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ORIGINAL

Faunal communities at sites of gas- and oil-bearing fluids in Lake Baikal

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Abstract Macro- and meiofaunal communities were examined at four geomorphologically distinct sites with different gas- and oil-bearing fluid characteristics in the northern, central and southern basins of Lake Baikal. All sites had elevated concentrations of bicarbonate, nitrate, sulphate and chloride ions in pore fluids, with highest values at the Frolikha vent. Elevated levels of iron ions were found in pore waters of the St. Petersburg methane seep and the Gorevoy Utes oil seep. The chemical composition of pore waters at the Malenky mud volcano was similar to that reported in earlier work. Consistent with published data, the Frolikha vent (northern basin) and the St. Petersburg methane seep (central basin) were characterised by methane of mixed genesis (thermogenic + biogenic), whereas the methane source was mainly thermogenic at the Gorevoy Utes oil seep (central basin) and biogenic at the Malenky mud volcano (southern basin). In contrast to marine seep ecosystems, the macrofauna was dominated only by amphipods, giant planarians and oligochaetes, whereas bivalves were absent; the meiofauna was similar to its marine counterpart, being dominated by nematodes, cyclops, harpacticoids and ostracods. A statistically significant positive relationship was revealed between faunal abundance and the availability of bacterial mats on seep sediments. Moreover, ANOVA tests showed significant increases in both meiozoobenthic and macrozoobenthic densities at "hot spot" vent/seep sites relative to discharge-free reference sites. The isotopic composition of carbon and nitrogen at various trophic levels of these benthic vent/seep communities was found to differ markedly from that reported by earlier studies for the pelagic and other benthic food webs in Lake Baikal. As in marine seeps, the macrofauna had variable isotopic signatures. Light δ^{13}C and δ^{15}N values suggest the utilization of chemosynthetically fixed and/or methane-derived organic matter. By contrast, the heavy δ^{13}C signatures of some mobile amphipods likely reflect consumption of photosynthetically derived carbon. These findings would at least partly explain why Lake Baikal is a notable outlier in global temperature–biodiversity patterns, exhibiting the highest biodiversity of any lake worldwide but at an extremely cold average temperature.

Introduction

Concentrated fluid and gas seeps are ubiquitous in the World's seas and oceans, existing in a wide variety of forms ranging from cold seeps (e.g. Sea of Okhotsk) to mud volcanoes (e.g. the Black and Caspian seas, and the Bay of Cadiz in the Mediterranean Sea). Similarly to hot vents, cold seeps support life at various trophic levels—e.g. tubeworms, shrimps and giant sulphur bacteria (e.g. MacDonald et al. 1989; Fisher 1990; Sassen et al. 1999; Sahling et al. 2002; Boetius and

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Suess 2004). Discharged fluids supply energy in the form of reduced compounds, enabling high productivity of biological communities. One main source of energy and carbon is methane (e.g. Gebruk et al. 2003; Thurber et al. 2010), which becomes incorporated into food webs through several pathways. Invertebrates can consume chemoautotrophic archaea (anaerobic methanotrophs; e.g. Valentine 2002) and aerobic methane-oxidising bacteria (e.g. Ding and Valentine 2008), as well as sulphide-oxidising or sulphate-reducing bacteria that assimilate methane-derived carbon from the dissolved inorganic carbon pool (e.g. Wegener et al. 2008). It is well established that examining the carbon and nitrogen isotope compositions of organisms inhabiting areas of fluid and gas discharge enables the detection of carbon and energy sources, as well as the determination of complex trophic interactions, including symbiosis and heterotrophy (e.g. Fisher et al. 1988; Van Dover and Fry 1989). Indeed, animals that contain chemoautotrophic symbionts typically have very low, often negative δ^{15}N values (e.g. Brooks et al. 1987), and biogenically sourced methane is isotopically depleted in ^{13}C (usually δ^{13}C of −50 to −110‰) and, thus, serves as its own biomarker (e.g. Whiticar 1999).

