Marine ecosystems based on chemoautotrophic and methylotrophic bacteria as possible refuge for living fossils

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ABSTRACT. *Marine ecosystems based on chemosynthesis are widely distributed in suitable areas with an abundance of reduced compounds. They are based on a strange symbiosis between chemoautotrophic (less often methylotrophic) bacteria and some invertebrates. Two basic types of these ecosystems exist: "hydrothermal" in the sites of hydrothermal venting and "cold seep" on various seeps with sufficient acceptable compounds. In the present review, their faunal composition, trophic organization and evolution are briefly discussed. The unusually high number of living fossils at hydrothermal ecosystems indicates the long evolutionary history and protective functions of these ecosystems. Some living fossils even underwent adaptive radiation. On the contrary, some groups of marine invertebrates could not settle vents due to their biological constraints.*

KEYWORDS: *marine ecosystems, hydrothermal vent, chemoautotrophy, methylotrophy, living fossils.*

Characterization and occurrence of ecosystems based on chemosynthesis

The geological research of deep-sea hydrothermal vents along the sea-floor spreading centers led to the surprising discovery of dense animal communities on the rocks in the venting sites on the Galapagos Rift (Lonsdale 1977, Weiss et al. 1977, Corliss et al. 1979) and East Pacific Rise (Desbruyères et al. 1982). Primary producers of this ecosystems are represented by free-living bacteria and symbiotic chemoautotrophic (less often methylotrophic) bacteria with strange giant obturate pogonophores and bivalves (Desbruyères and Laubier 1983, Grassle 1985). Symbiotic bacteria use energy of some reduced compounds emanating from vents (especially H_2S, CH_4) for chemosynthesis (Felbeck and Childress 1988). Bacteria and their hosts produce biomass for higher trophic levels that included especially detritovores, carnivores and also some parasites and symbionts (Laubier 1986).

The giant obturate pogonophore (= Vestimentifera) *Riftia pachyptila* is gutless. Its third body segment (gonomere) contains special voluminous tissue (trophosome) with sulfur bacteria (Jones 1981). *Riftia* supplies symbionts by H_2S, CO_2 and O_2 (Felbeck 1981). Other obturate and perviate (= "classical") pogonophores are also gutless, with symbiotic bacteria (Southward 1987). The exotic phylum Pogonophora is not widely known (for Czech review see Král et al. 1993).

The giant bivalve *Calyptogena magnifica* (Septibranchia, Vesicomyidae) possesses a functionless alimentary tract and its sulfur endosymbionts occupy specific regions of the gills (Fiala-Medioni and Metivier 1986). The mixotrophic bivalve *Bathymodiolus thermophilus* (Mytilidae) has a functional, but simplified alimentary tract. Sulfur endosymbionts live also in its gills (Le Pennec and Hily 1984).

In the higher trophic levels of hydrothermal community, various Mollusca predominate (Bivalvia, Gastropoda and Aplacophora), Polychaeta, Crustacea (Cirripedia and Malacostraca), Enteropneusta, siphonophores (Coelenterata) from the family Rhodaliidae and fishes (see Laubier 1986, 1989 for details).

Extremely thermophilous terebellomorph polychaetes of the genus *Alvinella* ("Pompeii worms") (Alvinellidae) inhabit the hottest zone of the hydrothermal community where anoxic hydrothermal fluid with sulfides is mixed with seawater (Desbruyères et al. 1982, Chevaldonné and Jollivet 1993, Jollivet et al. 1995). These worms exhibit peculiar development, reproductive behavior with pseudocopulation (Zal et al. 1995) and peculiar nutrition that is, they "cultivate" various morphological types of bacteria in an intersegmentary space, on parapodia, on special emergences of cuticle and on the inner surface of their tube (Desbruyères and Laubier 1980, Desbruyères et al. 1985, Alayse-Danet et al. 1987). Other polychaetes include detritophages, some carnivores and even commensals of the

mussel *Bathymodiolus* (*Branchipolynoe symmytilida*) (Desbruyères et al. 1985). Brachyuran crabs of the family Bythograeidae nip off pieces of individuals at colonies of Vestimentifera (*Bythograea thermydron*) or "Pompeii worms" (*Cyanagraea praedator*) (Williams 1980, Laubier 1986). Most species of anomuran decapods of the family Galatheidae live also on sea bottom in the neighborhood of hydrotherms and are so considered as "facultative hydrothermal" only (Fustec et al. 1987). Ectoparasitic copepods of the family Dirivultidae (Siphonostomatoida) live on the tentacular crowns of the Vestimentifera (Humes and Dojiri 1980).

