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Three-dimensional view of the Atlantic abyssal benthopelagic vent community

Alexander L. VERESHCHAKA and Mikhail E. VINOGRADOV
Shirshov Institute of Oceanology, Russian Academy of Sciences,
Nakhimovsky Prospekt 36, Moscow, 117851, Russia
Fax: (7) 095 124-7940. E-mail: alvereshchaka@yahoo.com

Introduction

Biological communities at hydrothermal vents have yielded many intriguing discoveries in deep-sea ecology, taxonomy, and morphology. Naturally, much research attention has been given to the benthic fauna, the most spectacular component of life at vents. Much less attention has been given to the distribution of plankton, although there has been intensive sampling of vent shrimp larvae, during the last few years, over vent fields of the Mid-Atlantic Ridge (Herring & Dixon, 1998). A recognizable benthopelagic fauna has been shown to be a ubiquitous and very important component of the near-bottom ecosystem in the deep ocean (Wishner, 1980; Vereshchaka, 1995). If a significant pelagic component exists above the Atlantic vents, then we need to modify our view of vent biology and ecology.

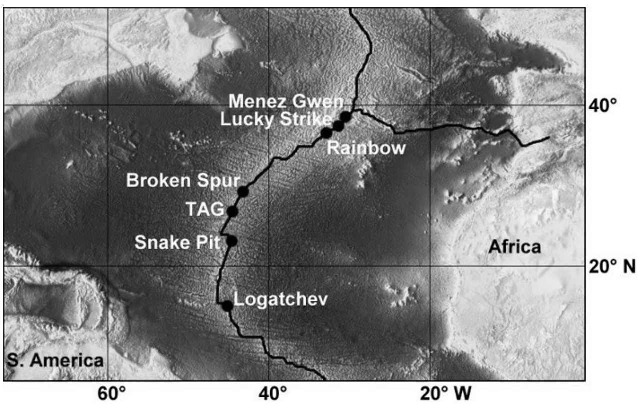

Figure 1. Location of study sites on the Mid-Atlantic Ridge (map kindly provided by A. J. Southward and A. Jory).

Material and methods

The Atlantic vent fields range from several tens to several hundreds of meters in diameter and are effectively studied only by submersible. Methods of visual observations and quantitative estimations of the plankton in water column and close to the bottom were developed during several cruises with two deep-sea submersibles (see details in Vereshchaka & Vinogradov, 1986). The data were collected during the 34th (August-October 1994), 39th (August-September 1996), and 41st (August-December 1998) cruises of the R/V "*Akademik Mstislav Keldysh*" (Institute of Oceanology, Russian Academy of Sciences, Moscow, Russia) that deployed the two "*Mir*" submersibles at four hydrothermal fields of the Mid-Atlantic Ridge: Logatchev, TAG, Rainbow and Broken Spur (Fig. 1). Animals were counted visually through the submersible port holes, within a counting frame, during vertical and oblique water column transects. The counting frame was positioned alongside the submersible in order to avoid the influence of the hydrodynamic "bow wave pillow" formed ahead of the horizontally moving vehicle (horizontal speed was about 1.0-1.5 m s^{-1}).

Plankton were counted during submersible descents and ascents, which occurred between 10 a.m. and 6 p.m. at a displacement speed of 10 to 25 m min^{-1}. For oblique transects, the submersible moved horizontally at 2 knots, while descending or ascending at 10 m min^{-1} vertical. The direction of horizontal movement was adjusted so that the submersible performed a helical movement and always remained above the vent field. Animal abundances were recorded during all vertical and oblique transects (Fig. 2).

The counting frames had graduation marks that allowed rough (± 1 cm) estimation of size of the observed animals.

