Geologic-Geochemical and Ecological Characteristics of Selected Hydrothermal Areas

Sergey V. Galkin and Liudmila L. Demina

Abstract In this paper we consider geologic-geochemical and ecological characteristics of the areas where the material for biogeochemical study (Demina, Trace metals in water in the hydrothermal biotope. Hdb Env Chem. doi:10.1007/698_2016_1; Demina, Galkin, Factors controlling the trace metal distribution in hydrothermal vent. Hdb Env Chem. doi:10.1007/698_2016_5) has been collected. In the Atlantic Ocean five hydrothermal areas (Menez Gwen, Rainbow, Lost City, Broken Spur, and Snake Pit) have been investigated. In the Pacific Ocean the 9°50′N vent area at the East Pacific Rise and hydrothermal manifestations in Guaymas Basin (Gulf of California) were studied. Observations and sampling were provided in 1996–2005 during numerous cruises of RV "Akademik Mstislav Keldysh" using deep-sea manned submersibles "Mir." Explored vent areas exhibit a wide range of environmental conditions, including great variation in depth (particularly on the MAR), associated physical parameters, and different geologic setting and underlying rocks. Faunal communities also vary greatly in taxonomic composition and spatial structure. Short characteristic of abiotic environment and structure of benthic communities is given for each explored area. With all the variety of hydrothermal manifestations, in the spatial structure of communities a number of general patterns can be revealed. At the analysis of bioaccumulation function of vent organisms in the case of each area particular habitat conditions and characteristics of spatial structure of communities (microdistribution of animal's populations, their association with a specific temperature zone and a particular type of substrate) must be taken into account.

Keywords Abiotic environment, East Pacific Rise, Guaymas Basin, Hydrothermal vents, Microdistribution, Mid-Atlantic Ridge, Taxonomic composition

S.V. Galkin (✉) and L.L. Demina
P.P. Shirshov Institute of Oceanology Russian Academy of Sciences (IORAN), Nakhimovsky pr., 36, 117997 Moscow, Russia
e-mail: galkin@ocean.ru; l_demina@mail.ru

L.L. Demina, S.V. Galkin (eds.), *Trace Metal Biogeochemistry and Ecology of Deep-Sea Hydrothermal Vent Systems*, Hdb Env Chem (2016) 50: 25–52,
DOI 10.1007/698_2016_3, © Springer International Publishing Switzerland 2016,
Published online: 30 April 2016

Contents

1 Introduction 26
2 Mid-Atlantic Ridge (MAR) 27
2.1 Menez Gwen 27
2.2 Rainbow 30
2.3 Lost City 32
2.4 Broken Spur 35
2.5 Snake Pit 38
3 East Pacific Rise (EPR) 42
3.1 9°50′N EPR 42
4 Guaymas Basin 45
4.1 Abiotic Environment 45
4.2 Taxonomic Composition and Spatial Structure of Community 46
5 Concluding Remarks 47
References 49

1 Introduction

The vent zone is the most chemically and spatially heterogeneous environment of a hydrothermal field.

In the hydrothermal ecosystem there is a strong relationship between abiotic and biotic components. Bottom fauna is able to influence the basic chemical environmental parameters: aggregated settlement of hydrothermal fauna, in particular symbiotrophic mussels and shrimps, redistribute chemical components of habitat, consuming from water hydrogen sulfide, sulfide ion, nitrates, and nitrites, followed by excreting ammonium ion and dissolved organic carbon into the water of biotope [1]

Obviously, at the analysis of bioaccumulation function of vent organisms in the case of each area particular habitat conditions and characteristics of spatial structure of communities (microdistribution of animal's populations, their association with a specific temperature zone and a particular type of substrate) must be taken into account.

Hydrothermal vent areas exhibit a wide range of environmental conditions, including great variation in depth (particularly on the MAR), associated physical parameters, and different geologic setting and underlying rocks. All these factors together with geographical distance determine taxonomic composition and spatial structure of associated vent communities.

In this chapter we consider geologic-geochemical and ecological characteristics of the areas where the material for our biogeochemical study [2, 3] has been collected (Table 1). Principal geologic-geochemical characteristics describe abiotic environment. Ecological characteristics include mean by taxonomic composition and spatial structure of hydrothermal vent communities. In all cases concentrations of metals in water over the fauna habitats are much higher than in the reference ocean water where trace metal concentrations are to 3 orders of magnitude less for Fe, Co, and Pb in comparison with biotope water [4]. All underwater deep-sea

Table 1 Basic characteristics of selected deep-sea hydrothermal vent areas

Vent Area	Locality	Maximal depth (m)	Fluid maximal temperature (°C)	pH of fluids
Menez Gwen	37°51′N, 30°31′W	875	284	4.2–4.8
Rainbow	36°14′N, 33°54′W	2,350	365	2.8–3.1
Lost City	30°15′N, 42°24′W	900	90	9–11
Broken Spur	29°10′N, 43°10′W	3,875	364	2.9–3.2
Snake Pit	23°22′N, 43°10′W	3,480	356	3.0–3.3
9°50′N EPR	9°48–51′N, 104°17′W	2,580	300	3.0–3.4
Guaymas Basin	27°00′N, 111°24′W	2,050	315	5.4

images of hydrothermal landscapes used in present paper were taken in situ with submersibles "Mir" cameras.

2 Mid-Atlantic Ridge (MAR)

By now, at MAR at least 10 hydrothermal areas to the north equator are more or less studied. The most areas are located between 37°N and 12°N. The depth of areas generally increases from north to south from 850 m (Menez Gwen) to 4,100 m (Ashadze). The investigations of hydrothermal vents at southern part of MAR were initiated relatively recently. Now several areas between 4°N and 10°S have been described [5].

In the present chapter we consider five hydrothermal areas at the MAR: Menez Gwen, Rainbow, Lost City, Broken Spur, and Snake Pit.

2.1 Menez Gwen

Locality: 37°51′N; 31°31′W. Depth: 840–875 m.

2.1.1 Abiotic Environment

Menez Gwen is the active, shallowest, and youngest (with an age less than 100 years) of all the fields of the MAR [6]. It is located on a volcanic segment, small chimneys (less than 5 m height) grow on the fresh pillows and are mainly composed of white anhydrite [1, 7]. The active area occupies approximately 200 m^2. Vent field is situated near the base of volcano and associated with axial magma chambers. Fluid temperature ranges from 8°C to 30°C [8]. Diffuse low-temperature hydrothermal vents dominate over focused ones, the black smokers are rare and there are no plumes. Rather low values of temperature and hydrostatic pressure determine relative lower (compared with other MAR vent areas) salinity of hydrothermal fluids [9]. The concentration of metals generally correlated with the salinity. Therefore, we anticipate lower concentrations of heavy metals in Menez Gwen fluids compared with other fields. Menez Gwen hydrothermal fluids ($pH > 4$) are enriched in gas (mainly CO_2 (75 %) and H_2S (10–20 %) [1]).

A characteristic feature of the landscape at Menez-Gwen is the presence of unconsolidated hydrothermal deposits of light gray, white or dark gray in most parts of the field. The most common type of fluid discharge within the area is the temperature diffuse flow through the sediments. Diffuse outflows run temperature of 10–40°C, pH 4.2–4.8. Emergence of relatively hot transparent fluid occurs at low (up to 0.5 m) edifices. The maximal recorded temperature of the fluid amounts up 284°C. The predominate substrates for the fauna are basaltic lavas, as well as white chimneys, consisting of anhydrite and barite. Fluids at Menez-Gwen are characterized by a number of features distinct from the fluids deep-water areas. It is connected with the process of subsurface phase separation [9–11]. Fluids at Menez Gwen showed low chlorinity, low salinity, low content of H_2S, low concentration of metals and silicon, the enrichment by gases and a high content of methane.

2.1.2 Taxonomic Composition and Spatial Structure of Community

Compared to communities of deeper areas, Menez-Gwen faunal community is impoverished in both abundance and diversity of vent fauna. Predominant macrofaunal group within the active zone of the field are mussels *Bathymodiolus azoricus* (Fig. 1). Population of the living mytilids seems quite small. The dimensions of continuous clusters never exceed a few tens of centimeters in diameter. According to [8], this may be due to a deficit of hard substrate appropriate for colonization by mytilids. Significant accumulations of large bivalves were observed on the ledges of solid rock, in the immediate vicinity of the most intensive vents, often in the shimmering water. Compared with other MAR vent areas, Menez Gwen characterized by very sparse population of the commensal polychaete *Branchipolynoe seepensis*. This peculiarity was mentioned by many authors [1].

From among bresilioid shrimps only *Mirocaris fortunata* has been recorded (in the initial version *Chorocaris* sp.), which also do not form clusters. Characteristic for deeper areas *Rimicaris exoculata* as well as carnivorous *Segonzacia mesatlantica* and *Phymorhynchus* are absent.

