduced vent fluids are mixing with oxic ambient bottom water. Both sulfide and oxygen are taken up across the plume and into its vascular blood, where they are bound by abundant hemoglobins with both high affinity and high capacity. The blood transports the sulfide and oxygen to the symbionts, which are densely packed in a well-vascularized internal organ, the trophosome. Due to their habit, morphology, and physiology these animals are able to take up and supply their symbionts with large quantities of sulfide and oxygen, and the symbionts in turn are apparently able to provide the host worm with the bulk of its nutritional needs. The efficiency with which this is accomplished is perhaps best evidenced by the most massive of the hydrothermal vent vestimentiferans, *Riftia pachyptila*, which has been suggested to be the fastest growing invertebrate (LUTZ et al. 1994) despite lacking a mouth, gut, or anus.

Another group of animals which thrives in areas of active mixing of reduced and oxic pools of water is the bathymodiolid mussels. Unlike the vestimentiferans or vesicomyid clams (which will be discussed below), bathymodiolid mussels such as *Bathymodiolus thermophilus* inhabit virtually the full range of hydrothermal vent microhabitats, from areas of barely detectable flow to areas of vigorous venting of diffuse fluids (FISHER et al. 1988). These animals have no physiological adaptations to take up, accumulate, or transport either sulfide or oxygen. Current thought is that mussels with chemoautotrophic symbionts like *B. thermophilus* detoxify the sulfide to thiosulfate and transport the thiosulfate to their symbionts, where it is further oxidized chemoautotrophically. This subject is reviewed in detail in CHILDRESS and FISHER (1992) and NELSON and FISHER (1995).

Animals which deal with sulfide exposure in part by binding the sulfide internally and transporting it to symbionts for oxidation require sulfide-oxidizing symbionts to avoid the toxic effects of sulfide build-up. Since sulfide is not accumulated by the mussels and the symbionts are not required to avoid the toxic effects of sulfide, these mussels may have been "pre-adapted" for symbiosis with other types of bacteria such as methanotrophs. Methanotrophic symbioses have been documented in several bathymodiolid mussels, and more recently several species harboring both methanotrophs and chemoautotrophs have been reported (reviewed in NELSON and FISHER 1995). Most seep environments are considerably less dynamic with respect to active mixing of the reduced seep fluids and the overlying oxic waters. As a result, the spatial extent of the zone where both oxygen and sulfide are present is much smaller than at hydrothermal vents. Methane, however, is much more stable than sulfide and thus is often present in high concentrations along with oxygen in mussel microhabitats at cold seeps (NIX et al. 1995). Although, as for sulfide, the mussels have no specialized molecules for accumulating or transporting methane to their symbionts, the ultrastructure of the symbiosis facilitates the supply of both oxygen and methane to the symbionts (see CHILDRESS and FISHER 1992). The symbionts pack the distal end of the bacteriocytes which line the surface of the numerous individual filaments of their hypertrophied gills. Like other bivalve gills these have evolved for gas exchange, and a very large gill surface area is in direct contact with the methane- and oxygen-rich water of their microhabitat. Largely because of the advantages of the metazoan body plan, mussel beds in seep environments in the Gulf of Mexico are capable of oxidizing methane and incorporating methane carbon at rates over three orders of magnitude greater than those found in any other aquatic environment (FISHER 1993).

B. Animals can spatially separate the acquisition of sulfide and oxygen by physically bridging the interface between the two environments and obtaining oxygen from one environment and sulfide from the other.

This option is not available to bacteria due to their small size. In order for a metazoan to spatially bridge the interface between two environments, there must be a mechanism which allows sulfide and oxygen uptake into different portions of the body. A classic example of an animal group which uses this strategy is the vesicomyid clams. Based on temperature measurements made around *Calyptogena magnifica* in 1982, on the anatomy of the clams, and the properties of their blood, ARP et al. (1984) postulated that *C. magnifica* takes up sulfide across the surface of its extensible foot, which is inserted into areas of pooling vent fluid, while obtaining oxygen across its gills from the overlying ambient bottom water. Vesicomyid blood contains hemoglobin in cells and an extracellular sulfide-binding component which allows the clams to concentrate sulfide into their blood by two to three orders of magnitude over environmental levels. Several studies have confirmed the spatial separation of the large pools of sulfide and oxygen in the vent clams' habitat and the ability of intact clams to accumulate sulfide from their environment (reviewed by CHILDRESS and FISHER 1992). Analysis of pore water from the habitats of seep clams in the Gulf of Mexico along with measurements of blood sulfide levels in freshly collected clams from these sites indicate that they use the same approach to obtain sulfide and oxygen from spatially separate pools. In the case of this seep habitat the sulfide is patchily distributed in the sediments and the clams apparantly "mine" the patches by moving through the sediments (SCOTT and FISHER 1995) .