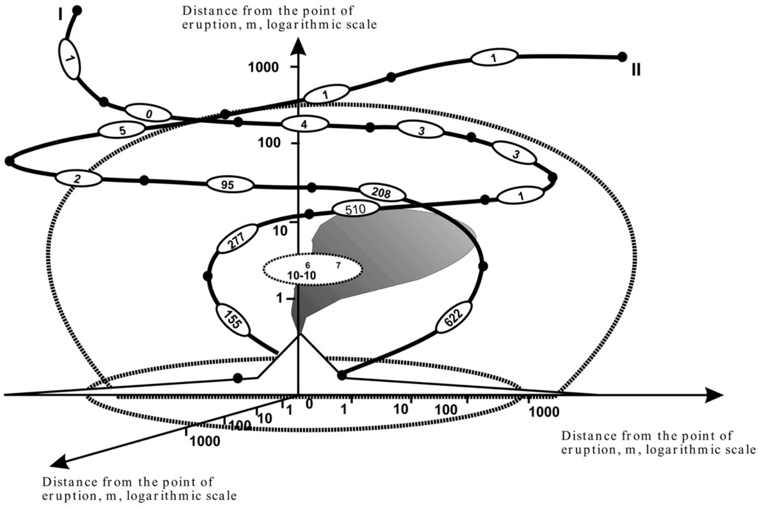

Figure 2. Observed plankton biomasses above Broken Spur vent field. Dives: I (observer A. L. Vereshchaka, St. 3678, "*Mir-2*", 2 Sept. 1996) and II (observer A. L. Vereshchaka, St. 3683, "*Mir-1*", 4 Sept. 1996). Different observations are separated by black dots, average plankton biomasses are shown within blank ellipses (mg m^{-3}). Biomasses in the central ellipse with dotted border indicate order of magnitude of the shrimp ["cloud"] biomass above black smokers (estimated from submersible window). Dotted line schematically marks outer border of vent community.

The counting volume was illuminated from the upper right- and upper left, in order to meet the following requirements: (1) minimum illumination so that the presence of transparent (ctenophores, etc.) and small (5-mm copepods) animals could be recorded; (2) illumination of the volume beyond the counting frame was minimized so as not to induce avoidance behaviour of animals. During the dives, information about observed animals (i.e. taxon and approximate length) was recorded onto audio tape. Depth was recorded simultaneously, usually every 5-10 m.

After transcribing the dive log tapes aboard the ship, the observer was able to estimate how many animals of each group had been observed within the selected depth ranges. For example, if six cyclothones (fishes) were observed between 400 and 420 m, the actual abundance of this animal in the 400-420 m layer was calculated as 6 ind examined volume^{-1} = 6 ind (3 m^2 * 20 m)$^{-1}$ = 0.1 ind m^{-3}. A specially designed computer program, PLANKTY, allowed fast treatment of plankton data and conversion of abundances to biomasses. The program calculated biomass from observed abundance and size data, using regressions of length and wet and carbon weight derived from animals sampled and analysed during several cruises of the Oceanology Institute Russia (see, for example, Vinogradov & Shushkina, 1987). The average wet weight of adult *Rimicaris exoculata* was estimated at 1 g, while the weight of 2-3 cm long juvenile vent shrimps of the genera *Rimicaris*, *Chorocaris,* and *Mirocaris* ranged from 0.2 to 0.4 g and 1-cm shrimp larvae were 0.01 g.

Results

The studied vent communities were dominated by bresilioid shrimp adults and larvae *(Alvinocaris markensis* Williams, 1988 and four undescribed species of the same genus; *Chorocaris chacei* Williams & Rona, 1986; *Rimicaris exoculata* Williams & Rona, 1986; *Iorania concordia* Vereshchaka, 1996 (this might be the juvenile stage of *R. exoculata*, but we followed the code of zoological nomenclature and kept a conservative approach, considering *I. concordia* as a valid species until a morphological revision of vent shrimps is done); *Mirocaris keldyshi* Vereshchaka, 1997 and *M. fortunata* Martin & Christiansen, 1995. On the seafloor, bivalves of the genus *Bathymodiolus,* bithograeid crabs, synaphobranchid fishes (*Ilyophis saldanhai* Karmovskaya & Parin, 1999)*,* copepods of the family Dirivultidae, *Globigerina*-like foraminiferans, and polynoid polychaetes were also significant components of the observed fauna. Previous studies have found that benthic organisms at these sites show horizontal zonation, this being most evident among the shrimp species (Segonzac et al., 1993). We also observed prominent zonation patterns in the water column, with similar patterns occurring at all the studied vent fields. Since the plankton communities over Broken Spur were surveyed in greater detail than the other fields, we will illustrate community structure using data obtained from this site. The plankton population, distribution, and biomass were similar at the other fields.