The most numerous forms within the hydrothermal community are limpets (*Lepetodrilus atlanticus*, *Protolyra thorvaldsoni* and *P. valvatoides*). These small (<0.5 cm) animals form aggregations on the surface of the mytilid shells, as well as on any hard substrate, including basalts. The density of their settlements reaches tens ind./dm^2. In these clusters other limpet species (in particular, *Shinkailepas briandi*) were recorded, but in single specimens. As the predominant form in the

Fig. 1 Menez Gwen hydrothermal area, Flores site. Depth 885 m. Settlement of mussels *Bathymodiolus azoricus*

inactive areas of the field the bresilioid shrimps *Mirocaris fortunata* and *Chorocaris chacei* were indicated in a number of papers (see, for example, [1]). However, during our observations, the first of these species was met only once, and the second was not marked at all, just as carnivorous crabs *Segonzacia mesatlantica*. The most notable carnivorous form within hydrothermal field was large geryonid crab *Chaceon affinis* (their number on the field at the moment of our observation was not less than 5).

The periphery of hydrothermal field is almost devoid of sedimentary cover. Background community is rather sparse. Dominating macrofauna is presented by gorgonian corals, hydroids, small sponges (including many encrusting forms) and alcyonarians. Peculiar element of the background landscape represent the accumulations of dead corals *Lophelia prolifera*, which form aggregates up to several square meters, mainly in the crevices of lava formations. These dead "reefs" are richly inhabited by diverse fauna, both attached forms (serpulids, hydroids, sponges, bryozoans, alcyonarians), and many mobile animals (Munidae crabs, errantia polychaetes, tanaids, amphipods (Stenothoidea), large Harpacticoida, brittle stars, gastropods Trochidae, Bursidae, and Opistobranchia). On the dead colonies are willing to settle live corals of different species (including numerous *Caryophyllia sarsiae*). The most abundant animals at the periphery of active vent field are the different species of hydroids (dominated by *Eudendrium* sp. and *Grammaria abietina*), sometimes completely covering the rocks. Both species are representatives of widespread boreal taxa and are known in a wide range of depths. Their presence in the hydrothermal community may be related to increased dynamics of the bottom water, due to thermal circulation.

2.2 Rainbow

Locality: 36°14′N, 33°54′W. Depth 2,260–2,350 m.

2.2.1 Abiotic Environment

The Rainbow vent area (36°14′N) discovered in 1997 [12] is located at a depth of 2,300 m and associated with ultramafic rocks; high-temperature serpentinization processes cause the highly acidic character (pH 2.8) of fluids enriched in methane up to 2.5 mmol kg^{-1} [13, 14]. There are many black smokers at the Rainbow vent field with high-temperature fluids enriched with sulfide particles; according to [1], this leads to very high total particle flux (up to 6.9 g m^{-2} day^{-1}) compared with other MAR vent fields (0.26–0.64 g m^{-2} day^{-1}). The Rainbow fluids that have passed phase separation [9] are enriched with chloride ions and associated with them heavy metals, most of which show here the maximal concentrations [14]. The fluids enriched with finely dispersed sulfides (black solutions) are common.

The area itself is a field about the size of 80 × 300 m, on which active sulfide buildings alternate with inactive ones. Black smokers are usually confined to the tops of buildings; diffuse outflows occur through the walls of buildings and through fractured basalts at the bottom of them.

The temperature of the outgoing fluid reaches 364°C. The content of H_2S, Si, Li is significantly lower, while that of Ca and Rb is higher than in the areas associated with basalts. Anomalously high concentrations of gases, primarily hydrogen and methane, are also associated with the process of serpentinization. Sharp fluid enrichment by Fe, Mn, Co, Ni, Cu, Zn, and other metals and increased amount of chlorine compared with the fluids of other hydrothermal areas are also associated with phase separation [10, 11, 15].

2.2.2 Taxonomic Composition and Spatial Structure of Community

The benthic community of the Rainbow hydrothermal area was explored by Russian expeditions in 1995, 1998, 1999, 2002, and 2005. Repeated studies have shown that faunal zonation at Rainbow area is very complex and subject to significant changes in a short time. During our 2005 expedition, we concentrated on researching specific structures, with the purpose of carrying out complete geological and biological surveys. One mature active structure in the central part of the field (mark AMKII) was investigated in great detail. During the dive of Mir-2 (St.4819) ten passes from base to top were carried out with continuous video-recording. The documentation of the ore-facial profile of the structure was carried out. At the same time, biological surveys were conducted and distribution of fauna was documented with reference to the rock facies. Faunal assemblages associated with different geo-morphological facies were described.

1. The basis of the structure (depth 2,317–2,313 m) is underlain by serpentinites and covered by metalliferous sediments and serves as a habitat for numerous Chaetopterids and hydroids (*Stegopoma plicatile*, *Candelabrum phrigium* a.o.). Settlements of the branchy xenophyophores *Luffamina* are characteristic for this zone. Numerous Nematoda, Harpacticoida, Tanaidacea, Foraminifera, and other small animals were found in the sediment.
2. Chaetopterids, hydroids, and xenophiophores are abundant and also present in an overlying zone (2,313–2,308 m), on a cone composed of fragments of tubes and massive blocks of sphalerite-pyrite ore. In this zone rare shrimps *Mirocaris fortunata* and rather abundant *Alvinocaris* sp. were observed. Gastropods *Protolyra thorvaldsoni*, *Pseudorimula mesatlantica*, *Peltospira smaragdina* and *Phymorhynchus* sp. are abundant. Polynoid polychaetes and picnogonids were recorded. Tanaids living in small houses constructed from particles of deposit material amounted to up to 200 individuals per several cm^2.
3. At a depth range of 2,309–2,303 m, the prevailing substratum consists of upright inactive pipes with a brown or dark surface. Shimmering water emissions are observed locally in this zone. The amount of dark rocks increases towards the top part of the structure. Shrimps *(Mirocaris fortunata;* up to 100 ind./m^2*)* are associated with these rocks. On a surface of the tubes, individual mollusks, *Bathymodiolus,* were observed that appear to be lifeless.
4. At a depth range of 2,303–2,301 m the vent structure consists of fused pipes of dark or orange color (Fig. 2). In this zone, shimmering water emissions and black smokes are most distinctive compared to the other zones. These water emission sites are marked by swarming shrimps *Rimicaris exoculata* (the swarm sizes are up to 0.5 m in diameter). The top of the structure (2,300 m) represents a multichannel, ramified smoker with no visible fauna.

Thus the spatial distribution of the fauna at Rainbow shows a similarity to that found at other MAR vent areas. There are an abundance of the *Rimicaris exoculata* adjacent to hot black smokes; predominance of *Mirocaris fortunata* in moderate temperature zone (sometimes also in shimmering water). The *Bathymodiolus* mussels mostly colonize the base of edifices, where the low temperature diffusors are located.

Mussel beds are inhabited by rather diverse fauna. There are polychaetes (Ampharetidae, Spionidae, Polynoidae, Capitellidae), fairly large picnogonids and limpets (*Peltospira smaragdina, Pseudorimula mesatlantica*).

Fig. 2 Rainbow hydrothermal area, depth 2,303 m. *Upper part* of the edifice AMKII. Dense swarms of bresilioid shrimps *Rimicaris exoculata* (*right*) and more sparse *Mirocaris fortunata* (*in center*)

2.3 Lost City

Locality: 30°15′N, 42°24′W. Depth 750–900 m.

2.3.1 Abiotic Environment

In Lost City hydrothermal area about 30 carbonate buildings with height from 30 to 70 m was described with a large number of smaller edifices [16, 17]. This field is distinctly different from all other known hydrothermal fields in that it is underlain by ultramatic rocks and is dominated by spectacular, steep-sided carbonate chimneys (Fig. 3) Weakly shimmering water with alkaline pH (up to 9.8) is found on the tops of and sometimes between the columns.

The slopes of the buildings are composed of white porous minerals: calcite, aragonite and brucite, and are often covered with bacterial mats [18]. ^{86}Sr isotope data, $^{12}C/^{13}C$, $^{16}O/^{18}O$, and ^{14}C isotope data suggest the approximate age of the hydrothermal activity equal to about 30,000 years. Thus this area is older than the

Fig. 3 Lost City hydrothermal area, depth ca. 760 m. Carbonate spires in the vicinity of the top of Poseidon edifice

areas with black smokers [16]. The unusual chemical composition of the fluids is controlled by the processes of serpentinization of ultramafic rocks. These subsurface reactions create fluids rich in hydrogen and methane [16, 17]. Although the influence of subsurface biosphere also could not to be excluded [15, 18].

2.3.2 Taxonomic Composition and Spatial Structure of Community

The fluid composition is controlled by the interaction between seawater and mantle peridotite. These subsurface reactions create fluids rich in hydrogen and methane, which are important energy sources for the primary producers of the Lost City ecosystem. These producers are represented by Archaea and eubacteria, their concentration reaches 10^7–10^8 cells per gram of wet carbonate. At the same time, communities of typical hydrothermal vent animals were not found at this field and it was originally thought that vent obligate (i.e., occurring only in hydrothermal vent environment) fauna at Lost City is absent.

