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Communities of Soil Invertebrates near Iska-Shor Hydrogen Sulfide Springs in the Adak Nature Reserve (Komi Republic)

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Abstract—The results are presented of studies on soil invertebrate communities (nematodes, springtails, and large invertebrates) in shore ecosystems near hydrogen sulfide springs in the valley of the Iska-Shor stream in the Adak reserve and along river valleys at the northern boundary of the taiga zone of the Komi Republic. The taxonomic richness of the studied invertebrate groups does not change between the sampling plots. The total abundance and the abundance of individual trophic groups of springtails and large soil invertebrates decrease in plant communities near the outlet of sulfide waters, but the structure of these groups remains similar between the plots. On the contrary, the structure of nematode complexes differs between the ecosystems of the river valleys and near the hydrogen sulfide springs, where the abundance of mycotrophs increases.

Keywords: nematodes, springtails, large soil invertebrates, coastal habitats, Adak Nature Reserve, Komi Republic

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The ecosystems of hydrogen sulfide springs are unique natural objects for studying adaptations of organisms to extreme natural factors. They are widespread throughout the world; however, most of them have balneological properties, are easily accessible, and, hence, has long been put to human use and lost their natural appearance. Therefore, such ecosystems located in hardly accessible regions of the Far North deserve special attention as unique sites where the entire complex of organisms associated with these springs has survived. In the north of Europe, hydrogen sulfide springs are usually in fault and rock-fracture zones formed mainly in calcareous rocks of different ages with pH above 7.5 [1, 2]. Studies under these conditions have been performed only on algal–bacterial mats formed mainly by alkalophilic cyanobacteria, colorless and pigmented bacteria adapted to the specific composition of mineral waters, diatoms [1, 3], and hydrobionts dominated by chironomids [4]. Terrestrial ecosystems near the hydrogen sulfide springs have not yet been studied; meanwhile, soil alkalization takes place there, and calcareous soils develop in areas with close limestone and dolomite deposition. They may be classified as rare soils because of small distribution area and atypical properties [1]. In addition, shore habitats representing a transitional zone between aquatic and terrestrial ecosystems play an important role in maintaining a high level of ecological heterogeneity and biological diversity [5, 6]. At the same time, such habitats can be considered extreme due to periodic floods and droughts to which only certain organisms can adapt.

Soil invertebrates are an important component of biological diversity; they play an essential role in the ecosystem functions of soil, since they are involved in processes such as organic matter decomposition, humus formation, and the cycle of matter [7]. Nematodes are the most numerous and diverse group in soil zoocenoses, in particular, in subarctic ecosystems [8]. Morphological plasticity, physiological adaptation, and ecological diversity allow these worms to absolutely prevail among multicellular organisms and be resistant to various environmental conditions [9]. No less important components of soil biota are microarthropods, among which two taxonomic groups are dominant: springtails and oribatid mites. Springtails possess features characteristic of *R*-strategists (rapid reproduction and high fecundity, while oribatids are *K*-strategists with low metabolic level, developmental rate, and fertility [10]. However, both groups are sensitive to environmental changes: moisture, acidity, temperature, and a number of other factors [11, 12].

Among large soil invertebrates, the highest sensitivity to changes in moisture level is characteristic of earthworms, which reach the highest diversity in temperate latitudes [13], and also of millipedes [5], while factors highly important for actively moving beetles and spiders include the species composition and spatial distribution of vegetation and the type and thickness of the litter [14]. Consequently, taxonomic groups of soil invertebrates with different levels of diversity, abundance, trophic structure, and mobility will differently respond to environmental changes [15].

In this study, we attempted to determine whether the communities of nematodes, springtails, and large soil invertebrates change near the outlet of hydrogen sulfide waters. For this purpose, we studied mixed herb communities growing directly along the shores of hydrogen sulfide springs and in river valleys in the north of the taiga zone. We put forward the hypothesis that complexes of soil invertebrates formed near the outlet of sulfide waters are characterized by low taxonomic richness and abundance and by changes in the ratio of trophic groups.