Ongoing studies continue to support the hypothesis that many adult seep vestimentiferans spatially separate the acquisition of sulfide and oxygen, obtaining sulfide across the thin-walled portions of the buried posterior end of their tubes and obtaining oxygen across their plume. Sulfide is rarely detectable around the plumes of the Gulf of Mexico seep vestimentiferans, and it is often absent in the top 5-10 cm of sediment around the base of large aggregations (SCOTT and FISHER 1995). During the 1995 summer field season, direct measurements of sediment depth around the bases of tube worm aggregations confirmed that the posterior ends of adult vestimentiferan tubes in the Gulf of Mexico are normally buried by one-half meter or more of sediment. Furthermore, sulfide concentrations in interstitial water samples taken between the tubes in vestimentiferan assemblages from sediment depths of 25 to 70 cm ranged up to 1 mM (FISHER unpubl.). This represents a significant pool of sulfide potentially available to the animals. However, sulfide uptake will be limited by the sulfide diffusion rate from interstitial waters across their tube and body wall and into their coelomic fluid (which also contains a sulfide-binding hemoglobin). Seep vestimentiferans are therefore likely exposed to a stable energy source whose uptake rate is significantly limited compared with vent vestimentiferan species. From this one can hypothesize that seep vestimentiferans are slow-growing and perhaps long-lived. Four years of data from banded worms in the Gulf of Mexico (Fig. 3) indicate this is the case with both species of vestimentiferan present between 500 and 1000 m around hydrocarbon and saline seeps (SIMPKINS 1994, SCOTT and FISHER 1995, unpubl. data). Yearly growth increments have now been determined for 53 individuals from 14 aggregations at 3 different sites. The largest growth increment recorded for any individual in any year was 3.1 cm. Average yearly growth rates were under 1 $cm \cdot a^{-1}$ for both species. Although this technique does not allow measurement of growth of small individuals, the data on animals between 47 and 216 cm in length clearly indicate that the seep vestimentiferans are slow growing and long lived. The efficacy of a new technique was recently confirmed when tubeworms stained in 1994 were revisited in 1995. The past year's growth is clearly visible on the tubes of animals stained with a blue chitin dye one year earlier (Fig. 4). With this technique much smaller animals can be studied, and the first year's data indicates that although the smaller (younger) animals can grow up to twice as fast, the seep vestimentiferans clearly grow much more slowly than their hydrothermal vent relatives and can live well over 100 years.

C. Animals can temporally separate the acquisition of the sulfide and oxygen by accumulating the substrates one at a time in either a variable environment or by moving between microhabitats.

Both oxygen and reduced sulfur compounds must be present simultaneously for an aerobic chemoautotroph to obtain energy from the oxidation of the sulfur compound. However, if an organism has the ability to store either substrate, it can temporally separate the acquisition of the two and combine the two subsequently. There are two types of environments in which the ability to temporally separate the acquisition of sulfide and oxygen can be beneficial to an organism with a chemoautotrophic life style. One is in habitats where the chemistry is variable and both substrates are present in the same space, but at different times. This is the case in some of the hydrothermal vent tube worm habitats. Local variations in vent flow and bottom currents can make a vent vestimentiferan habitat one in which either sulfide or oxygen can be absent for periods ranging from seconds to hours, and in extreme cases perhaps more (JOHNSON et al. 1988). The ability to accumulate and store both oxygen and sulfide in their blood allows vestimentiferans to acquire each at different times if necessary and yet supply them together to their intracellular symbionts. JOHNSON et al. (1988) have demonstrated that *Riftia pachyptila* can and does take up sulfide and oxygen from separate "packets" of water in situ.

There are also free-living chemoautotrophic bacteria which live in a variable habitat and may be able to take up oxygen and sulfide at separate times yet use them together. At the sediment-covered vent site in Guaymas Basin there are mats of the filamentous chemoautotroph *Beggiatoa* spp. which are 20 times as thick as coastal mats (GUNDERSEN et al. 1992). The pulsatory flow of cold ambient bottom water into the sediments and warm vent fluid out of the sediments creates an environment of changing oxygen and sulfide levels. The 2 to 10 mm-long *Beggiotoa* filaments have a large intracellular vacuole which GUNDERSEN et al. (1992) speculate may serve as the storage reservoir for either reduced or oxidized substrates during exposure to the other.

Mobile hosts to chemoautotrophic symbionts may also temporally separate the acquisition of sulfide and oxygen by moving back and forth between the two environments. There are two groups of animals for which this strategy has been investigated in some detail. One group is the solemyid clams, which harbor abundant intracellular chemoautotrophic sulfur bacteria in their gills. These clams live in a U- or Y-shaped burrow and it has been proposed that the clams acquire sulfide from the stagnant base of their burrow and oxygen by moving into the upper portions and ventilating the burrow (DOELLER et al. 1988). Supply of either sulfide or oxygen to the symbionts, while the host is exposed to the other, could be accomplished through the use of cytoplasmic gill hemoglobin which reversibly binds either sulfide or oxygen (DOELLER et al. 1988); this would allow a temporal separation of acquisition and use.

Meiofauna with epibiotic chemoautotrophic symbionts may also acquire sulfide and oxygen from different places and at different times. OTT et al. (1991) document a migratory behavior of nematodes from the sub-family *Stilbonematinae* which exposes the worms repeatedly to sulfide and then to oxygen. Since both must be present for reaction together, a mechanism must exist to store either oxygen or reduced forms of sulfur. Although binding mechanisms have not been elucidated for either substrate, SCHIEMER et al. (1990) documented at least partial decoupling of the uptake and oxidation of reduced sulfur species by the intact symbiosis and postulated that the worms "recharge" their sulfur stores with periodic excursions into anoxic regions. Based on migration to the sulfide/oxygen interface and the distribution of

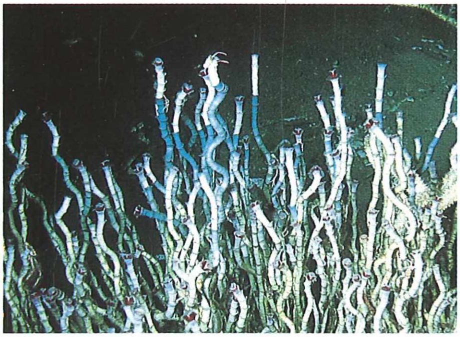

Fig. 1: Thick filamentous bacterial growth on tubes of *Ridgeia piscesae* at 2180 m depth on the Endeavour segment of the Juan de Fuca Ridge. Photo courtesy V. TUNNICLIFFE.