In July 2002 Lost City was revisited on the 47th cruise of the RV "Akademik Mstislav Keldysh." During the dives with Mir submersibles several samples of bottom fauna were recovered including obligate (occurring only in hydrothermal vent environment) hydrothermal species (limpets Peltospiridae, amphipods, archinomid polychaetes, etc.) inhabiting porous interiors of the carbonate edifices. Two subfossil valves and six fragments of bivalve shells presumably belonging to *Bathymodiolus* were collected at the base of the tower complex at a depth of 830 m [19, 20]. In 2003 during 19 dives with the submersible Alvin [17] ten discrete, active vent sites were sampled. Recovered samples revealed that over 65 morpho-species were present, and >90 % of these fauna were in the order of hundreds of micrometers or less in size.

The task of our 2005 expedition was to make comprehensive observations of and take samples from the different biotopes. Active chimneys, inactive tower flanges, and the base of the complex were explored. Initial analysis of recovered samples revealed the presence of at least 55 species. Of the most abundant taxa, polychaetes are most diverse (>14 species). Coelenterates (11 species) and small crustaceans (not less 7 species) are also abundant.

Our observations reveal qualitative differences in species abundance and composition relative to substrate type.

Active Tower Tops and Walls

White friable carbonate prevails; thermal discharges are often visible by characteristic shimmering of the water. Temperatures of up to 50°C were measured. Bacterial mats are often visible on the surface. Porous channels and crevices of carbonate that is rich in bacterial mats provide habitat for many small animals including typical vent species. The most characteristic fauna in this biotope are amphipods *Bouvierella curtirama*, limpets *Protolyra valvatoides*, harpacticids, ostracods, tanaids, giant (up to 1 cm long) nematodes, and representatives of several families of polychaetes (*Ophriotrocha* sp. and Ceratulidae were observed only in this zone). Bivalves Cuspidariidae and Thyasiridae were recorded. Sessile animals are almost absent. Numerous euphasiids *Nematoscelis* and hyperiids *Paraphronima* and *Streetsia* swarms were present in the water.

Inactive Chimneys and Tower Walls

These are made up of relatively hard, glaucous or yellowish rocks. There is no visual evidence for current hydrothermal activity. Non-vent animals are fairly abundant, corals *Lophelia* sp. and *Cariophyllia sarsiae* are often observed. *Lophelia* forms bushes of up to 2 m in diameter. Gorgonian corals, alcionarians (*Stolonifera*) and actinians *Sideractis glacialis* and *Amphianthus* sp. are common. Diverse hydroids associated with corals and rocks were collected and include *Halecium tenellum, Sertularella gayi, Zanclea costata, Mirocomella polydiademata,* and other species. Also common in this zone were the sponges Demospongia and Hexactinellida (*Farrea*). Polychaete fauna is also rich in species: representatives of Serpulidae (two species) and Spirorbidae are common. Polynoidae, Eunicidae, Spionidae, Dorvilleidae, Sabellidae, Phyllodocidae, *Archinome rosacea* were observed, often in association with corals. Among larger mobile animals, gerionid crabs, galateids (*Munidopsis scabra*), *Agononida* and *Munida,* the swimming crab *Bathynectes maravigna*, echinoids *Araeosoma fenestratum* and Cidaridae, asteroids resembling *Ceramaster*, and brittle stars are common.

The Complex Base at 850–900 m

At the base of the tower complex, carbonate structures and hard rocks are locally covered with sediment. Macrofaunal composition and appearance in this zone is similar to the previous one. Analyses of our sediment samples revealed that fauna of this sediment are similar to ordinary background fauna and typically represented by meiobenthic taxa: Nematoda, Harpacticoida, small Polychaeta, and numerous diverse foraminifera.

Observations and sampling show that there is a well-defined boundary between vent and non-vent habitats at Lost City. This is generally true for all small, in particular vent-typical, animals. However we repeatedly observed large crabs, fishes, and echinoderms in active zones near the tops of the central complex. In the stomach of a sea-urchin *Araeosoma fenestratum* bacterial clots were found. The question which remains unclear is how far chemosynthetically derived production can be consumed by non-vent fauna and to what degree hydrothermal processes can influence the surrounding background community.

The most remarkable find on our 2005 expedition was the discovery of an extinct hydrothermal community which we named Lost Village [21]. Having discovered this community, we now know that Lost City area hosts (at least from time to time) large populations of *Bathymodiolus azoricus*, which may be compared (in terms of biomass and abundance) with dense populations of the same species living at other fields along the mid-Atlantic Ridge.

2.4 Broken Spur

Locality: 29°10′N, 43°10′W. Depth 3,050–3,875 m.

2.4.1 The Abiotic Environment

Hydrothermal area Broken Spur, discovered in 1993 [22, 23], is situated on a basaltic substrate and consists of massive sulfide structures. Broken Spur is one of the youngest MAR hydrothermal areas. Active hydrothermal manifestations are observed in the western part of the rift valley on about 6,000 m^2. Hydrothermal edifices with different morphology and activity are located at the bottom of the axial graben and marginal terraces. There are five buildings with active black smokers and seven inactive buildings. The height of buildings varies from 5 to 40 m. Several main morphological types of hydrothermal edifices include high, column-like (Triple Chimney, Judy's Tower, Spire), high massive (Saracen's Head, Bogdanov Site), and relatively low, platform structures with fattened tops (White Mushroom, White Button, point "K"). Most high-temperature outflows in the form of black smokers and intense shimmering water are observed in the upper part and especially on the tops of columnar and massive buildings. Fungiform edifices are less active, dominant form of hydrothermal discharge – shimmering water expiration through the cracks in a flat surface.

Predominate forms of hydrothermal discharges are the focused high- and low-temperature vents. The main feature of the fluids is an extremely high hydrogen sulfide content (up to 11 mmol kg^{-1}) [24]. The fluids are characterized by high temperature: 56–364°C. Presence of high-temperature hydrothermal sulfide deposits indicates that in this area emerges almost not modified primary fluid. It is characterized by a high content of H_2S, Fe, and Mn. On the contrary, the enrichment in methane and chlorine is low [9, 10].

2.4.2 Taxonomic Composition and Spatial Structure of Community

Initial observations made in 1993 at Broken Spur [22] suggested a low biomass relative to other deep-water Mid-Atlantic vent communities (e.g., TAG, Snake Pit, Logachev).

Vent fauna at Broken Spur is associated with isolated chimney structures of various morphologies. During the expedition of RV "Akademik Mstislav Keldysh" in 2005, attention was focused on detailed research of spatial distributions of animals associated with the different types of vent structures. Communities were studied at seven sites: White Mushroom, Saracen's Head, Bogdanov Site, Triple Chimney, Judy's Tower, White Button, and Spire.

Several spatial faunal assemblages associated with discrete biotopes were identified:

1. "Swarms" of shrimps *Rimicaris exoculata* were concentrated near relatively high-temperature vents that discharge characteristic black smoke or turbid shimmering water. The continuous, extremely dense swarms of shrimps usually did not exceed a distribution zone of 1 m around, and commonly stayed within a limit of a few tens of centimeters of the vents. As analysis of the recovered samples from this zone shows, fauna other than shrimps was rare and represented by sporadic individuals of polychaetes (fam. Spionidae). The most dense aggregations of *Rimicaris exoculata* were observed on massive structures and sometimes in the upper part of column-like structures. In all cases, dense aggregations of *Rimicaris exoculata* were found where the topography of vent structures provided enough substrate that was washed over with warm shimmering water.
2. The second dominant shrimp, *Mirocaris fortunata,* was common in weakly shimmering water and formed aggregations of hundreds of individuals per m^2. Slow-flow areas were covered with bacterial mats (Fig. 4). Crabs *Segonzacia*

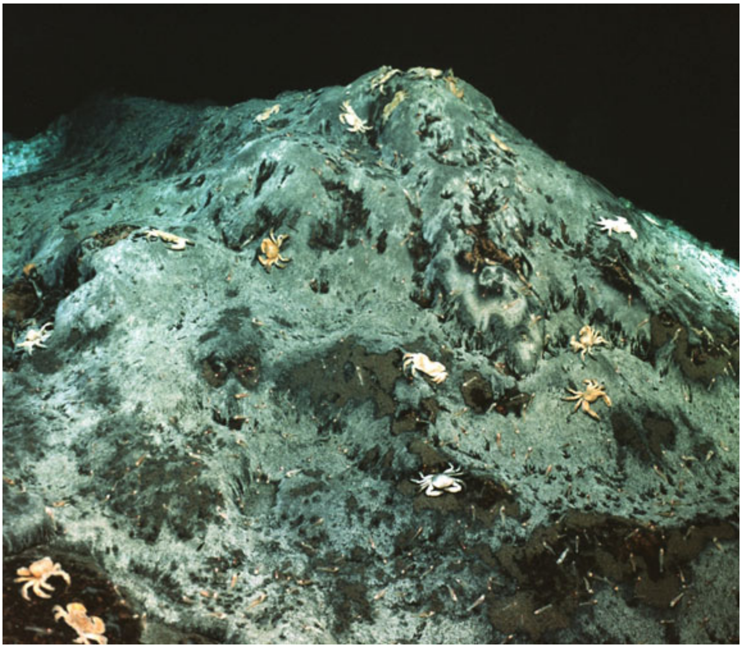

Fig. 4 Broken Spur hydrothermal area, depth 3,036 m. The *central part* of the White Mushroom edifice. Bythograeid crabs *Segonzacia mesatlantica*, shrimps *Mirocaris fortunata,* and bacterial mats

mesatlantica, gastropods *Phymorhynchus*, brittle stars *Ophioctinella acies* (tens of individuals per dm^2), and *Alvinocaris sp.* were all common in this area. Gastropods Peltospiridae (especially *Peltospira smaragdina*) and Fissurelidae formed patches of very dense aggregations. In samples recovered in this zone a number of polychaets (Polynoidae, Spionidae, Capitellidae, Hesionidae, *Archinome rosacea)* were recorded. The low-temperature discharge biotope marked by weakly shimmering water was sometimes inhabited by small aggregations of *Bathymodiolus puteoserpentis.* Single picnogonids were observed together with mussels. This assemblage was topographically associated with horizontal flanges of column-like structures and was especially common when associated with low and mushroom-like structures that had flat tops. A few meiofaunal taxa (Nematoda, Harpacticoida, Foraminifera) were collected in sediment from this habitat.