MATERIAL AND METHODS

Characteristics of the study area. The Adak Nature Reserve was established in 1984 to preserve the landscape of the Usa River valley flowing in the taiga zone of the Komi Republic. A group of hydrogen sulfide springs in its territory is located the valley of the Iska-Shor stream (66°28′ N, 59°34′ E), which originates from a swamp 6 km above the springs. The waters of the hydrogen sulfide springs are formed due to penetration of highly saline formation waters into the zone of active water exchange along faults and fractures. The waters of the stream are transparent upstream of the hydrogen sulfide springs and milky white downstream to the mouth (about 3.5 km). The salinity of its waters varies from 0.9 to 1.4 g/L.

A total of five zones of discharge of hydrogen sulfide waters were distinguished. The first (I) and second (II) zones are located in the lower, swampy part of the valley on both sides of the stream. The third group of hydrogen sulfide springs (III) is about 2 km from the Usa River in a gorge where ascending bubbling-up flows are observed in the spring and a swampy hollow is located, which V.V. Rammo (cited from [2]) described as "nonfreezing small swamp that clearly stands out in color against the dark background of the rock and green vegetation." The fourth outlet of sulfide waters (IV), where they are discharged as a numerous jet flows, is 100 m upstream of the Iska-Shor. Finally, the fifth group of hydrogen sulfide waters (V) is at a distance of 3.2 km from the stream mouth. The water flow rate is about 20 L/s in discharge zones IV and V, decreasing to less than 2 L/s in zones I–III. Everything (soil, rocks, moss, etc.) in areas exposed to sulfide waters is covered with a gel-like film formed by accumulations of bacteria, algae, and fungi and sulfur deposits. The temperature of the spring waters is 5.0–9.8°C at pH 7.4–7.8. The air in the discharge zones has a strong odor of hydrogen sulfide, whose concentration in the water may vary from 39 to 92 mg/L [1, 2].

Sampling plots. Soil samples from mixed herb communities growing at a distance of 1–2 m from the hydrogen sulfide springs (discharge zones I, III, IV, and V) were taken in July 2018. A floodplain willow copse located 50 m upstream of the last discharge zone was selected as a control plot. In addition, we used previous data on floodplain meadows and willows in the Pechora and Bolshaya Rogovaya river valleys lying in the northern taiga subzone. A total of eight plots were selected; four of them were located near the hydrogen sulfide springs and the other four (control plots) were along river valleys. A more detailed description of the plots is given in Table 1.

Field methods. Five soil samples for nematodes (5 × 5 × 10 cm) and eight samples for springtails (10 × 10 × 10 cm) were taken from each plot (a total of 40 and 64 samples, respectively). Eight samples for studying large soil invertebrates were collected from each plot in the Pechora and Bolshaya Rogovaya valleys (a total of 24 samples). They had a size of 25 × 25 × 10 cm, in correspondence with the standard methods of macrofauna inventory [16]. In the Adak Reserve plots, it was impossible to take samples of this size in plots lying at the established distance from the hydrogen sulfide springs; therefore, eight 10 × 10 × 10 cm were taken from each of them (a total of 40 samples). The data on the macrofauna abundance based on the inventory of the lower number of samples were adjusted using a factor of 6.25 calculated as the size ratio of the largest sample (0.0625 m^2) to the smallest sample (0.01 m^2). It should be noted that the weather in the study region was dry and hot in 2018 (no rain for more than 20 days).

Soil physicochemical properties. Soil parameters were analyzed based on eight samples taken from the organogenic horizon in each plot. The analysis was performed in the Ecoanalytical Laboratory of the Institute of Biology, Komi Science Center. Soil moisture was determined gravimetrically by drying the samples at 105°C for 12 h; soil pH was measured potentiometrically in 0.01 M $CaCl_2$ extract; mass fractions of total nitrogen (N_{total}) and total carbon (C_{total}) were determined by gas chromatography on an EA 1110 CHNS element analyzer (Carlo Erba, Spain). Soil sulfur was not determined, since it was mainly in the form of hydrogen sulfide acid (H_2S) and its salts, and this acid is weak and cannot be quantified at pH 5.0–6.0. Soil samples were.