Within the first few metres above the sea floor, adults and juveniles of *R. exoculata* and *I. concordia* occurred in moving swarms. Locally, the biomass within this zone reached several kg m^{-3}, approximately seven orders of magnitude more than the total plankton biomass in the ambient water column (tenths of mg m^{-3}).

Outside the dense swarms of *R. exoculata* and *I. concordia,* sparser groups of small shrimps were regularly observed in the water column at distances of a few or several tens of metres above the hydrothermal mineral structures. Several slurp-gun samples, taken at different sites, contained only juveniles of *Chorocaris chacei.* From visual observations, these juveniles created a "cloud" of biomass about 50 m high and 100 m thick above the black smokers. Estimated biomass values ranged from 0.02 to 0.03 g m^{-3} outside the shrimp patches to 0.5-3.0 g m^{-3} within the shrimp patches, approximately two orders of magnitude more than the plankton biomass in the ambient water.

Beyond the "cloud" of *Chorocaris chacei,* dispersed shrimp were still the dominant group in the water column. These were small larvae that could not be sampled from the submersible. However, we were able to examine them carefully when the vehicle moved very slowly. Some were 1.5-2.0 cm long and identified as larvae and juveniles of *Alvinocaris* sp. and *Mirocaris* sp.. Smaller individuals about 1 cm long were impossible to identify morphologically and could have been younger stages of any of the vent shrimps. These animals were evenly distributed and dominated at 50 to 200 m, sometimes 300 m, above the bottom. Estimated biomass values range from 0.005 to 0.0l g m^{-3}, several times the plankton biomass in the background communities.

True pelagic animals (ctenophores, medusae, appendicularians, siphonophores, calanoid copepods, pelagic shrimps, etc.) were sporadically observed in the near-bottom layer. Their total abundance and estimated biomass did not exceed either 0.001 ind m^{-3} or 0.0005 mg m^{-3}. In essence, pelagic animals did not make a significant contribution to the near-bottom hydrothermal communities.

There were some notable differences in the distribution of shrimp and other plankton observed at Broken Spur compared to other MAR fields. At TAG, the species composition and vertical zonation were similar to those at Broken Spur. At Logatchev and Rainbow, the faunistic composition and the vertical scales were somewhat different. Bivalves of the genus *Bathymodiolus* became dominant along with *R. exoculata* and the total biomass of the benthic component was greater. More pronounced changes were observed in the plankton component of the Rainbow field; no zone of *Alvinocaris* + *Mirocaris* was seen and the biomass within the *C. chacei* zone was only one order of magnitude higher than in the ambient water column.

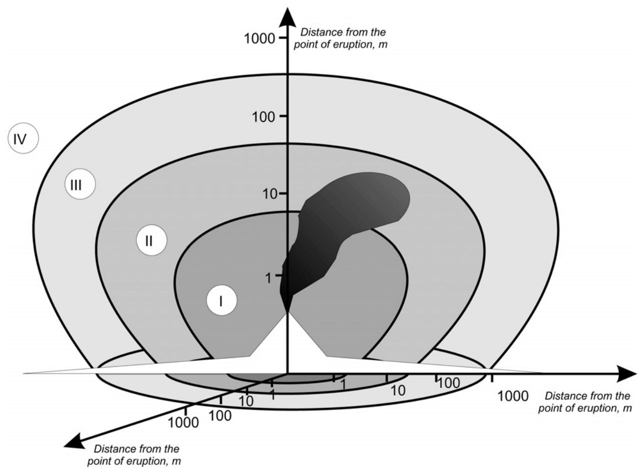

Figure 3. Schematic representation of the 3-dimentional structure of the hydrothermal community (a composite of all sites). Zones from the centre to periphery: (I) *Rimicaris exoculata* + *Iorania concordia* (biomass is seven orders of magnitude greater than background communities; (II) *Chorocaris chacei* (biomass two orders of magnitude greater than background); (III) *Alvinocaris* spp. + *Mirocaris* spp. + youngest unidentified stages of vent shrimps (biomass 2 to 3 times background); (IV) typical deep sea community.