3. Settlements of actinostolid actinians *Maractis rimicarivora* (originally incorrectly identified as *Parasicyonis ingolfi*) occupied the closest peripheral zones of vents. These settlements are characteristic for the inactive base of all types of vent structures. In this zone chaetopterid polychaetes and *Phymorhynchus* are also abundant. Spionid and archinomid polychaetes, and *Ophioctinella acies* were recorded on friable hydrothermal deposit material near the base of chimneys. More or less dense populations of actinians and chaetopterids are also distributed throughout the field between venting structures.

Remarkable features of the Broken Spur hydrothermal community compared to other MAR areas are reduced total biomass of benthos and relatively high biomass of crabs *Munidopsis* and *Segonzacia* relatively with shrimps. According to [25], unusual quantitative predominance of carnivorous forms compared with symbiotrophs indicates that the community is not in a mature state. At the same time, the large size of the edifices and the abundance of dead shells do not allow to consider Broken Spur hydrothermal system as a "young." It is possible that the observed pattern is related to short-term decrease of hydrothermal activity in the recent past, which resulted in the extinction or emigration of mobile obligate symbiotrophs and gradual extinction of populations of *Bathymodiolus*, a few of which mixotrophic mode of feeding allowed to survive unfavorable conditions [25].

2.5 Snake Pit

Locality: 23°22′N, 44°57′W. Depth 3,420–3,480 m.

2.5.1 The Abiotic Environment

Snake Pit hydrothermal area was discovered in 1985 [26]. It is located in the most deep central part of the rift valley. Within the area there are three active hydrothermal hills, separated from each other by 50–100 m. Every hill is 20–60 m in diameter and from 20 to 26 m high. Snake Pit characterized by the focused high-temperature fluids outflowing from pipes of black smokers and diffusers. The surface of the rift valley is composed of basalts typical for ocean ridges. According to the classification of Y. A. Bogdanov, fluids of the Snake Pit represent the primary hydrothermal solutions which were not subject to phase separation. Black smokers are concentrated at the tops of hills [25, 27, 28]. The maximal measured temperature of the fluid is 356°C. Characteristic hydrothermal formations at Snake Pit area present also so-called diffusers (edifices up to 80 cm in diameter, with porous walls) emerging fluids with the temperature up to 70°C. Hydrothermal fluid of the Snake Pit area is slightly modified compared with the primary solution. The fluid is characterized by a high concentration of chlorine, H_2S, metals, and relatively low concentrations of gases and methane [9]. Researches performed by Russian expedition in 2002 have allowed to describe the landscape-ecological structure of the area. Active sites Beehive and Moose in the eastern part of the hydrothermal field were investigated especially in detail. The bottom at Beehive site is composed of sulfide deposits of different degree of fragmentation. Central part of the site on an area a diameter 20 m at a depth of 3,471 m is occupied by the complex of active smokers (diffusers and pipes) on a single base. Its basis is fused sulfide chimneys and honeycomb structures (diffusers) with a diameter of 1 m. The main forms of hydrothermal discharge within a site – diffuse outflows, visible on the shimmering water, warm black smoke emanating from cracks in the edifice, the hot discharge from the diffusers (sometimes with black smoke in the upper half) and hot black smoke coming out of the vertical chimneys to 1.5 m high.

The active site of Moose is located approximately 40 m east-northeast of the Beehive. The site itself presents a hydrothermal building of about 12 m high (Fig. 5). Measured in our dive diameter of the building at a depth of 3,488 m is about 6 m, the top reaches approximately 3,476 m. The basement of the building is composed of brown cemented sulfide blocks. The edifice in the lower part consists of overlapping each other cornices from a few centimeters to almost a meter in thickness and sometimes protruding more than 1 m. The main forms of hydrothermal discharge within a site are: diffuse outflows through cracks in the basement and walls of edifice, between the cornices on the upper surface of the cornices rods and diffusers; warm black fumes escaping from cracks in the buildings and some diffusers; as well as the thick black smoke flowing from a vertical chimneys. The most active hydrothermal manifestations were observed in the upper third of the building, especially the top, where shimmering water is visible almost everywhere, and black smoke from numerous pipes merge together in the cloud.

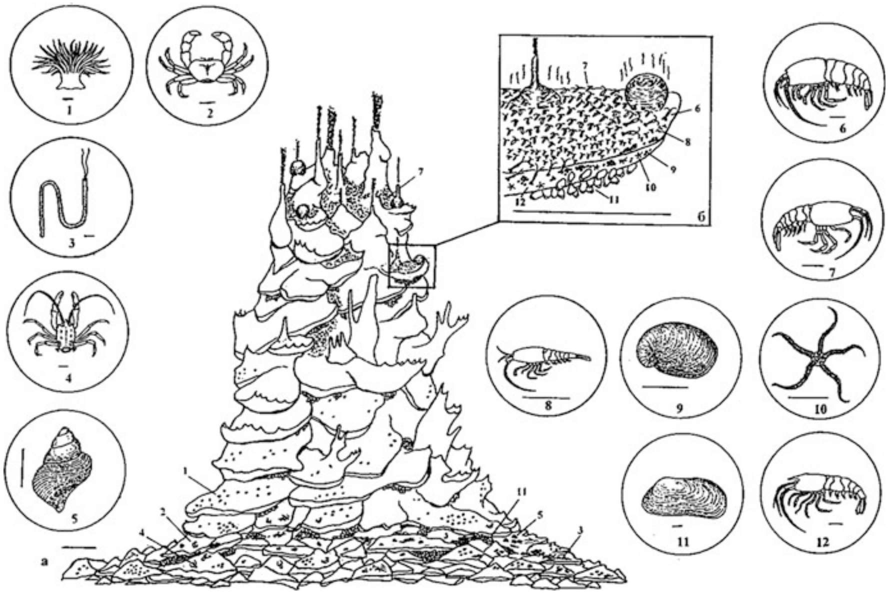

Fig. 5 The distribution of fauna on the edifice of Moose, Snake Pit hydrothermal area according to observations in the 47th cruise of RV "Akademik Mstislav Keldysh" (2002). (a) General view of the building from the south-west side, (**b**) the cornice at the top of the building. The main representatives of macrofauna: *1 Maractis rimicarivora*, *2 Segonzacia mesatlantica*, *3* Polychaeta: Chaetopteridae, *4 Munidopsis crassa, 5 Phymorhynchus* sp., *6 Chorocaris chacei*, *7 Rimicaris exoculata* (adult), *8 R. exoculata* (juvenile), *9* Gastropoda: Peltospiridae, *10 Ophioctinella acies*, *11 Bathymodiolus puteoserpentis*, *12 Alvinocaris markensis*. Scale: a, **b** – 1 m; animals – 1 cm (Peltospiridae – 0.5 cm). Depth of the base of edifice 3,490 m

2.5.2 Taxonomic Composition and Spatial Structure of Community

The distribution of fauna in the immediate vicinity of black smokers of the Snake Pit hydrothermal area was first described by Segonzac [29], they also made the first landscape reconstruction. The total number of species of invertebrates recorded in the area, according to different sources, is at least 50. Taxa marking the zone directly adjacent to the hot vents are the Alvinocarididae shrimps. *Chorocaris chacei* and *Alvinocaris markensis* are more than *Rimicaris exoculata* confined to the base of edifices, away from the vent. Sea anemones *Maractis rimicarivora*, gastropods *Phymorhynchus* sp., galatheid crabs *Munidopsis crassa,* and the brittle stars *Ophioctinella acies* are common at the foot of the active buildings. In the same habitat the aggregations of the tubes of chaetopterid polychaetes were recorded [25]. Bivalves *Bathymodiolus puteoserpentis* form clusters on the active sites of the edifices not occupied by shrimps [30]. According to the data of Fornari et al. [31], the temperature in the area of mussels habitat reaches approximately 5°C.