Soil-zoological parameters. To assess the abundance and composition of nematodes, they were extracted from a 50-g soil sample by the modified Berman method for 48 h, and the resulting material was fixed in 4% formalin. The taxonomic composition of nematodes was assessed by identifying no less than 100 specimens from each sample. Based on the classification of Yeates et al. [17], nematodes were divided into five trophic groups: bacteriotrophs, mycotrophs, polytrophs, predators, and phytotrophs. Each taxon was assigned a value based on the *c–p* Bongers scale (Bongers, 1990): from 1 (*R*-strategists, or colonizers,

Table 1. Brief characteristics of sampling plots

Plot no.	Coordinates	Locality	Plant community	Vegetation
		Hydrogen sulfide springs		
1	66°28′ N 59°35′ E	Adak (Iska-Shor stream, zones I–II)	Mixed herb communities	*Filipendula ulmaria* (L.), *Equisetum palustre* E., *E. fluviatile* L., *Cirsium heterophyllum* (L.) Hill, and *Archangelica officinalis* (Moench)
2	66°28′ N 59°34′ E	Adak (Iska-Shor stream, zone III)		*Filipendula ulmaria* (L.), *Equisetum palustre* E., *E. fluviatile* L., *Angelica archangelica* L., *Carex cespitosa* L., *Caltha palustris* L., etc.
3	66°28′ N 59°34′ E	Adak (Iska-Shor stream, zone IV)		*Filipendula ulmaria* (L.), *Geum rivale* L., *Carex cespitosa* L., *Angelica archangelica* L., *Galium boreale* L., etc.
4	66°27′ N 59°33′ E	Adak (Iska-Shor stream, zone V)		*Filipendula ulmaria* (L.), *Carex cespitosa* L., *C. vaginata* Tausch., *Angelica archangelica* L., *Veratrum lobelianum* Bernh., etc.
		Control area		
5	66°27′ N 59°33′ E	Adak (Iska-Shor stream)	Tall grass–sedge willow copse	*Filipendula ulmaria* (L.), *Veronica longifolia* L., *Cirsium heterophyllum* (L.) Hill, *Galium boreale* L., *Deschampsia cespitosa* (L.), *Equisetum fluviatile* L., and other herbaceous plants and sedges
6	66°54′ N 52°19′ E	Ermitsa (Pechora River)	Grass–herb willow copse	*Phalaroides arundinacea* L., *Deshampsia cespitosa* (L.), *Equisetum arvense* L., *Angelica archangelica* L., *Galium boreale* L., and other herbaceous plants and sedges
7	67°01′ N 61°38′ E	Bolshaya Rogovaya River	Grass–herb willow copse	*Deschampsia cespitosa* (L.), *Equisetum palustre* E., *E. fluviatile* L., and other herbaceous plants and sedges
8	64°52′ N 57°36′ E	Kedrovy Shor (Pechora River)	Herb–sedge community	*Carex cespitosa* L., *Galium palustre* L., *Filipendula ulmaria* (L.), *Deschampsia cespitosa* (L.), *Geranium sylvaticum* L., and other herbaceous plants and sedges

are characterized by short life cycles, significant fluctuations in abundance, high fecundity, and resistance to environmental damage) to 5 (*K*-strategists, or persistors, have low fecundity and are highly sensitive to environmental disturbances). Maturity index (ΣMI) was used as an indicator of soil ecosystem disturbance. It is calculated based on the ratio of nematode taxa with different ranks on the *c–p* scale [18]. To estimate the abundance of springtails, they were extracted using Berlese–Tulgren funnels in 96% alcohol for 7–10 days (the period sufficient for achieving the air-dry state of the soil). The life forms of springtails were identified according to Stebaeva [19] and their trophic guilds, according to Potapov et al. [20]. To estimate the abundance and structure of soil macrofauna communities, the samples were manually sorted out, and large soil invertebrates were extracted in the laboratory. They were divided into three trophic groups according to [21]. On the whole, about 3000 nematodes, 25000 microarthropods, and 740 large soil invertebrates were extracted from the soil samples.

Statistical data processing. Soil samples taken from the same plot were regarded as pseudoreplicates; therefore, they were pooled into one true replicate [22]. The quantitative parameters of physicochemical soil properties and soil invertebrates were calculated as mean values ± standard error of the mean. The significance of differences between the samples was estimated using the nonparametric Mann–Whitney test at $p < 0.05$. The ordination of soil fauna communities from different plots was performed by the method of nonmetric multidimensional scaling (NMDS) using the Bray–Curtis index, based on the relative abundance of their individual taxa. The results were statistically processed in PAST 3.0.

RESULTS

Soil physicochemical properties. Most of the estimated soil parameters did not significantly differ between the plots. However, the total nitrogen concentration proved to be significantly twice higher in the shore ecosystems of river valleys (Table 2).