Subsequent expeditions documented the occurrence of similar hydrothermal ecosystems at other regions of the Pacific and Atlantic oceans:

(1) axial seamount of the Juan de Fuca Ridge (depth 1570 m) (Tunnicliffe et al. 1985) and Explorer Ridge (Tunnicliffe et al. 1986)

(2) Guaymas basin in the Gulf of California (2000 m) (Grassle 1982)

(3) spreading axes of the Fiji, Lau, Manus and Mariana Back-Arc Basins (1700 – 3800 m) (Jollivet et al. 1989; Nautilau group 1990; Both 1986, Galchenko 1995; Hessler et al. 1987, Desbruyères and Laubier 1989)

(4) Mid-Atlantic Ridge (3600 – 3800 m) (Williams and Rona 1986)

It is evident that hydrothermal communities occur on active oceanic ridges, and in back-arc basins where oceanic crust is extending (Laubier 1989). These communities can occupy even hydrothermal vents on the slopes of active axial volcanoes at some regions (Craig et al. 1987). The Guaymas Basin is exceptional because in this case hydrothermal fluid percolates up through a thick sequence of hemipelagic sediments (Lonsdale et al. 1980, Simoneit and Lonsdale 1982). The observed differences in species composition are caused mainly by different ages of hydrothermal vents (Fustec et al. 1987), different hydrostatic pressure (Laubier 1989), temperature and chemical composition of hydrothermal fluid (Laubier 1986), and major distances and geographical barriers (Denis et al. 1993).

Recent discoveries established great differences in composition of hydrothermal communities in some distant geographical areas. Primary consumers in hydrothermal communities of the West Pacific Back-Arc Basins are radically different from those of the Eastern Pacific (Denis et al. 1993). The primary biomass of these Western Pacific communities is dominated by great mixotrophic

mesogastropods of the genera *Alviniconcha, Ifremeria* and *Olgaconcha* (Denis et al. 1993, Stein et al. 1988, Bouchet and Warén 1991, Galchenko 1995); the obturate pogonophores and mussel *Bathymodiolus* are less abundant, and the mussel *Calyptogena* is missing (Laubier 1993). Some tissues of snails *Alviniconcha* (beds of mantle) and *Olgaconcha* (gill) contain sulfur and methylotrophic bacteria (Stein et al. 1988, Galchenko 1995). The Mid-Atlantic Ridge hydrothermal community seems to be different also from "classical" East Pacific type. Decapods *Alvinocaris, Chorocaris* and *Rimicaris* (Bresiliidae), *Segonzacia mesatlantica* (Bythograeidae), *Munidopsis sp.* (Galatheidae) and some polychaetes prevail in this simple assemblage; obturate pogonophores and bivalves are missing (Williams and Rona 1986, Segonzac et al. 1994). Bresiliids, which consume mats of the bacteria on the bottom, form the key link of the food web here. Lastly, some differences are also obvious between communities of the northern and southern part of East Pacific (different families of Vestimentifera, sister species in some groups). The present explanation rests on subduction of the Farallon plate below the North American plate, resulting in rather recent separation of the northern and the southern East Pacific ridges 35 million years ago (Tunnicliffe 1988).

The hydrothermal vent environment is highly unstable and harsh for life (Moraga et al. 1994). The hydrothermal vent continues its activity for only 20 – 100 years, chemical composition of fluid can also vary considerably (Lalou et al. 1985). This apparent instability is connected with variations in convection of magmatic heat and tectonic activity (Fustec et al. 1987, Tunnicliffe 1988, 1991). Therefore, hydrothermal assemblages have only ephemeral life and their populations can be at genetic disequilibrium due to extinctions (Jollivet et al. 1995). Moreover, hydrothermal vent fauna can be stressed by high temperature (Chevaldonné et al. 1991, 1992), natural radioactivity (Cherry et al. 1992), hypoxia and colossal concentrations of sulfide, ammonia and some heavy metals (Johnson et al. 1988, Edmond et al. 1982, Michard et al. 1984, Jollivet et al. 1995). This unfavourable environment is very selective and gave rise to a special adaptations (see Felbeck and Childress 1988, Laubier 1988, Jollivet et al. 1995 for details). Numerous adaptations and rich sources of chemical energy cause high rates of metabolism, rapid growth, continuous reproduction and good dispersal ability among hydrothermal species (Grassle 1984, Laubier 1989, Lutz et al. 1984).