Summarizing all the available data, on the distribution of the main representatives of the macrofauna one can identify the following patterns. The indicator species of the far periphery of the hydrothermal field are galatheid crabs *Munidopsis crassa* whose abundance is apparently increasing in 50–100 m from the edifices, and the chaetopterid polychaetes, single tubes of which are starting to occur on the surface of the lava pillows at about the same distance. Sharp increase of the abundance of chaetopterids and the appearance of sparse sea anemones approximately coincide with the advent of hydrothermal incrustation on basalts and sulfide crusts. The outlook of the nearest peripheral zone of the field in the studied area determines the mass settlements of *Maractis rimicarivora*, clusters of Chaetopteridae and gastropods *Phymorhynchus* sp. (probably represented by two species: *P. carinatus* и *P. ovatus*). At the basement of edifice the abundance of gastropods amounts up to 3–10 specimens per m^2. In the same zone crabs *Munidopsis crassa* and *Segonzacia mesatlantica* are common. The shrimps *Alvinocaris*, *Chorocaris,* and sparse *Rimicaris* (especially juveniles of the last) were also observed in this area.

The biotope of low-temperature outflows is occupied by the mussels *Bathymodiolus puteoserpentis*, whose existence required at least a weak inflow of fluid. Mytilids are most abundant at the base on Moose edifice and on the surfaces of the building outside settlements of shrimps. Mussels form dense aggregations (several hundred individuals per m^2) in the places of low-temperature fluid discharge, sometimes in weakly shimmering water. Generally they are confined to cracks and depressions of relief. Mussel beds are inhabited by diverse small animals. Numerous limpets, polychaetes Hesionidae and Ampharetidae, brittle stars Ophioctinella acies, small Bryozoa, nematodes, Harpacticoida (fam. Ectinosomatidae), ostracods and copepods were found associated with mussels.

The appearance of the zone of intense shimmering water and warm black smokes determine dense swarms of *Rimicaris exoculata* that occupy the largest area in the upper third of the building. Juveniles of *Rimicaris* generally gravitate to the external less temperature zone, although single specimens occur also in the clusters of adult forms. Carnivorous shrimps *Chorocaris* and *Alvinocaris* are found at all hydrothermal field, but there are most abundant at the surfaces of active edifices, free from accumulations of *Rimicaris*.

Limpet gastropods *Peltospira smaragdina* (fam. Peltospiridae) were often observed in dense aggregations (several hundred individuals) on cornices close to shimmering water zone. They are also abundant on sulfide surfaces occupied by shrimp's populations. As against, limpets *Pseudorimula mesatlantica* (also fairly abundant) are obviously associated with mussels.

Overall an exceptionally complex morphology of the Moose edifice, a variety of forms of the fluid discharge, and a complex picture of the local convective flows exclude simplified version of zonation. Diverse microhabitats within the active site are used by different groups of organisms (Fig. 6). Besides some aggregations (as,

Fig. 6 Snake Pit hydrothermal area, depth 3,485 m. Microdistribution of animals at Moose hydrothermal edifice. *On the left center* is a white smoker. *At the top* – the settlement of bivalves *Bathymodiolus puteoserpentis* and clusters of adult shrimps *Rimicaris exoculata*. On the walls of the smoker *Rimicaris exoculata* juveniles. *Below* – an accumulation of carnivorous gastropods *Phymorhinchus* sp. *Centre right* – gastropod's egg masses attached to sulfide formations

for example, clusters of mobile *Alvinocaris* or clusters of different age stages of *Rimicaris*) are obviously ephemerous.

However in general terms the zonation of hydrothermal fields of Snake Pit quite fit into the scheme, known in other deep-sea MAR vent areas. The main feature is the dominance of sea anemones, gastropods, and chaetopterids in the peripheral part of the field and at inactive sites and domination of bresilioid shrimps (primarily, *Rimicaris exoculata*) in the zones of shimmering water and black smokes. Bathymodiolin mussels occupy in some sense an intermediate biotope of low-temperature seeps. Mussels don't occur outside the active zone as well as in the accumulation of shrimps (although sometimes live side by side with them).

It should be noted that in quantitative terms the population of shrimps on the Beehive site is, apparently, one of the largest in the Atlantic. The complete absence of mytilids on the Beehive site (in the presence of abundant clearly independent population on the nearby Moose) remains a fact requiring explanation.

3 East Pacific Rise (EPR)

Hydrothermal areas of the northern part of EPR are characterized by sulfide edifices, black smokers and diffuse emissions through the sulfide and fractures in the basalts. The temperature of the fluids amounts up to 340°C. Hydrothermal fluid at EPR is weakly modified in comparison with primary solution. The fluid is characterized by a high concentration of chlorine, H_2S, metals, and methane [4, 10, 32, 33]. The surface of the rift valley is composed of basalt. Hydrothermal ecosystems of the East Pacific rise (ECP) have a high species diversity, complex, and changeable structure of hydrothermal communities.

At the East Pacific Rise we studied one hydrothermal area: 9°50′N.

3.1 9°50′N EPR

Locality: 9°48′–51′N; 104°17′W. Depth 2,480–2,580 m.

3.1.1 Abiotic Environment

The 9°50′N vent field at the EPR is interesting primarily for two reasons. First, it is located in the axial rift zone of the most fast-spreading basalt ridge (>11 cm year^{-1}). Second, repeated volcano eruptions periodically happened during the last 15 years and destroyed most of the living communities, resulting in evolutionary changes of the geochemical medium and recovery of the biotopes [34]. Two types of hydrothermal vents are developed at this field: low-temperature diffuse seeps and high-temperature vents with sulfide mounds and black smokers. Examined in our expeditions active hydrothermal sites are located along the deep canyon (axial cracks), stretching from North to South. The bottom and walls of the canyon are composed of very young pillow lavas. A characteristic element of background landscape are high lava columns with ribbed surface. During the recent eruptions these columns served as channels for molten lava. Later some of them became part of the hydrothermal circulation system.

3.1.2 Taxonomic Composition and Spatial Structure of Community

The distribution of fauna at the sites of 9°N EPR was studied in detail during the expedition of RV "Akademik Mstislav Keldysh" in 2003.

Most high-temperature hydrothermal faunal assemblage is confined to diffuse seeps on the walls of active sulfide structures adjacent to places of discharge of the hot fluid (black and white smokers) (Fig. 7). The greatest tolerance to high temperature demonstrates "Pompeii worms" – polychaetes *Alvinella pompejana*. These animals are able to withstand temperatures of over 40°C. Tubes of polychaetes densely covered with bacterial owergrow. With Pompeii worms are associated *Alvinella caudata*, and motile polychaetes (Nereidae and Polynoidae).

The most characteristic representatives of the hydrothermal fauna of the immediate environment of the field are the giant vestimentiferans *Riftia pachyptila*. Tubes of this species reach over a meter in length. The requirement of vestimentiferans of high enough concentrations of fluids causes their localized distribution on hydrothermal field. They usually occur in groups, in places of warm outflows marked by shimmering water. At a relatively young hydrothermal sites vestimentiferans dominate. In the older sites mature tubes of vestimentiferans are often hidden under mussel beds (*Bathymodiolus thermophylus*). Vestimentiferan clusters and mussel beds are inhabited by numerous and diverse fauna [35]. On mytilid shells small limpets (fam. Lepetodrilidae) were abundant. Among them, *Lepetodrilus ovalis*, *L. elevatus,* and *L. cristatus* are most numerous. Small gastropods from the family Trochidae (*Bathymargarites* sp.) were common in this zone. In the water column above the clumps of vestimentiferans, and sometimes above mussel beds, in places of diffuse outflows dense clusters of obligate (endemic) amphipods *Halice hesmonectes* (fam. Pardaliscidae) were observed. These "swarms" represent a rare example of purely pelagic hydrothermal assemblage. According to the estimation of Van Dover et al. [36], the density of amphipods reaches more than 1,000 ind./L and represent the most massive accumulations of pelagic animals at great depths.