Fig. 2: White bacterial growth on shells of an undescribed seep mytilid at 2200 m depth in Alaminos Canyon in the Gulf of Mexico. Photograph by C. FISHER.

Fig. 3: A banded vestimentiferan, *Lamellibrachia* sp., from 600 m depth in the Gulf of Mexico. Yearly growth increments are determined by videoscopic measurement of the distance between the band and the apical end of the tube. Video image by I. URCUYO.

Fig. 4: Stained *Lamellibrachia* sp. from 600 m depth in the Gulf of Mexico. The tubes were stained blue in the previous year and subsequent growth is visible as unstained tube material deposited anterior to the stained tubes. Photograph by A. FIALA. Copyright National Geographic Magazine.

some oligochaetes with endosymbiotic chemoautotrophs around this interface, GIERE et al. (1991) hypothesize a similar behavior for these meiobenthic worms. This behavior is likely not limited to species with chemoautotrophic symbionts. MEYERS et al. (1987) suggest that aerobic meiofauna living in sulfidic sediments must migrate occasionally to oxic sediments to obtain and store oxygen for their extended excursions into anaerobic microhabitats.

At first consideration, moving between oxidized and reduced microhabitats might not appear to be a viable option for free-living chemoautotrophs. However, FOSSING et al. (1995) recently reported on a mat-forming bacteria whose physiological and behavioral adaptations for the acquisition of sulfide and an oxidant may exceed those of many metazoan symbioses. *Thioploca* spp. form multicellular filaments of up to 7 cm in length and can glide up and down in sheaths 10 to 15 cm long and 1.5 mm in diameter. In one mat found at 87 m off the Chilean coast in the oxygen minimum zone, the wet weight of the sheathed *Thioploca* was "nearly 1 kg m^{-2}" (FOSSING et al. 1995). The massive filament moves between the nitrate-rich surface of the sediments and nitrate-free depths where sulfide is abundant. About 80 % of the cell volume is occupied by a large, central, liquid vacuole, and nitrate concentrations inside the cells are as high as 20 000 times that of the surface seawater (where nitrate concentrations are highest in this environment). This would provide a viable mechanism for the storage and transport of oxidant to the reduced microhabitat. The bacteria also accumulate elemental sulfur in their cytoplasm around the central vacuoles, which may serve as a mechanism to transport a reductant back up into the nitrate-rich upper zone. Thus, this prokaryote can accumulate, store, and transport both oxidant and reductant within its cells, allowing it to temporally separate the acquisition of the two.

The impact of vent and seep primary production in the deep sea

One of the immediately obvious and outstanding aspects of the chemoautotrophic communities in the deep sea is the very high biomass associated with these communities, which is in stark contrast to the benthos in the surrounding deep sea. The contrast itself suggests that the primary production supporting vent and seep communities is of endogenous origin. This suggestion has been supported in several studies of the tissue stable carbon and nitrogen composition of hydrothermal vent fauna (reviewed recently in FISHER 1995 and KENNICUTT and BURKE 1995). These studies are based on the fact that the $\delta^{13}C$ and $\delta^{15}N$ values of organic carbon and nitrogen produced chemoautotrophically within the vent communities are discernible from organic C and N produced photoautotrophically (Fig. 5). Because there is very little change in the $\delta^{13}C$ values between a consumer and its food source and only a -3.5 ‰ change in the $\delta^{15}N$ values (MACKO et al. 1987), stable isotopes are good tracers of hydrothermal vent production in the deep sea.

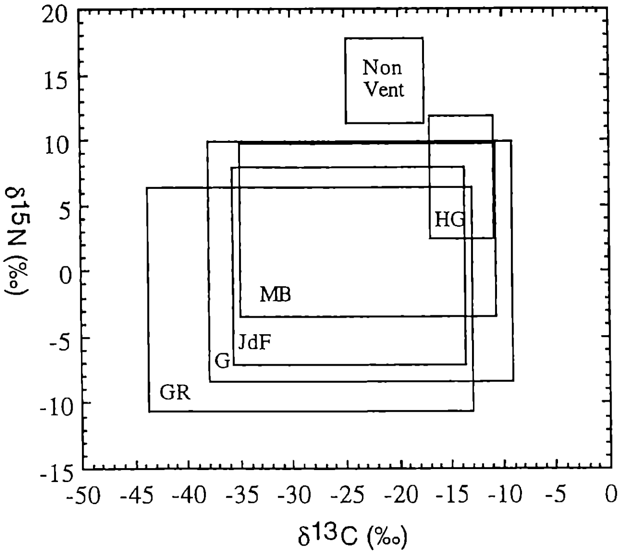

Fig. 5: Summary of $\delta^{13}C$ and $\delta^{15}N$ values for deep sea vent and non-vent fauna. Each box includes the entire range of $\delta^{13}C$ and $\delta^{15}N$ values for vent fauna from a particular geographical area, with the exception of the Non Vent box which delineates data from 8 species of ambient fauna collected in the general area of vent sites. G represents values from 215 individuals of 21 species collected at three sites on the Galapagos Rift. GR represents 17 values from 12 species collected from 4 distinct sites on the Gorda Ridge. HG represents 17 values from 13 species collected from the Hanging Garden vent at 21°N on the EPR. JdF represents 47 values from at least 15 species collected at two sites on the Endeavour Segment of the Juan de Fuca Ridge. MB represents 25 values from 8 species collected from the Marianas Back Arc Spreading Center. Figure is modified from FISHER (1995) and includes additional unpublished data from JdF samples.