According to proposed models (Hessler and Smithey 1983, Fustec et al. 1988), primary consumers form 75%– 90% of the biomass at hydrothermal communities. Biomass of suspension feeders exceeds that of deposit feeders considerably. The high biomass of the hydrothermal communities ($10 - 70$ kg/m^{-2} fresh weight) is comparable to shallow-water ecosystems with the highest production of biomass (coral reefs, for example) (Laubier 1989).

Rich benthic fauna based on symbiotic chemoautotrophic and methylotrophic bacteria was found later also at other environments with numerous acceptable compounds (H_2S, CH_4, ethylene, NH_4, CO_2) on passive or active sea margin areas:

(1) cold water seeps on accretionary prisms of the subduction system near Oregon (depth 2000 m) (Suess et al. 1985, Kulm et al. 1986), Barbados (Jollivet et al. 1990). Three different communities (700 – 900, 3000 – 3500, 5800 – 6000 m) have been studied on water seeps of the Japanese subduction system (Okutani and Egawa 1985, Ohta and Laubier 1987)

(2) cold water brine seep at the base of the limestones of Florida Escarpment, Gulf of Mexico (3260 m) (Cary et al. 1989)

(3) ephemeral cold water seeps at disturbances of unhardened sediments on the continental slope, Newfoundland (Laubier 1986)

(4) hydrocarbon (= petroleum) seeps on the Louisiana Slope, Gulf of Mexico (600 – 700 m) (Kennicutt et al. 1985), off the California coast (Spies et al. 1980) and at Sea of Okhotsk (Galchenko 1995)

The so-called "cold seep communities" enumerated above display fauna similar to the hydrothermal assemblage, but seem to be less diverse (Laubier 1989, 1993). The Vestimentifera and bivalves of the genus *Calyptogena* represent the primary producers. Dominant bacterial symbionts of bivalves from hydrocarbon seeps and some types of cold seeps are methylotrophic bacteria which oxidize CH_4 (Childress et al. 1986, Kulm et al. 1986, Galchenko 1995). Carbon dioxide produced here is exploited by methanogenic bacteria living in the sediment below oxygen/sulfide boundary. The rest of this gas is the carbon source for the authigenic carbonates that cement the sediment and form crusts and deep-sea stromatolites above seeps (Kulm et al. 1986, Lein et al. in Galchenko 1995).

Different type of chemosynthetically-based communities (Laubier 1989) represents simple food webs formed by bacterial mats and their consumers only. This type was found at some sea areas with sulfide of biological or geothermal origin, lakes and even in some caves (Stein 1984).

Nevertheless, the chemosynthetically-based ecosystems would occupy a wider area. Vestimentifera and/or bivalves with symbiotic bacteria are able to found simple analogies of the cold seep communities at shipwrecks (Dando et al. 1992) or on the dead body of whales (Laubier 1993). Perviate pogonophores occupy extensive areas on cold sea bottom, especially in the deep sea. This group lead a solitary, sessile life, buried in sediments (Ivanov 1963). Animals with symbiotic chemosynthetic bacteria can constitute a part of the benthos and meiofauna at ecosystems with high organic sedimentation based on photosynthesis (mangroves, for example) where this fauna employs accumulations of simple reduced compounds. Such species have been discovered among gutless tubificid oligochaetes (Giere 1981), gutless polychaetes of the genus *Astomus* (Jouin 1978), gutless bivalves of the family Solemyidae (Reid and Bernard 1980, Felbeck 1983), bivalves of the families Lucinidae and Thyasiridae (Schweimanns and Felbeck 1985, Reid and Brand 1986, Southward 1986), acoel turbellarians (Fox and Powell 1987), gnathostomulids (Powell and Bright 1981) and nematodes (Polz et al. 1992). Hence, our knowledge of the number of ecosystems which are based on chemosynthesis will increase probably dramatically.

Remarks to the evolution of marine ecosystems based on chemosynthesis

All ecosystems based on chemosynthesis are noted for high levels of energetic isolation. Reduced compounds for "cold seep communities" and similar assemblages arise still partially by bacterial conversion of organic material from ecosystems based on photosynthesis (Cary et al. 1989). The hydrothermal vent ecosystem exploits the compounds of geothermal origin and thus appears to be

the most isolated ecosystem on the earth. Clearly, this isolation cannot be absolute. Other ecosystems supply the hydrothermal community with oxygen, for example (Southward et al. 1994).

The environment of hydrothermal vents seems to be a likely candidate for the origin of life (Baross and Hoffman 1985) and its macrofauna may be of very ancient origin. On the contrary, cold seeps can be rather recent environments that must be supplied by preexisting organic material (Laubier 1989).