The areas devoid of mytilids, in the zone of low-temperature seeps are inhabited by large vesicomyid bivalves *Calyptogena magnifica* (see Figure 10 in the Chapter Galkin S.V. "Structure of hydrothermal vent communities"). They reach a length of 20 cm and usually are imbedded in crevices of basalt. Near the clam's settlements gastropods, serpulid polychaetes and barnacles are common. Near the accumulations of bivalves and outside of the active sites is quite common giant picnogonids *Collosendeis colossea*. On the active sites large mobile carnivorous

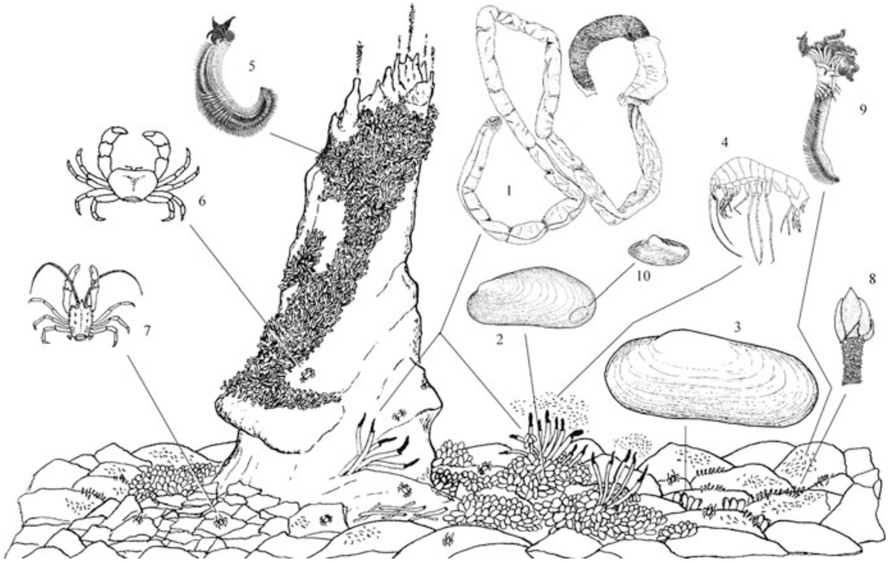

Fig. 7 9°N EPR hydrothermal area. Distribution of animals at the site BV (9°50,97′N; 104°17,59′W; depth 2,517 m). The hydrothermal edifice is 5 m high, diameter at base about 2 m. The view from the North-East. The reconstruction is performed on the basis of direct observations, analysis of videos and photographs obtained in the DSRV "Mir-2" (dive #22/360). Dominant fauna: *1 Riftia pachyptila, 2 Bathymodiolus thermophilus*, *3 Calyptogena magnifica, 4 Halice hesmonectes*, *5 Alvinella pompejana, 6 Bythograea thermidron, 7 Munidopsis subsqamosa, 8 Neolepas zevinae, 9 Laminatubus alvinae, 10 Lepetodrilus* aff. *elevatus*

crabs *Bythograea thermidron* are quite numerous. They eat live mussels and (or) their remains. Similar type of feeding is characterized the large gastropods *Phymorhynchus*, also common in the settlements of mytilids.

At the periphery of hydrothermal sites the aggregations of serpulid polychaetes of two obligate (endemic) hydrothermal species *Laminatubus alvinae* and *Protis hydrothermica* are common. According to our estimates, the number of polychaetes reaches up to 180–220 ind./m^2. Other typical inhabitants of the nearest periphery of the field were lepadomorph barnacles of the genus *Neolepas*. These sessile suspension-feeding animals sometimes form a thick "brush" on the rocks. Food for suspension-feeding assemblages of the peripheral zone provides the bacterial suspension, which is present in abundance in water surrounding the vent field. At the base of the basalt columns in crevices of lava pillows a small white octopuses *Vulcanoctopus hydrothermalis* (obligate hydrothermal genus) were repeatedly observed. At inactive sites of the canyon red and white shrimps (fam. Nematocarcinidae) and galatheid crabs *Munidopsis subsquamosa* are common. These animals do not belong to a specific hydrothermal taxa, however, the number of them markedly increases when approaching the active sites.

4 Guaymas Basin

Locality: 27°00′N, 111°24′W. Depth: 1,950–2,050 m.

4.1 Abiotic Environment

The vent area of the Guaymas Basin in the Gulf of California has some differences from other fields. The intense tectonic activity in this area is caused by the displacement of the Baja California peninsula towards the NW at a spreading rate of about 6 cm per year [37, 38]. An exceptional feature of the semi-enclosed Guaymas Basin (Gulf of California) hydrothermal vent area is the thick (>500 m) organic-rich sedimentary cover on the seafloor. This cover is a result of high (1–2 mm/year) sedimentation rates due to Colorado River sediment input directly before dam construction or tidal resuspension of previously supplied terrigenous sediments in the Upper Gulf of California [39, 40] and biogenic particles from the highly productive euphotic zone (>500 mg/m^2 per day) [41, 42]. High-temperature fluids are discharged to the surrounding seawater through the vents and by ascending through the overlying sediments, which are rich in Mn. This leads to the enrichment of fluids for Mn relative to Fe [43], which is a characteristic feature of Guaymas Basin fluids compared to other vent fields. This differs from the hydrothermal vent fluids of the Mid-Atlantic Ridge and 9°50′N of the East Pacific Rise, where Fe is found in higher concentrations than Mn [14, 44]. The surface sediments of the Guaymas Basin also have a Mn-oxide-rich and (relatively) Fe-oxide-rich turbidite layer that affects the distribution of C, Fe, Mn, S, and some trace metals [45]. Iron is mainly pyritized in the sediments, while Mn is found predominantly in carbonates (41 ± 12 %) and is associated with pyrite to a much lesser degree; Co, Cr, Cu, Ni, and Zn were highly pyritized (>80 %) in the sediments of the Guaymas Basin [45]. The low-temperature hydrothermal mineral associations on the floor of the Guaymas Basin are represented by opal and barite, while pyrrhotite, sphalerite, and chalcopyrite are the dominant ore minerals in high-temperature areas [46]. It is interesting to note that both mineral formations contain oil hydrocarbons, with a content of Corg in the surface sediments ranging from 0.15% (high-temperature area) to 2.23% (low-temperature area) [46] and reaching up to 6.21% in some deposits saturated with hydrocarbons. More than a hundred high-temperature hydrothermal mounds (black smokers) in an area of 30 km^2 were discovered and described by [41]. Sulfide chimneys commonly grow through overlying sediments and can reach heights of more than 25 m. High-temperature fluids (maximum temperatures of up to 315°C) are emitted from the vents into the surrounding water. Warm fluids flow through the chimney walls and ascend past the sedimentary cover, which is enriched with organic matter. This leads to a complicated transformation of organic matter into hydrocarbons and methane [43] that is characteristic of the Guaymas Basin fluids compared to other known vent fields. A characteristic element of the Guaymas Basin landscape are extensive bacterial mats of white, cream, and orange, reaching a few centimeters in thickness and covering the space of hundreds of square meters.

4.2 Taxonomic Composition and Spatial Structure of Community

In 1986 and 1990, hydrothermal communities of the Guaymas Basin were studied by Russian expeditions using the submersibles "Pisces" and "Mir." In the area of hydrothermal activity around 40 species of macrofauna were recorded, their distribution was visually studied in a series of dives.

Abundant settlements of vestimentifera *Riftia pachyptila*, reaching up to 1 m length and occupying areas of up to hundreds m^2, were detected in the shimmering water at the hydrothermal chimney surfaces. These thickets are inhabited by numerous organisms, most notable of which are polynoid polychaetes, limpets, and bythograeid crabs. All vestimentiferans tubes are covered with bacterial fouling, obviously used as food by grayzers and deposit feeders. In areas free of vestimentiferans, but covered with bacterial mats, the settlements of alvinellid polychaetes *Paralvinella bactericola* were observed. The population of small (1–2 cm) anemones is located on the surface of the edifices often in shimmering water. At the basement of the buildings accumulate dead vestimentiferans tubes. Here carnivorous galatheids *Munidopsis* and some gastropods are most numerous. Large crabs Lithodidae were often observed near the edifices but also noted in the settlements of vestimentifera. On sediments, in areas of diffuse seepage, thick bacterial mats are developed (Fig. 8), under which the polychaetes *Ophryotrocha* are abundant.

The basic group of fauna inhabiting the soft sedimentary cover is the vesicomyid clam *Archivesica gigas* whose settlements can accumulate up to hundreds specimens per m^2. These communities of organisms are nutritionally dependent on the chemosynthetic bacterial community and are typically surrounded by accumulations of the bivalve mollusks *Nuculana grasslei* [47]. Sediments soaked with hydrocarbons serve as a substratum for these organisms. Chimney walls and bases are inhabited by *Munidopsis alvisca* crabs (predator), *Spongia* (filter-feeder), and *Phelliactis pabista* (filter-feeder and predator). The latter were often attached to the shells of the vesicomyid clam *Archivesica gigas*. Thick bacterial mats (with a thickness of up to a few cm) cover significant areas (hundreds of m^2).