In many hydrothermal vent communities, such as those on the East Pacific Rise, the biomass is dominated by species with endosymbiotic chemoautotrophic bacteria, such as vestimentiferans, mussels, and clams. This, however, is not always the case; the shrimp-dominated communities of the Mid-Atlantic Rise provide an excellent example of communities not dominated by species with endosymbionts (VAN DOVER 1995). An apparently intermediate situation occurs at some sites on the Juan de Fuca Ridge, such as on the Endeavour segment, where vestimentiferans are abundant but accompanied by a wide variety of other fauna without endosymbionts (TUNNICLIFFE and FONTAIN 1987, TUNNICLIFFE 1988). The endosymbiotic bacteria in the symbiotic species apparently provide the bulk of their hosts' nutritional needs, although filterfeeding by the bivalves can provide additional nutritional input (reviewed by NELSON and FISHER 1995). The endosymbiont-containing species can therefore be considered among the primary producers at vents and seeps. On the other hand, there is growing evidence that the endosymbiont-containing species are directly important in the nutrition of only a small subset of the associated fauna (VAN DOVER and FRY 1994) . For example, a study at three Galapagos Rift sites revealed that very few species of vent consumers analyzed had tissue stable isotope values which supported tight nutritional links between all individuals of the consumer species and either the symbiotic bivalves or tubeworms abundant at those sites (Fig. 6). Although a few individuals of some consumer species had tissue stable isotope values similar to the symbiont-containing species, most individuals could not be nutritionally linked to either tubeworms or bivalves from this data, and nutritional input from free-living bacteria was implicated (FISHER et al. 1994). Data from other studies at various hydrothermal vent sites yield similar conclusions (reviewed in FISHER 1995 and VAN DOVER 1995).

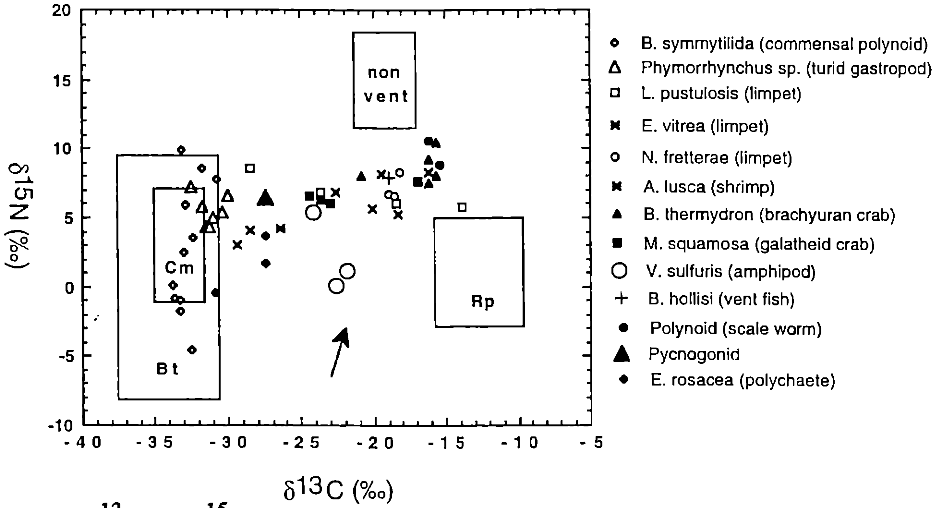

Fig. 6: $\delta^{13}C$ and $\delta^{15}N$ values for fauna from Galapagos Rift hydrothermal vent fields. Each plotted symbol represents the values from a single individual. The lower rectangles represent the range of values found in the tissues of symbiont-containing animals; *Bathymodiolus thermophilus* (Bt), *Calyptogena magnifica* (Cm), and *Riftia pachyptila* (Rp). The upper rectangle (non vent) represents the range of values from 8 species of ambient deep-sea fauna. The arrow indicates the direction and magnitude of change in tissue isotope values to be expected between a prey item and its consumer. Modified from Fisher et al. (1994).

Tab. 3: $\delta^{13}C$ values of benthic deep-sea fauna from the Gulf of Mexico.

Chemosynthetic primary producers		
Seep mytilid Ia		-40 to -66 ‰
Vestimentiferan tube worms		-17 to -43 ‰
Vesicomyid and Lucinid clams		-31 to -40 ‰
Bacterial mats		-26.8 to -30.9 ‰
Ambient benthic megafauna **		-17.7 ±1.2 ‰
Heterotrophic endemic seep fauna		
Munidopsis sp.	(galatheid crab)	-37.6 ‰*
Alvinocaris statophila	(shrimp)	-34.1 ‰*
Orbinid polychaete		-47.0 ‰*
Bathynertia naticoidea	(snail)	-32.4 ‰*
Other heterotrophic fauna collected at seeps		
Sclerasterias	(starfish)	-50.1 ‰*
Nezumia aequalis	(rat tail fish)	-40.2 ‰*
Buccina canatea	(snail)	-32.8 ‰*
Brachyuran crabs***		-16 to -31 ‰

The lowest value measured for an individual of each species

** 132 specimens of 42 species trawled from non-seep areas of the Gulf of Mexico (avg ± SO)

***Most of these samples were identified simply as "brachyuran crab", but *Chaceon* spp. and *Rochinia crassa* were occasionally identified and are the commonly collected species at these sites.