Discussion

We used the horizontal and vertical distributions of the shrimp to develop a three-dimensional model of the MAR hydrothermal vent community, schematically represented in Fig. 3. Communities are organized around the point of fluid venting and are distinguished by three zones of decreasing biomass.

(1) The first zone is a few metres in diameter and dominated by *R. exoculata* and *I. concordia.* The benthic component is represented by the adults of the same species and, at some vent fields, by bivalves of the genus *Bathymodiolus* and gastropods of the family Peltospiridae. The biomass within this zone is seven orders of magnitude more than in the ambient water column.

(2) The second zone is tens of metres in diameter and dominated by the larvae of *C. chacei* and polynoid polychaetes. Abundances of shrimp larvae ranged from 0.04 to 0.06 ind m^{-3} outside the shrimp patches, to 1-5 ind m^{-3} inside the patches. Abundances of Polynoidae however, did not exceed 0.001-0.003 ind m^{-3} and their contribution to the total biomass was insignificant. The benthic component is represented by adults of the same species, *Mirocaris* sp. and by bythograeid crabs. The biomass within this zone is two orders of magnitude more than in the ambient water column.

(3) The third zone is a few hundred metres in diameter and is dominated by the larvae of *C. chacei* and *Mirocaris* sp.. The benthic component consists of adult *Alvinocaris markensis* plus synaphobranchid fishes, polyps, actinians, etc.. The biomass within this zone is several times more than in the ambient water column.

Some shrimp larvae may be found as far as 50-100 km from the vent fields (Herring, 1996), however it is unlikely that they play a significant ecological role outside the described zones, at distances of hundreds or thousands metres from the point of venting. Where the hydrothermal animals are generally absent, the community turns from hydrothermal to typical deep-sea water column species.

A simplified representation with a single vent site and a single point of fluid venting is shown Fig. 3. In fact, black smokers may have several orifices (e.g. Saracen's Head at Broken Spur field) in which case there would be several first level zones encompassed by a single second level zone. For hydrothermal fields with several vent sites and black smoker edifices, the three-dimensional picture becomes even more complex, with each black smoker edifice having its own second level zone and with the whole field being contained by a common third level zone. Furthermore, in order to accurately represent the complexity of the zones, we must eventually add the influence of near-bottom currents, as they constantly modify the shapes of the planktonic zones.

A similar three-dimensional structure is probably also characteristic of the Pacific vent communities where larvae of dominant benthic animals along with benthopelagic crustaceans can be abundant in the water column above vent fields (Wiebe et al., 1988; Kaartvedt et al., 1994; Mullineaux et al., 1995).

Conclusion

Vent communities should be regarded as three-dimensional, rather than two-dimensional, systems. Significant rates of dark CO_2 fixation and active chemosynthetic bacteria were found above the TAG and Broken Spur vent fields during the period of our study (Lein et al., 1997), confirming that chemosynthetically produced food is present in the zones where our observations were conducted. Conceptualizing vents in 3-D, to include the overlying water column, is a more accurate representation of the vent site in that it includes pelagic organisms that are able to utilise the organic matter dispersed into the near-vent environment. The outward flux of organic matter from the vents would be “caught” by these living “filters”. Food passing through the inner (first) zone would be assimilated in the second and third zones. As the organic flux decreases with distance from the source of venting, the community biomass also decreases. As a result, organic flux from the hydrothermal community into the background ecosystem appears to be extremely low (Vinogradov, 1997; Vinogradova, 1997), which accounts for the absence of enrichment of the typical deep sea fauna outside the vent fields.

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