Complex configuration of edifices (overhanging eaves, ledges, secondary chimneys) increases habitat diversity and strongly masks the zonal distribution of animals. However, a few prominent zones can be identified in the Guaymas Basin's hydrothermal vent field, each of which is dominated by certain megafaunal groups: (1) the euthermal or shimmering water zone (ambient temperature of about 25–30°C), where vestimentiferans commonly live; (2) the oligothermal zone

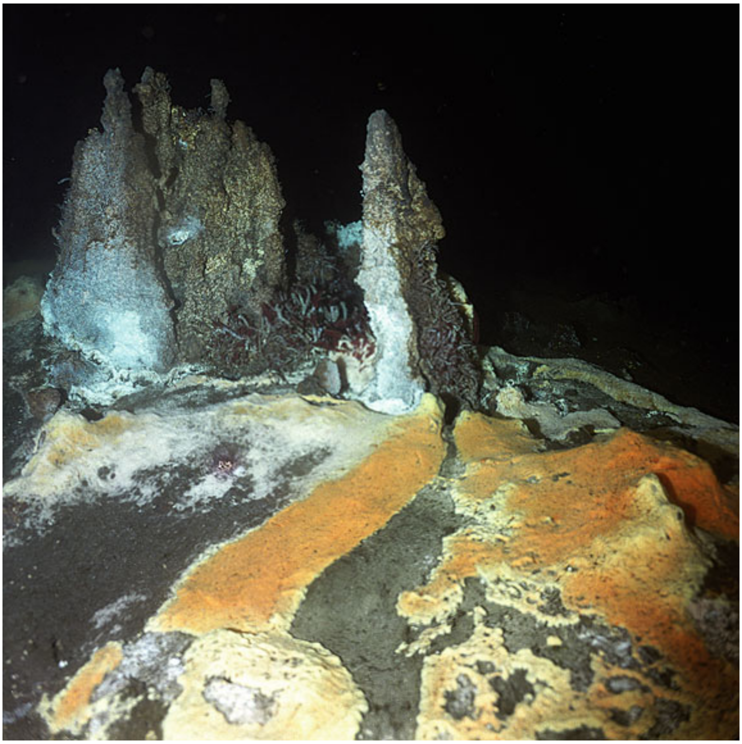

Fig. 8 Guaymas Basin hydrothermal area, depth ca. 2,000 m. Bright bacterial mats with thickness up to several centimeters on loose sediment at the foot of the sulfide structures – a characteristic element of the landscape of the Southern Trough

(temperatures of 3–6°C to 25°C), which is populated by vesicomyid clams; (3) the periphery of the vent zone (near-field, with very low or absent temperature anomalies), where specialized suspension-feeders consuming bacteria are the predominant taxa; and (4) the periphery of the vent zone (far-field, without temperature anomalies), which is occupied by non-vent suspension-feeders and carnivores and deposit feeders [32].

5 Concluding Remarks

The discussed above hydrothermal vent areas exhibit a wide range of environmental conditions, including great variation in depth (particularly on the MAR), associated physical parameters, and different geologic setting and underlying rocks. The MAR is a slow spreading ridge (spreading rate <6 cm/year), and the EPR is a fast-spreading ridge (>6 cm/year). In addition, the hydrothermal fields differ in depth, geologic structure, and rock composition, which results in different maximum fluid temperatures, pH, and concentration levels of reduced compounds and metals. The youngest (less than 100 year) and shallowest (850 m deep) Menez Gwen field is located at the base of a volcano and associates with axial basaltic magma chambers. Low-temperature diffuse vents with T° up to 274°C are dominant in this field. Other fields comprise mainly high temperature (highest temperature of 405°C) vents (black smokers). In contrast to other sites considered in this paper, hydrothermal circulation at the Rainbow field is confined to ultrabasic rocks, the interaction of which with seawater penetrating along fractures results in anomalously high contents of hydrogen (low pH) in the fluids and extensive abiogenic methane formation. A distinctive feature of the hydrothermal field of the Guaymas Basin (Gulf of California) is the presence of a thick sedimentary cover enriched in organic matter owing to the very high sedimentation rates and the high productivity of the photic zone. At this site, high temperature fluids discharge into the bottom water through vents and also percolate through the overlying reduced sediments enriched in Mn. This results in the enrichment of fluids in Mn relative to Fe which is a characteristic feature of fluids from the Guaymas Basin, distinguishing them from the fluids of other fields. Faunal communities of studied areas also vary greatly in taxonomic composition and spatial structure. Especially strongly differences in taxonomic composition exhibit the communities of the Pacific and Atlantic Oceans. Between these two regions there are practically no shared species. The shallowest Atlantic area Menez Gwen has a lot of differences from deeper areas of the MAR. Herewith the depth was suggested as the main factor determining the differences between MAR hydrothermal vent communities [48]. Besides landscape circumstances, type of substrate, morphology of hydrothermal edifices, etc. are also important factors determining microdistribution of animals. Of the variety of factors determining fauna distribution, temperature and substratum characteristics are the easiest to estimate during bottom observation. Precise data is lacking in most cases, but numerous visual observations accompanied by temperature estimations have found that black smokers have a temperature in the range 275–400°C, while white smoker temperature varies from 100°C to 250°C [49]. Diffuse outflows of different types have a lower temperature, and are marked by a characteristic "shimmer" of water (the optical effect appearing by mixing of fluids of different density). This effect is clearly observed in the temperature anomalies in 3–6°C and more [50]. The heat extreme for most vent zone inhabitants seems to be about 25–40°C. Along with all the variety of hydrothermal manifestations, in the spatial structure of communities a number of general patterns can be revealed. Thus, the high temperature zone directly adjacent to black and white smokers is occupied in the Atlantic by the assemblage of shrimps *Rimicaris exoculata* while in the Pacific – by the assemblage of alvinellid polychaetes (*Alvinella pompejana* and *A.caudata*). Shrimps and alvinellids inhabit warmer zones with temperatures ranging from 20°C to 40°C. The bathymodiolin mussels under investigation reside in the zone of warm diffuse outflows at temperatures from 2°C to 20°C. Due to mixotrophic mode of feeding, bathymodiolins are widely distributed within the field and occur not only in shimmering water zone but also outside them. Siboglinids (vestimentiferans) may occur together with mytilids, but more often they settle closer to hydrothermal vent emissions and live at temperatures exceeding 20°C. On the contrary, vesicomyid clams are confined to weak outflows and practically never were recorded in shimmering water. Mobile predators and scavengers (mostly crustaceans, large gastropods) are distributed all over the field. The scavengers are especially abundant at the periphery of vent sites and at the foot of high edifices where organic remains accumulate. Filter feeders using advective currents of water are characteristic for the periphery of the fields. Their distribution is largely determined by the availability of suitable substrate.

At the analysis of bioaccumulation function of vent organisms in the case of each area particular habitat conditions and characteristics of spatial structure of communities (microdistribution of animal's populations, their association with a specific temperature zone and a particular type of substrate) must be taken into account.

Acknowledgements The authors are grateful to Captain Yuri Gorbach of the R/V *Akademik Mstislav Keldysh* and his crew for their essential collaboration during the cruises. We also acknowledge Dr. A. Sagalevich and the *MIR* pilots and team for their constant support. We thank all submersible observers for sharing observations and samples and a great many of experts for identification of animals. This work was funded by the Russian Science Foundation (Grant No. 14-50-00095) (analyses and generalization of the material). The research has also received funding from the European Union Seventh Framework Programme (FP7/2007-2013) under the MIDAS project, grant agreement Nr 603418.

References

1. Desbruyères D, Biscoito M, Caprais J-C et al (2001) Variations in the deep-sea hydrothermal vent communities on the Mid-Atlantic Ridge near the Azores Plateau. Deep-Sea Res 48:1325–1346
2. Demina LL. Trace metals in water in the hydrothermal biotope. Hdb Env Chem. doi:10.1007/698_2016_1
3. Demina LL, Galkin SV. Factors controlling the trace metal distribution in hydrothermal vent organisms. Hdb Env Chem. doi:10.1007/698_2016_5
4. Demina LL, Holm NG, Galkin SV, Lein AY (2013) Some features of the trace metal biogeochemistry in the deep-sea hydrothermal vent fields (Menez Gwen, Rainbow, Broken Spur at the MAR and 9°50′N at the EPR): a synthesis. J Mar Syst 126:94–105
5. Haase KM, Petersen S, Koschinsky A et al (2007) Young volcanism and related hydrothermal activity at 5°S on the slow-spreading southern Mid-Atlantic Ridge. Geochem Geophys Geosyst 8(11):1–17
6. Desbruyères D, Almeida A, Biscoito M et al (2000) A review of the distribution of hydrothermal vent communities along the northern Mid-Atlantic Ridge: dispersal vs. environmental controls. Hydrobiologia 440:201–216
7. Charlou JL, Donval JP, Douville E et al (2000) Compared geochemical signatures and the evolution of Menez Gwen (37°50′N) and Lucky Strike (37°17′N) hydrothermal fluids, south of the Azores Triple Junction on the Mid-Atlantic Ridge. Chem Geol 171:49–75
8. von Cosel R, Comtet T, Krylova E (1999) *Bathymodiolus* (Bivalvia, Mytilidae) from hydrothermal vents on the Azores triple junction and the Logachev hydrothermal field, Mid-Atlantic Ridge. Veliger 42(3):218–248
9. Bogdanov YA (1997) Hydrothermal ore manifistations of rifts of the Mid-Atlantic Ridge. Nauchnii Mir, Moscow, 166 p. (in Russian)