Values for the symbiotic megafauna are selected from KENNICUTT et al. (1992) (only data from living animal tissue are included). Bacterial mat values are from SASSEN et al. (1993). Values for the heterotrophic fauna are unpublished data from R. BROOKS, C. KENNICUTT, I. MACDONALD and R. CARNEY.

Stable isotopes are equally useful to study nutritional interactions of seep fauna, although published values for heterotrophic animals from these environments are scarce. Tab. 3 present a selection of $\delta^{13}C$ values for benthic deep Gulf of Mexico fauna. Most of the benthic primary producers (chemoautotrophic and methanotrophic symbioses, and free-living bacteria) have significantly more negative values than ambient deep-sea fauna collected away from seep areas, whose tissue $\delta^{13}C$ values reflect consumption of surface-derived organics. Several species of heterotrophs are endemic to the seeps, including a shrimp, galatheid crab, orbinid polychaete, and nerite gastropod (Figs 7-8). The negative $\delta^{13}C$ values for the endemic seep fauna is expected; unlike published data from hydrothermal vent communities, however, there is a clear signal of seep organic carbon in the tissues of a variety of common vagrant fauna collected in or near seeps (Tab. 3) . The starfish *Sclerasterias* sp. (Fig. 9) is often seen both in mussel beds and climbing on tubeworms. The brachyuran crabs *Chaceon* sp. and *Rochinia crassa* (Fig. 10) are also regular visitors to both mussel beds and tube worm aggregations, as are a variety of other large decapods. The tissue $\delta^{13}C$ values of most fish collected in traps near seep sites reflect surface-derived detrital values; however, rat tails (*Nezumia aequalis*) near a large mussel bed associated with a methane-rich brine-pool (MACDONALD et al. 1990a) show a clear signal of vent-derived organics (Tab. 3). Several other species of fish such as the eels shown in Fig. 11 are locally abundant in many mussel beds and have yet to be analyzed. Each of these animals is of substantial size and mobile, and is therefore a potentially effective vehicle for the export of seep-produced organics to the surrounding deep sea.

Although insufficient data currently exists to quantify the input of seep organics to the background fauna in the Gulf of Mexico, several additional considerations suggest that it may be significant on more than a very local scale:

1. Individual communities are not distributed over point sources of hydrothermal emission, arrayed linearly along spreading centers, but instead are often diffusely distributed over square kilometers (MACDONALD et al.

Fig. 7: Gulf of Mexico seep mussels and some of the endemic fauna commonly associated with the seep communities. Numerous galatheid crabs (*Munidopsis* sp.) are visible. A single shrimp (*Alivanocaris stactophila*) is visible in the upper right hand corner of the photograph and two clumps of undescribed orbinid polychaetes can be seen near the right edge. Photo from Brine Pool NR-1 at 700 m depth in the Gulf of Mexico. Photograph by J. BLAIR. Copyright National Geographic Magazine.

Fig. 8: Extensive aggregations of orbinid polychaetes from the same site as in Fig. 7. The edge of the brine pool is visible on the bottom of this photograph. Photograph by J. BLAIR. Copyright National Geographic Magazine.

Fig. 9: The starfish, *Sclerasterias* sp., in a seep mussel bed at 700 m depth in the Gulf of Mexico. Photograph by J. BLAIR. Copyright National Geographic Magazine.


10.37
24.24
0.8.

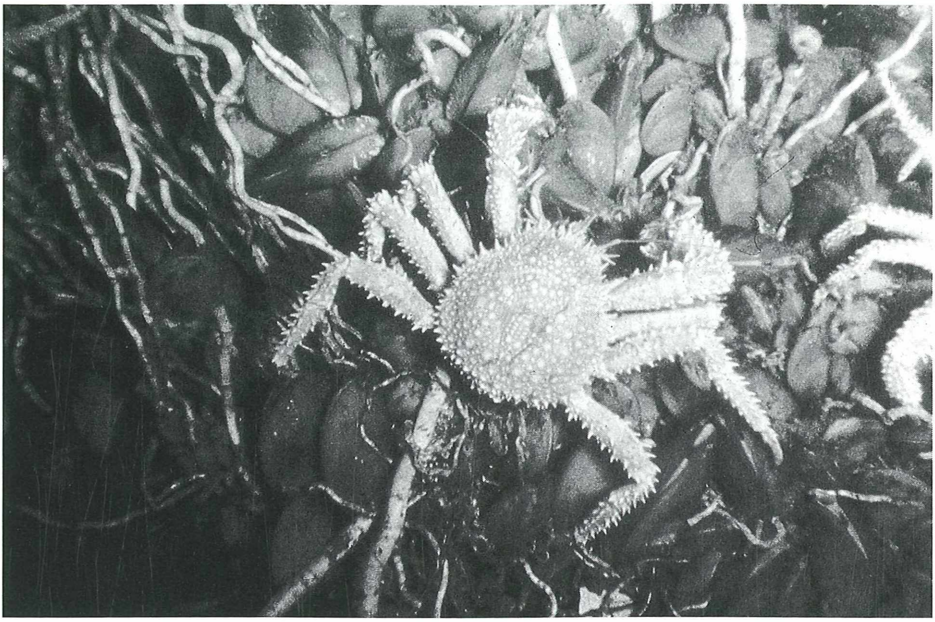

Fig. 10: The majid crab, *Rochinia crassa* in a mixed tubeworm-mussel bed at 600 m depth in the Gulf of Mexico. Photograph by C. FISHER