Soil invertebrate complexes. The species richness of all studied soil invertebrate groups did not vary between the plots. In total, 49 nematode genera, 41 springtail species, and 16 families of large invertebrates were recorded near the outlet of hydrogen sulfide waters, compared

Table 2. Physicochemical soil properties and parameters of the community of soil invertebrates (mean ± SE) in plant communities near hydrogen sulfide springs and in river floodplains (control) in the Komi Republic

Parameter	Hydrogen sulfide springs ($n = 4$)	Control ($n = 4$)
Physicochemical soil properties		
Moisture, %	49.5 ± 3.0	54.6 ± 4.5
pH	5.6 ± 0.2	5.7 ± 0.2
N, %	0.7 ± 0.1^{a}	1.4 ± 0.2b^{b}
C, %	13.7 ± 2.2	17.6 ± 2.3
Taxonomic richness of soil invertebrates		
Nematodes (number of genera)	27.5 ± 3.0	27.5 ± 2.9
Collembolans (number of species)	21.5 ± 1.0	21.3 ± 3.8
Macrofauna (number of families)	10.5 ± 0.9	8.3 ± 1.1
Abundance of soil invertebrates		
Nematodes, ind./100 mg	1860 ± 684	1429 ± 127
Oribatids, ind./m^2	18600 ± 3884	38333 ± 13684
Collembolans, ind./m^2	8094 ± 1284^{a}	15828 ± 2524^{b}
Macrofauna, ind./m^2	112 ± 23^{a}	174 ± 26^{b}
Abundance of trophic groups of nematodes (ind./100 mg)		
Bacteriotrophs	628 ± 228	366 ± 50
Mycotrophs	537 ± 206^{a}	213 ± 58^{b}
Polytrophs	105 ± 28^{a}	328 ± 58^{b}
Predators	71 ± 21	185 ± 63
Phytotrophs	523 ± 418	341 ± 128
Maturity index (ΣMI)	2.5 ± 0.1^{a}	3.2 ± 0.1^{b}
Abundance of life forms of springtails (ind./m^2)		
Epiedaphic	1013 ± 210^{a}	5225 ± 867^{b}
Hemiedaphic	4913 ± 923^{a}	15466 ± 2969^{b}
Euedaphic	2168 ± 447	1478 ± 373
Abundance of trophic guilds of springtails (ind./m^2)		
EPMC	487 ± 117^{a}	3900 ± 935^{b}
EAMC	548 ± 125^{a}	2313 ± 413^{b}
HMC	5452 ± 1062^{a}	14809 ± 2807^{b}
EMC	1116 ± 238^{a}	431 ± 187^{b}
Abundance of trophic groups of macrofauna (ind./m^2)		
Saprophages	77 ± 18	120 ± 26
Zoophages	30 ± 8^{a}	52 ± 9^{b}
Phytophages	4 ± 2	11 ± 5

EPMC, epigeic plant and microorganism consumers, EAMC, epigeic animal and microorganism consumers, HMC, hemiedaphic microorganism consumers, EMC, euedaphic microorganism consumers. Different letters indicate significant differences between the plots (Mann–Whitney test, $p < 0.05$).

to 51 nematode genera, 46 springtail species, and 14 macrofauna families in samples from plant communities near the river valleys.

The average abundance of oribatid mites and nematodes also did not differ significantly between the plots. However, different trends were observed for mycotrophic and polytrophic worms: representatives of the former group increased in abundance in mixed herb communities near the outlet of sulfide waters, whereas the abundance of the latter decreased in this zone. The maturity index, calculated from the data on the soil nematode community, had lower values near the outlets of sulfide waters (Table 2). Unlike roundworms, the abundance of springtails, including epiedaphic and hemiedaphic species, and trophic groups (except euedaphic microorganism consumers) significantly decreased in soils near hydrogen sulfide springs. A similar trend towards a decrease in average abundance was revealed for the soil macrofauna, in which zoophages proved to be most sensitive (see Table 2).

The NMDS ordination demonstrated distinct differentiation between the structures of nematode complexes in the plots. The differences are conditioned by changes in soil acidity and moisture content, as well as by the nitrogen content (Fig. 1a). On the contrary, the communities of springtails and large soil invertebrates had similar structure in all shore ecosystems (Figs. 1b, 1c).