10. Lein AY (2006) Geochemistry and biogeochemistry of hydrothermal fluids. Bacterial production on active hydrothermal fields. In: Vinogradov M.V., Vereschaka A.L. (eds) Hydrothermal ecosystems of the Mid-Atlantic Ridge. Nauka, Moscow, pp 68–94 (in Russian)
11. Gebruk AV, Mironov AN (2006) Biogeography of Mid-Atlantic Ridge hydrotherms. In: Hydrothermal ecosystems of the Mid-Atlantic Ridge. Nauka, Moscow, pp 119–162 (in Russian)
12. Fouquet Y, Charlou JL, Ondreas H et al (1997) Discovery and first submersible investigations on the Rainbow hydrothermal field on the MAR (36°14′N). EOS Trans AGU 78(46):F832
13. Holm NG, Charlou JL (2001) Initial indications of abiotic formation of hydrocarbons in the Rainbow ultramafic hydrothermal system, Mid-Atlantic Ridge. Earth Planet Sci Lett 191:1–8
14. Douville E, Charlou JL, Oelkers EH et al (2002) The Rainbow vent fluids (36°14′N, MAR): the influence of utramaphic rocks and phase separation on trace metals content in Mid-Atlantic Ridge hydrothermal fluids. Chem Geol 184(1):37–48
15. Bogdanov YA (2006) Geological preconditions of the diversity of Mid-Atlantic Ridge hydrothermal fauna. Hydrothermal ecosystems of the Mid-Atlantic Ridge, Nauka, Moscow, pp 19–36 (in Russian)
16. Kelley DS, Karson JA, Blackman DK, Frűh-Green GL, Butterfield DA, Lilley MD, Olson EJ, Schrenk MO, Roe KK, Lebon GT, Rivizzigno P, The AT3-60 Shipboard Party (2001) An off-axis hydrothermal vent field near the Mid-Atlantic Ridge at 30°N. Nature 412:145–149
17. Kelley DS, Karson JA, Früh-Green GL, Yoerger DR, Shank TM, Butterfield DA, Hayes JM, Schrenk MO, Olson EJ, Proskurowski G, Jakuba M, Bradley A, Larson B, Ludwig K, Glickson D, Buckman K, Bradley AS, Brazerlton WJ, Roe K, Elend MJ, Delacour A, Bernasconi SM, Lilley MD, Baross JA, Summons RE, Sylva SP (2005) A serpentinite-hosted ecosystem: the Lost City hydrothermal field. Science 307(5714):1428–1434
18. Lein AY (2004) Role of bacterial chemosynthesis and metanotrophy in ocean biogeochemistry. In: New idea in oceanology I. Physics, chemistry, biology. Nauka, Moscow, pp 280–324
19. Gebruk AV, Galkin SV, Krylova EM, Vereshchaka AL, Vinogradov GM (2002) Hydrothermal fauna discovered at Lost City (30°N, Mid-Atlantic Ridge). InterRidge News 11(2):18–19
20. Vereshchaka AL, Galkin SV, Gebruk AV, Krylova EM, Vinogradov GM, Borowski C, The "Mir" submersibles team (2002) Biological studies using Mir submersibles at six North Atlantic hydrothermal sites in 2002. InterRidge News 11(2):23–28
21. Galkin SV (2006) Lost Village – a "faubourg" of Lost City: benthic studies using Mir submersibles at North Atlantic hydrothermal sites in 2005. InterRidge News 15:18–24
22. Murton BJ, Klinkhammer G et al (1993) Direct measurements of the distribution and occurrence of hydrothermal activity between 27°N and 37°N on the Mid-Atlantic Ridge. EOS 74:99
23. Murton BJ, Van Dover C (1993) Alvin dives on the Broken Spur hydrothermal vent field at 29°10′N on the Mid-Atlantic Ridge. BRIDGE Newsl 5:11–14
24. James RH, Elderfield H, Palmer MR (1995) The chemistry of hydrothermal fluids from the Broken Spur site, 29°N Mid-Atlantic Ridge. Geochim Cosmochim Acta 59(4):651–659
25. Van Dover CL (1995) Ecology of Mid-Atlantic Ridge hydrothermal vents. In: Parson LM, Walker CL, Dixon DR (eds) Hydrothermal vents and processes, vol 87, Geological Society special publication. Geological Society, London, pp 257–294
26. Kong L, Solomon LC, Pudry GM (1985) Microearthquake characteristics of a mid-ocean ridge along axis high. J Geophys Res 97:1659–1685
27. Mevel C, Auzende J-M, Cannat M, Donval J-P, Dubois J, Fouquet Y, Gente P, Crimand D, Karson JA, Segonzac M, Stievenard M (1989) La ride du Snake Pit (dorsale medio-Atlantique, 23°22′N): resultats preliminaires de la compagne HYDROSNAKE. C R Acad Sci Paris Ser II 308(6):545–552
28. Fouquet J, Wafik A, Cambon P, Mevel C, Meyer G, Gente P (1993) Tectonic setting and mineralogical and geochemical zonation in the Snake Pit sulfide deposit (Mid-Atlantic Ridge at 23°N). Econ Geol 88:1018–1036
29. Segonzac M (1992) Les peuplements associes a l'hydrothermalisme oceanique du Snake Pit (dorsal Medio-Atlantique; 23°N, 3480 m): composition et microdistribution de la megafaune. C R Acad Sci Paris 314(III):593–600

30. von Cosel R, Metivier B, Hashimoto J (1994) Three new species of *Bathymodiolus* (Bivalvia: Mytilidae) from the hydrothermal vents in the Lau Basin and the North Fiji Basin, Western Pacific, and the Snake Pit area, Mid Atlantic Ridge. Veliger 37(4):374–392
31. Fornari DJ, Van Dover SL, Shank T, Lutz R, Olsson MA (1994) Versatile, low-cost temperature sensing device for time-series measurements at deep-sea hydrothermal vents. BRIDGE Newsl 6:40–47
32. Galkin SV (2002) Hydrothermal vent communities of the World Ocean. Structure, typology, biogeography. GEOS, Moscow, 99 p (in Russian)
33. Demina LL, Galkin SV, Lein AY, Lisitzin AP (2007) First data on microelements composition of benthic organisms of the hydrothermal field 9°50′N (East-Pacific Rise) Dokladi Akademii Nauk 415(4):528–531 (in Russian)
34. Von Damm KL, Lilley MD (2004) Diffusive from hydrothermal fluids from 9°50′N East Pacific Rise: origin, evolution and biogeochemical controls. In: Wilcock WSO (ed) The subseafloor biosphere at midoceanic ridges, vol 144, Geophysical monograph. American Geophysical Union, Washington, DC, pp 245–269
35. Goroslavskaya EI, Galkin SV (2010) Composition and structure of mytilid and alvinellid assemblages at 9°N East Pacific Rise: comparative analysis. Cah Biol Mar 51:389–392
36. Van Dover CL, Kaartwedt S, Bollens S et al (1992) Deep-sea amphipod shwarms. Nature 6381:25–26
37. Klitgord KD, Mudie JD, Bischoff JL, Henyey TL (1974) Magnetic anomalies in the northern and central Gulf of California. Geol Soc Am Bull 85:815–820
38. Lonsdale P (1984) Hot vents and hydrocarbon seeps in the Sea of Cortez. Oceanus 27(3):21–24
39. Calvert SE (1966) Accumulation of diatomaceous silica in the silica sediments of the Gulf of California. Geol Soc Am Bull 77:569–596
40. Carriquiry JD, Sánchez A (1999) Sedimentation in the Colorado River delta and Upper Gulf of California after nearly a century of discharge loss. Mar Geol 158:125–145
41. Lonsdale PF, Bischoff JL, Burns VM, Kastner M, Sweeney RE (1980) A high-temperature hydrothermal deposit on the sea bed at Gulf of California spreading center. Earth Planet Sci Lett 49:8–20
42. De la Lanza-Espino G, Soto LA (1999) Sedimentary geochemistry of hydrothermal vents in Guaymas Basin, Gulf of California, Mexico. Appl Geochem 14:499–510
43. Von Damm KL, Edmond JM, Measures CI, Grant B (1985) Chemistry of submarine hydrothermal solutions at Guaymas Basin, Gulf of California. Geochim Cosmochim Acta 49:2221–2237
44. Von Damm KL (2000) Chemistry of hydrothermal vent fluids from 9-10°N, East Pacific Rise: "Time zero", the immediate posteruptive period. J Geophys Res 105:11203–11222
45. Otero XL, Huerta-Diaz MA, Macías F (2003) Influence of a turbidite deposit on the extent of pyritization of iron, manganese and trace metals in sediments from the Guaymas Basin, Gulf of California (Mexico). Appl Geochem 18:1149–1163
46. Bogdanov YA, Lisitzin AP, Sagalevitch AM, Gurvich EG (2004) Hydrothermal ore formation at the ocean floor. Nauka, Moscow, 528 p (in Russian)
47. Allen JA (1993) A new deep-water hydrothermal species of *Nuculana* (Bivalvia: Protobranchia) from the Guaymas Basin. Malacologia 35:141–151
48. Rybakova (Goroslavskaya) E, Galkin S (2015) Hydrothermal assemblages associated with different foundation species on the East Pacific Rise and Mid-Atlantic Ridge, with a special focus on mytilids. Mar Ecol 36:45–61
49. BRIDGE (1994) Workshop report no. 4. Diversity of vent ecosystems (DOVE), Marine Biological Association, Plymouth
50. Desbruyeres D, Alayse-Danet AM, Ohta S et al (1994) Deep-Sea hydrothermal communities in Southwestern Pacific Back-Arc Basins (the North Fiji and Lau Basins): composition, microdistribution and food-web. Mar Geol 116(1–2):227–242