Hydrothermal phenomena have also long been known for freshwater bodies, in particular Lake Tanganyika along the East African Rift (e.g. Tiercelin et al. 1993), geothermal lakes of North America (e.g. Klump et al. 1988) and Lake Baikal in Siberia (e.g. Crane et al. 1991; Gebruk et al. 1993). Hovland et al. (2012) have recently provided a selective review of the environmental significance of seepage-related processes in both the marine and freshwater realm. In Lake Baikal, thermal vents associated with elevated temperatures and electro-conductivity in bottom water layers occur in, for example, Frolikha Bay in the vicinity of a low-temperature vent at the crossing of tectonic faults (Golubev 1993; Kipfer et al. 1996). Here, pore waters are enriched in microelements—Sr, Sc, Zn, Mo, Cr, W, Be, As, Nb, Ba—due to leaching of host rocks, as well as influx of fluids from deeper beneath the Earth's crust (Callender and Granina 1997; Granina 2008). Similarly to active hydrothermal sites in the Atlantic and Pacific, specific natural microbial communities that form microbial mats and consume deepwater reduced substances characterise this and other such areas in Lake Baikal (e.g. Crane et al. 1991; Namsaraev et al. 1994; Zemskaya et al. 2001, 2010; Kadnikov et al. 2012). At the Frolikha vent, the consumption of this microbial pool has been shown based on the carbon isotopic signatures of various benthic organisms, including sponges and turbellarians with δ^{13}C values reaching −60‰ (Kuznetsov et al. 1991; Grachev et al. 1995).

Besides vents, the last decade has seen a substantial advance in knowledge on the geomorphological and biogeochemical aspects of mud volcanoes, pockmarks, cold seeps, natural gas, oil and gas hydrates detected at the bottom of Lake Baikal, including the St. Petersburg methane seep, the Gorevoy Utes oil seep and the Malenky mud volcano (e.g. De Batist et al. 2002; Klerkx et al. 2003; Matveeva et al. 2003; Khlystov 2006; Kalmychkov et al. 2006; Khlystov et al. 2007; Granin et al. 2010; Krylov et al. 2010; Cuylaerts et al. 2012; Naudts et al. 2012; Poort et al. 2012). Many sites show discharge of variably sourced methane into the water column, in some cases accompanied by enrichment in other chemical compounds (e.g. Callender and Granina 1997; Kalmychkov et al. 2006; Granina 2008) that may serve as additional sources of energy and organic carbon for benthic communities. Yet, there are very few quantitative data on zoobenthic distribution patterns in the deeper waters of Lake Baikal. Takhteev et al. (1993) reported meio- and macroinvertebrate densities for some sites in the southern, central and northern basins but provided essentially no information on local geomorphological and geochemical characteristics. Based on newest findings by Cuylaerts et al. (2012), it can confidently be assumed that those sites were not associated with vents or seeps. Moreover, to date there have been no studies aimed specifically at evaluating benthic invertebrate density at deepwater hydrothermal vents and seeps in the lake. Based on C and N isotopic proxies, earlier works on shallow-water and, to a lesser extent, deepwater benthic food webs demonstrated an important role of autochthonous organic matter from primary production (Kiyashko et al. 1991, 1998; Yoshii 1999; Yoshii et al. 1999; Ogawa et al. 2000).

Within this context, the present study aimed primarily at examining (1) some key geochemical characteristics of sediments and benthic fauna at four different hydrocarbon discharge sites in Lake Baikal and (2) the structure of faunal communities at these sites. Combined with corresponding information from reference sites free of discharge, these data served to assess the importance of discharge-rooted carbon and nitrogen sources for these food webs.

Physical setting

This study was performed in 2008–2010 from aboard the RV *Koptyug* and RV *Vereshchagin* at four geomorphologically distinct sites: a low-temperature vent in Frolikha Bay in the northern Baikal basin (400–470 m water depth), an oil seep at Gorevoy Utes (900 m) and the St. Petersburg methane seep (~1,400–1,480 m) in the central Baikal basin, and the Malenky mud volcano (~1,360 m) in the southern Baikal basin. Concurrent observations from a *Mir* submersible revealed discharge of methane and other gases at all sites, and of liquid oil at the Gorevoy Utes site. Massive layers of methane hydrates occurred at the lake bottom at the St. Petersburg site. For inter-comparison of biological communities, two reference sites were selected in the central Lake Baikal sector: site 1 at 337 m water depth and site 2 at 1,425 m (Table 1).