Fig. 11: Cutthroat eels, *Synaphobranchus* sp., among mussels at Brine Pool NR1 at 700 M depth in the Gulf of Mexico. Photograph by J. BLAIR. Copyright National Geographic Magazine.

1989). This is due to dispersion of seeping fluids passing through over a kilometer of sediment before emerging at the sea floor (COLEMAN et al. 1991).

2. Individual vestimentiferan aggregations at these seeps can cover large areas due to the same factors. Aggregations of hundreds of thousands of individuals covering hundreds of square meters are not uncommon (MACDONALD et al. 1990b, personal observation).
3. The vestimentiferans grow slowly and provide a stable and long-lived habitat for associated fauna.
4. The mussel communities in the Gulf of Mexico are extremely productive (FISHER 1993).
5. Hydrocarbon and saline seeps are distributed widely in the Gulf of Mexico. Over 42 communities have been located by trawling or visited by submersible at depths ranging from 400 to 3200 m (pers. comm. Ian MACDONALD). Using satellite imagery, persistent oil seeps have been visualized over large surface areas of the Gulf of Mexico (MACDONALD et al. 1993).
6. The seep communities seem less hostile to non-endemic fauna than most vent habitats. A variety of "normal" deep-sea fauna are often seen in and among the tube worms, mussels, and bacterial mats.

Hydrothermal vent and cold seep communities are proving to be quite widespread in the world's oceans. Due to numerous evolutionary adaptations, the chemosynthetic primary production by free-living and symbiotic bacteria in these communities can be very high and results in communities with high biomass in the often nutrient-limited deep sea. Studies to determine the routes and magnitude of transfer of this deep-sea primary production to the surrounding fauna are still in their infancy. However, data is accumulating that in at least some regions of the deep sea the impact of chemosynthetic primary production may extend well beyond the boundaries of the seep or vent communities themselves.

Acknowledgements

The authors work is supported by the US National Science Foundation, the US NOAA National Undersea Research Program. Special thanks are due to J. BROOKS, R. CARNEY, M. KENNICUTT, I. MACDONALD, K. SCOTT, and I. URCUYO for making unpublished data available to me and to the National Geographic Society and Harbor Branch Oceanographic Instituion for support of recent field work and allowing the publication of copyrighted photographs.

References

ARP, A. J., CHILDRESS, J. J., FISHER, C. R., Jr., 1984: Metabolic and blood gas transport characteristics of the hydrothermal vent bivalve, *Calyptogena magnifica*. - Physiol. Zool. **57**: 648-662.

BAUER-NEBELSICK, N-M., BARDELE, C. F., OTT, J. A., 1996: Redescription of *Zoothamnium niveum* (HEMPRICH & EHRENBERG, 1831), a ciliate with ectosymbiotic, chemoautotrophic bacteria. - Euro. J. Protozool. **32**: 18-30.

CHILDRESS, J. J., FISHER, C. R., 1992: The biology of hydrothermal vent animals: physiology, biochemistry and autotrophic symbiosis. - Oceanogr. Mar. Biol. Annu. Rev. **30**: 337-441.

COLEMAN, J. M., ROBERTS, H. H., BRYANT, W. R., 1991: Late quarternary sedimentation. - In SALVADOR, A., (Ed.): The Gulf of Mexico Basin, pp. 325-352. - Boulder, CO: Geol. Soc. Am.

DE ANGELIS, M. A., REYSENBACH, A. L., BAROSS, J. A., 1991: Surfaces of hydrothermal vent invertebrates: Sites of elevated microbial CH_4 oxidation activity. - Limnol. Oceanogr. **36**: 570-577.

DOELLER, J. E., KRAUS, D. W., COLACINO, J. M., WITTENBERG, J. B., 1988: Gill hemoglobin may deliver sulfide to bacterial symbionts of *Solemya velum* (Bivalvia, Mollusca). - Biol. Bull. Woods Hole Mass. **175**: 388-396.

FISHER, C. R., 1990: Chemoautotrophic and methanotrophic symbioses in marine invertebrates. - Rev. Aquat. Sci. **2**: 399-436.

FISHER, C. R., 1993: Oxidation of methane by deep-sea mytilids in the Gulf of Mexico. - In OREMLAND, R. S., (Ed.): Biogeochemistry of Global Change: Radiatively Active Trace Gases, pp. 606-618. - New York: Chapman & Hall Inc.

FISHER, C. R., 1995: Toward an appreciation of hydrothermal-vent animals: Their environment, physiological ecology, and tissue stable isotope values. - In HUMPHRIS, S. E., ZIERENBERG, R. A., MULLINEAUX, L. S., THOMSON, R. E., (Eds): Seafloor Hydrothermal Systems: Physical, Chemical, Biological, and Geochemical Interactions, pp. 297-316. - AGU Monographs Series.