The hydrothermal and cold seep fauna exhibit rather low diversity (Grassle 1985), but 95% of described species are endemic and restricted to these areas (Laubier 1993). Phyllum Pogonophora represents an enigmatic group that is often related to the Upper Proterozoic and Cambrian enigmatic group Sabellitida. Unusual body construction supports assumptions about origin of Pogonophora during explosive radiation of animal kingdom during Upper Proterozoic and Lower Cambrian (Král et al. 1993). However, a large proportion of the recent hydrothermal vent fauna may be of Mesozoic age (Tunnicliffe 1992). Some of the endemic species belong to genera with many species from deep sea environments (*Munidopsis*) and are probably Cenozoic immigrants (Newman 1985, Laubier 1993).

Unfortunately, we have available only a few records of fossils in hydrothermal vent deposits. Several types of tube structures (some reminiscent of those of Vestimentifera and *Alvinella* species) have been described from massive sulfides of two Cretaceous localities: Samail ophiolite, Oman (Haymon and Koski 1985) and Troodos ophiolite, Cyprus (Oudin and Constantinou 1984). Well-preserved Middle Devonian fauna of the Sibai ophiolite complex (south Ural) also have a "modern" character. This community is dominated by tubes of the Vestimentifera, vesicomyid bivalves and tubes similar to those of "Pompeii" worms (Kuznetsov et al. 1991). On the contrary, Carboniferous tube fossils from Tynagh (Ireland) are morphologically different from Devonian and Cretaceous tube forms from hydrothermal deposits (Banks 1985). Sediments of the Tynagh strata arose in relatively shallow basin and contain Pb-Zn deposits that were precipitated from hot hydrothermal fluid percolating through the carbonate mud (like Guaymas Basin).

It would be noteworthy to start sedimentological research at recent hydrothermal vents and cold seep areas and to find fossil analogues of their sediments (Malahoff 1982). Systematic search for fossils of these deposits is also needed to explain the evolution of unusual hydrothermal and seep ecosystems.

A remarkably large number of living fossils have been described from hydrothermal vent ecosystems. Most of these animals occupy positions at higher trophic levels of the hydrothermal community.

The slight bivalve *Bathypecten vulcani* (Pectinidae) was found on Galapagos Rift and East Pacific Rise. This primitive pectinid mussel is probably related to the ancestors of related families Propeamussiidae and Pectinidae. These families separated during Triassic period (Fatton 1985). Bivalves of the family Vesicomyidae and bivalve *Bathymodiolus thermophilus* are also Paleozoic or Early Mesozoic relicts (Kuznetsov et al. 1991, Newman 1985). Cirripedians of the genera *Neolepas*, *Eochionelasmus*, *Scillaelepas* and *Verruca* are descendants of Jurassic and Cretaceous lineages of this group (Newman 1979, Laubier 1993). The Galapagos rift limpet *Neomphalus fretterae* and some related archaeogastropods are probably descendants of the superfamily Euomphalacea. This species-rich group underwent a major radiation in the Paleozoic and became extinct during the Cretaceous Period. Shells of *Neomphalus* reach 30 mm in diameter and are cap-shaped with a horizontally lying initial coil (McLean 1981). Unusual bipectinate gill is modified for filter feeding. *Neomphalus* is a sedentary form, associated with groups of *Riftia pachyptila* (McLean 1981).

New immigrants to hydrothermal ecosystems had to evolve adaptations for life in a specific harsh environment. Species from tropical shelves came to hydrothermal vents probably along active ridges (Newman 1979). Deep-sea immigrants could conform to hydrothermal activity at similar environment of cold seeps. Up till now, we do not have any description of living fossils from this place. Cold seeps probably do not represent environments suitable for long-term survival of living fossils.

Highly isolated ecosystems of hydrothermal vents could offer a rich source of food, warm water for thermophilic tropical species during periods of decreasing temperature of sea water, protection from ultraviolet irradiation, meteoritic impacts and an absence of some predators (McLean 1981, Laubier 1989). Some groups of living fossils (Cirripedia, Archaeogastropoda) even went through successful adaptive radiations.

Compared with usual rock substrates of deep-sea environments, absence (or scarcity) of some major groups (corals, sponges, bryozoa, echinoderms, peracarids) at hydrothermal communities is apparent (Grassle 1985, Laubier 1989). Potential immigrants from these groups have a lesser chance to settle the hydrothermal environments due to their biological constraints.

Acknowledgements

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