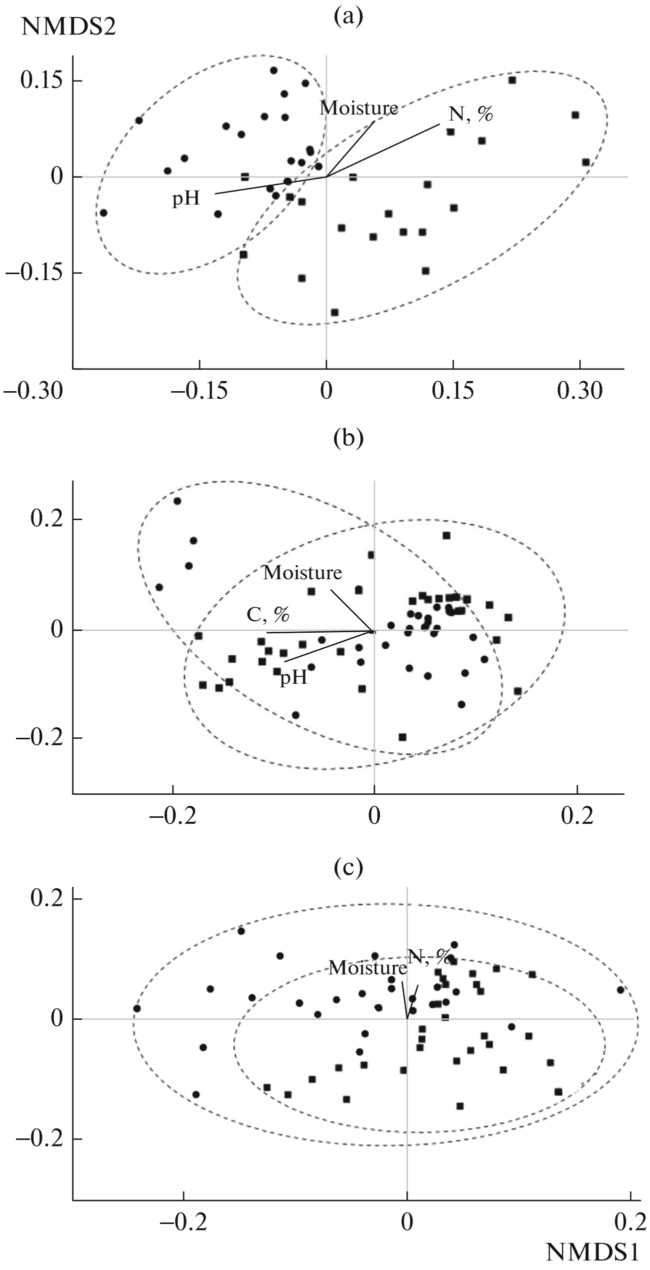

Fig. 1. NMDS ordination of (a) soil nematode, (b) springtail, and (c) large invertebrate communities in plots near hydrogen sulfide springs (circles) and control plots (squares).

DISCUSSION

The results indicate that the trophic structure and abundance of the studied groups of soil invertebrates change near the outlets of hydrogen sulfide waters, while their taxonomic richness remains unchanged. The absence of significant differences in the latter parameter among all representatives shows that the studied plant communities are inhabited by species that are relatively tolerant and ecologically flexible to shore conditions. Hydrological conditions in these biotopes are unfavorable, and species with different ecological strategies can survive there due to the high spatial heterogeneity of floodplains, which contributes to long-term stability of the communities as a whole [23]. In addition, the physicochemical properties of the soil in the studied plots showed no significant differences, except for the higher content of total nitrogen in the ecosystems of river valleys (see Table 2). According to the published data [24], increased soil nitrogen has no negative effect on the taxonomic richness of the soil biota.