FISHER, C. R., CHILDRESS, J. J., ARP, A. J., BROOKS, J. M., DISTEL, D., FAVUZZI, J. A., FELBECK, H., HESSLER, R., JOHNSON, K. S., KENNICUTT, M. C., II, MACKO, S. A., NEWTON, A., POWELL, M. A., SOMERO, G. N., SOTO, T., 1988: Microhabitat variation in the hydrothermal vent mussel *Bathymodiolus thermophilus*, at Rose Garden vent on the Galapagos rift. - Deep-Sea Res. **35**: 1769-1792.

FISHER, C. R., CHILDRESS, J. J., BROOKS, J. M., MACKO, S. A., 1994: Nutritional interactions in Galapagos Rift hydrothermal vent communities: inferences from stable carbon and nitrogen isotope analyses. - Mar. Ecol. Prog. Ser. **103**: 45-55.

FOSSING, H., GALLARDO, V. A., JØRGENSEN, B. B., HÜTTEL, M., NIELSEN, L. P., SCHULZ, H., CANFIELD, D. E., FORSTER, S., GLUD, R. N., GUNDERSEN, J. K., KÜVER, J., RAMSING, N.B., TESKE, A., THAMDRUP, B., ULLOA, O., 1995: Concentration and transport of nitrate by the mat-forming sulphur bacterium *Thioploca*. -Nature **374**: 713-715.

GAILL, F., DESBRUYÉRES, D., PRIEUR, D., 1987: Bacterial communities associated with the "Pompeii worms" from the East Pacific rise hydrothermal vents: SEM, TEM observations. - Microb. Ecol. **13**: 129-139.

GIERE, O., 1981: The gutless marine oligochaete *Phallodrilus leukodermatus*. Structural studies on an aberrant tubificid associated with bacteria. - Mar. Ecol. Prog. Ser. **5**: 353-357.

GIERE, O., CONWAY, N. M., GASTROCK, G., SCHMIDT, C., 1991: "Regulation" of gutless annelid ecology by endosymbiotic bacteria. - Mar. Ecol. Prog. Ser. **68**: 287-299.

GUNDERSEN, J. K., JØRGENSEN, B. B., LARSEN, E., JANNASCH, H. W., 1992: Mats of giant sulphur bacteria on deep-sea sediments due to fluctuating hydrothermal flow. - Nature **360**: 454-456.

JOHNSON, K. S., CHILDRESS, J. J., HESSLER, R. R., SAKAMOTO-ARNOLD, C. M., BEEHLER, C. L., 1988: Chemical and biological interactions in the Rose Garden hydrothermal vent field. - Deep-Sea Res. **35**: 1723-1744.

JØRGENSEN, B. B., REVSBECH, N. P., 1983: Colorless sulfur bacteria. *Beggiatoa* sp. and *Thiovulum* sp. in O_2 and H_2S microgradients. Appl. Environ. Microbiol. **45**: 1261-1270.

KENNICUTT, M. C. II. Jr., BURKE, R. A. Jr., 1995. Stable isotopes: clues to biological cycling of elements at hydrothermal vents. - In KARL, D. M., (Ed.): Microbiology of Deep-Sea Hydrothermal Vents, pp. 275-287. -Boca Raton: CRC Pr.

KENNICUTT, M. C. II., BURKE, R. A. Jr., MACDONALD, I. R., BROOKS, J. M., DENOUX, G. J., MACKO, S. A., 1992: Stable isotope partitioning in seep and vent organisms: chemical and ecological significance. - Chem. Geol. **101**: 293-310.

LUTZ, R. A., SHANK, T. M., FORNARI, D. J., HAYMON, R. M., LILLEY, M. D., VON DAMM, K. L., DESBRUYERES, D., 1994: Rapid growth at deep-sea vents. - Nature **371**: 663-664.

MACDONALD, I. R., BOLAND, G. S., BAKER, J. S., BROOKS, J. M., KENNICUTT, M. C. II, BIDIGARE, R. R., 1989: Gulf of Mexico hydrocarbon seep communities. II. Spatial distribution of seep organisms and hydrocarbons at Bush Hill. - Mar. Biol. **101**: 235-247.

MACDONALD, I. R., REILLY, J. F. I., GUINASSO, N. L. J., BROOKS, J. M., CARNEY, R. C., BRYANT, W. A., BRIGHT, T. J., 1990a: Chemosynthetic mussels at a brine-filled pockmark in the northern Gulf of Mexico. - Science **248**: 1096-1099.

MACDONALD, I. R., GUINASSO, N. L., ACKLESON, S. G., AMOS, J. F., DUCKWORTH, R., SASSEN, R., BROOKS, J.M., 1993: Natural oil slicks in the Gulf of Mexico visible from space. - J. Geophys. Res. **98**: 16351-16364.

MACDONALD, I. R., GUINASSO, N. L., REILLY, J. F., BROOKS, J. M., CALLENDER, W. R., GABRIELLE, S. G., 1990b: Gulf of Mexico hydrocarbon seep communities: VI. patterns in community structure and habitat. - Geo-Marine Lett. **10**: 244-252.

MACKO, S. A., FOGEL, M. L., HARE, P. E., HOERING, T. C., 1987: Isotopic fractionation of nitrogen and carbon in the synthesis of amino acids by microorganisms. - Chem. Geol. (Isot. Geosci. Sec.) **65**: 79-82.

MEYERS, M. B., FOSSING, H., POWELL, E. N., 1987: Microdistribution of interstitial meiofauna, oxygen and sulfide gradients, and the tubes of macro-infauna. - Mar. Ecol. Prog. Ser. **35**: 223-241.

NELSON, D. C., FISHER, C. R., 1995: Chemoautotrophic and methanotrophic endosymbiotic bacteria at vents and seeps. - In KARL, D. M., (Ed.): Microbiology of Deep-Sea Hydrothermal Vents, pp. 125-167. -Boca Raton: CRC Pr.

NELSON, D. C., JANNASCH, H. W., 1983: Chemoautotrophic growth of a marine *Beggiatoa* in sulfide-gradient cultures. - Arch. Microbiol. **136**: 262-269.

NELSON, D. C., JØRGENSEN, B. B., REVSBECH, N. P., 1986: Growth pattern and yield of a chemoautotrophic *Beggiatoa* sp. in oxygen-sulfide microgradients. - Appl. Environ. Microbiol. **52**: 225-233.

NIX, E. R., FISHER, C. R., VODENICHAR, J., SCOTT, K. M., 1995: Physiological ecology of a mussel with methanotrophic endosymbionts at three hydrocarbon seep sites in the Gulf of Mexico. - Mar. Biol. **122**: 605-617.

OESCHGER, R., SCHMALJOHANN, R., 1988: Association of various types of epibacteria with *Halicryptus spinulosus* (Priapulida). - Mar. Ecol. Prog. Ser. **48**: 285-293.

OTT, J., RIEGER, G., RIEGER, R., ENDERES, F., 1982: New mouthless interstitial worms from the sulfide system: Symbiosis with prokaryotes. - P.S.Z.N.I.: Marine Ecology **3**: 313-333.

OTT, J. A., NOVAK, R., SCHIEMER, F., HENTSCHEL, U., NEBELSICK, M., POLZ, M., 1991: Tackling the sulfide gradient: A novel strategy involving marine nematodes and chemoautotrophic ectosymbionts. - P.S.Z.N.I: Marine Ecology **12**: 261-279.

REID, R. G. B., BRAND, D. G., 1986: Sulfide-oxidizing symbiosis in Lucinaceans: implications for bivalve evolution. - Veliger **29**: 3-24.

SASSEN, R., ROBERTS, H. H., AHARON, P., LARKIN, J., CHINN, E. W., CARNEY, R., 1993: Chemosynthetic bacterial mats at cold hydrocarbon seeps, Gulf of Mexico continental slope. - Org. Geochem. **20**: 77-89.

SCHIEMER, F., NOVAK, R., OTT, J., 1990: Metabolic studies on thiobiotic free-living nematodes and their symbiotic microorganisms. - Mar. Biol. **106**: 129-137.

SIMPKINS, M. A., 1994: Hydrocarbon seep vestimentiferans: growth and condition in a variable environment. - M.Sc. Thesis Pennsylvania State Univ.

SCOTT, K. M., FISHER, C. R., 1995: Physiological ecology of sulfide metabolism in hydrothermal vent and cold seep vesicomyid clams and vestimentiferan tube worms. -Am. Zool. **35**: 102-111.

SOMERO, G. N., ANDERSON, A. E., CHILDRESS, J. J., 1989: Transport, metabolism and detoxification of hydrogen sulfide in animals from sulfide-rich marine environments. - Rev. Aquat. Sci. **1**: 591-614.

SOUTHWARD, E. C., 1982: Bacterial symbionts in pogonophora. - J. Mar. Biol. Ass. U.K. **62**: 889-906.

TEMARA, A., RIDDER, C. D., KUENEN, J. G., ROBERTSON, L. A., 1993: Sulfide-oxidizing bacteria in the burrowing echinoid, *Echinocardium cordatum* (Echinodermata). - Mar. Biol. **115**: 179-185.

TUNNICLIFFE, V., 1988: Biogeography and evolution of hydrothermal-vent fauna in the eastern Pacific Ocean. - Proc. R. Soc. London, Ser. B **233**: 347-366.

TUNNICLIFFE, V., FONTAIN, A. R., 1987: Faunal composition and organic surface encrustations at hydrothermal vents on the southern Juan de Fuca Ridge. - J. Geophys. Res. **92**: 11303-11314.

VACELET, J., BOURY-ESNAULT, N., FIALA-MEDIONI, A., FISHER, C. R., 1995: A methanotrophic carnivorous sponge. - Nature **377**: 296.

VAN DOVER, C. L., 1995: Ecology of Mid-Atlantic Ridge hydrothermal vents. - In PARSON, L. M., WALKER, C L., DIXON, D. R., (Eds.): Hydrothermal Vents and Processes. - Geol. Soc. Spec. Publ. **87**: 257-294.

VAN DOVER, C. L., FRY, B., 1994: Microorganisms as food resources at deep-sea hydrothermal vents. - Limnol. Oceanogr. **39**: 51-57.

Address of the author:

Charles R. FISHER, Department of Biology, The Pennsylvania State University, University Park, PA, 16802 - USA.
e-mail: cfisher@psu.edu

Zeitschrift/Journal: Biosystematics and Ecology

Jahr/Year: 1996

Band/Volume: 11

Autor(en)/Author(s): Fisher Charles

Artikel/Article: IV. Unusual energy sources. Ecophysiology of primary production at deep-sea vents and seeps. 313-336