As could be expected, the abundance of microarthropods decreased in herbaceous communities near the outlets of hydrogen sulfide waters (see Table 2). On the one hand, this may be due to the influence of vegetation; on the other hand, to a change in the fungi/bacteria ratio. It is known that oribatid mites and springtails have strong feeding preferences for certain plant species [11, 25]. For example, it was found that the abundance of springtails decreased mainly on account of epigeic and hemiedaphic species, which is confirmed by reduction in the number of trophic groups that consume plant and animal remains and microorganisms (see Table 2). This presumably indicates that the abundance of epiedaphic springtails greatly depends on the availability of suitable microhabitats (forest litter). In turn, the abundance of euedaphic forms and the corresponding trophic group of springtails increased in this case, which may be explained not only by their habitation in deeper soil horizons [12] but also by their relative independence from colonization substrate [26]. It is considered that representatives of this group feed on mycorrhizal fungi [27], regulate the microbial community in the rhizosphere, and are involved in decomposition of soil organic matter [20]. Despite the change in the total abundance of springtails and the abundance of their individual trophic groups and life forms, their community structure does not vary between the plots (Fig. 1b), which is apparently explained by similarity of soil physicochemical properties.

A similar trend towards a significant decrease in total abundance in the herbaceous communities near the outlets of hydrogen sulfide springs was recorded for large invertebrates (see Table 2), which are highly dependent on the "biotopic" factor, i.e., on the species composition and spatial distribution of vegetation and the pattern and thickness of the litter [14]. In addition, a significant decrease in the abundance of zoophages was recorded in these ecosystems. In our opinion, this may be due to a low supply of these areas with water that carries amphibiotic insects, aquatic organisms, and dead organic matter, which is then assimilated by terrestrial saprophages and microbophages [28]. It was previously found that the aquatic fauna in the hydrogen sulfide springs of the Iska-Shor creek was depleted and its quantitative development was low [4], which has probably accounted for the decrease in the abundance of oribatid mites, springtails, and a number of other saprophages serving as a potential prey for zoophages. This phenomenon is mentioned in the literature [28, 29] but has not been studied sufficiently. One should particularly note the dominance of saprophages in the plots (see Table 2), which is characteristic of shore ecosystems [30] where since organic remains are retained near the water edge in the form of silt, plankton, and plant detritus. This creates favorable conditions for the development of saprotrophic microorganisms, which are the main food resource of terrestrial saprophages [31]. Apparently, this is why the structure of large soil invertebrate communities proved to be similar between the plots (Fig. 1c).

On the contrary, the structure of the soil nematode complex differed between the sites near the outlets of hydrogen sulfide springs and the biotopes of the river valleys. This response, opposite to that of arthropods, may probably be explained by differences in their habitat. Being primary aquatic organisms, nematodes live in soil water droplets, while microarthropods inhabit pore spaces, and large invertebrates, which can make tunnels, inhabit the soil as such [32]. It is very problematic to determine the leading factors responsible for differences in the trophic and taxonomic structure between soil nematode communities from different plots. However, the obtained data indicate a higher stress level for nematocenoses near the outlets of sulfide waters. The abundance of polytrophic and predatory nematodes (*K*-strategists sensitive to environmental disturbances) [17] and the maturity index (ΣMI) decreased in these plots, which is evidence for significant disturbances in the soil food web [18] and implies a low level of trophic interactions in it [33, 34]. Having a wide range of trophic strategies, nematodes can be used as indicators of energy and nutrient fluxes through the bacterial and fungal channels in the soil [33, 35]. The increase in the abundance of mycotrophs in the ecosystems near the outlets of hydrogen sulfide waters shows that the role of the fungal component in the functioning of the soil food web is greater in these ecosystems than the valleys of large rivers.

CONCLUSIONS

The results presented above partially confirm the hypothesis that soil invertebrate complexes formed near the outlets of sulfide waters are characterized by a low level of taxonomic richness and abundance and by changes in the ratio of trophic groups. They show that the taxonomic richness of nematodes, springtails, and large soil invertebrates in plant communities near hydrogen sulfide springs has not changed, compared to that in river valleys. However, the abundance of microarthropods and macrofauna in shore ecosystems near hydrogen sulfide springs is decreased primarily on account of epiedaphic and hemiedaphic species and the corresponding trophic guilds of springtails and zoophages among large soil invertebrates. At the same time, the structure of springtail and macrofauna communities is very similar between the study sites, unlike that of nematodes. A decrease in the abundance of polytrophic and predatory worms and lower values of the maturity index (ΣMI) has been revealed for nematode complexes near the outlet of sulfide waters. The increase in the abundance of nematode mycotrophs and edaphic consumers of microorganisms among springtails in the shore ecosystems near the outlets of hydrogen sulfide waters indicates that the fungal component in these ecosystems plays a greater role in the functioning of the soil food web than in the valleys of large rivers.

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