Table 1 Site information (station, sampler, water depth, sediments, sampling date, number of samples, *n*) and meiozoobenthos density in Lake Baikal "hot spots" (*SQ* semi-quantitative sample)

Density (ind. m^{-2}), mean ± standard error, minimum–maximum

Nematoda	Cyclopoida	Harpacticoida	Ostracoda	Turbellaria	Others	Total
Frolikha vent, 55°30.94′N, 109°46.58′E						
St-F-1, MIR-BC, 404 m, light-brown silty sand, bacterial mats, 21.07.2010, *n*=2						
116,109 (110,580–121,638)	6,635 (6,635–6,635)	0	2,212 (0–4,423)	1,106 (0–2,212)	1,106 (0–2,212) (bdelloid rotifers)	127,168 (117,215–137,120)
St-F-2, MIR-BC, 430 m, silt, blue sand, bacterial mats, smell of hydrogen sulphide, 21.07.2010, *n*=3						
2,950±2,949 (0–8,846)	11,058±6,635 (4,423–24,328)	0	5,898±3,900 (0–13,270)	1,474±1,474 (0–4,423)	0	21,380±9,584 (4,423–37,580)
St-F-3, MIR-BN, 409 m, boulders, fine grey sand, detritus, bacterial threads, cyanobacteria, 24.07.2010, *n*=1 (SQ)						
10,000	24,000	1,000	45,000	0	0	80,000
St-F-4, MIR-BC, 473 m, oxic silt with sand, bacterial threads, 23.07.2010, *n*=2						
6,635 (6,635–6,635)	0	4,423 (4,423–4,423)	2,212 (2,212–2,212)	0	0	13,270 (13,270–13,270)
St-F-5, MIR-BC, 441 m, sponges, thin layer of oxic silt, bacterial mats, 25.07.2010, *n*=1 (SQ)						
1,300	2,560	0	2,340	0	31,200 (bdelloid rotifers)	37,400
Reference site 1, 53°17.06′N, 108°28.73′E						
St-6, GR, 337 m, oxic silt about 1 mm thick, then anoxic clay, 20.08.2009, *n*=4						
2,426±1,053 (422–4,641)	105±105 (0–422)	0	0	527±316 (0–1,266)	0	3,058±1,186 (422–5,063)
St. Petersburg methane seep, 52°53′N, 107°10′E						
St-SPb-7, MIR-BC, 1,425 m, oxic silt, diatom aggregations, 23.08.2008, *n*=1						
260	780	1,040	520	0	0	2,600
St-SPb-8, GC, 1,443 m, oxic silt, diatom aggregations, 23.08.2009, *n*=1						
764	127	255	382	127	0	1,655
St-SPb-9, GC, 1,464 m, anoxic clay, blue sand, bacterial threads, 22.08.2009, *n*=5						
2,278±544 (1,266–4,219)	169±103 (0–422)	0	1,181±450 (421–2,954)	422±189 (0–844)		4,051±807 (2,532–7,173)
St-SPb-10, GC, 1,483 m, oxic silt, diatoms, Fe-Mn concretions, 23.08.2009, *n*=1						
509	382	0	127	0	0	1,018
St-SPb-11, MIR-BC, 1,396 m, oxic silt, gas fluids, bacterial threads, 15.05.2010, *n*=3						
31,552±12,407 (8,404–50,876)	6,782±3,234 (442–11,058)	37,081±2,003 (7,298–75,195)	16,882±7,554 (1,990–26,539)	1,622±590 (442–2,212)	0	93,919±38,774 (18,577–145,966)
Malenky mud volcano, 51°91′N, 105°63′E						
St-M-12, GR, 1,357 m, thin oxic silt layer, then anoxic clay, 13.09.2010, *n*=6						
1,414±347 (303–2,424)	859±354 (0–2,424)	0	51±51 (0–303)	51±51 (0–303)	0	2,374±633 (303–4,545)
St-M-13, GR, 1,368 m, brown silt with crust, bacterial threads, 20.06.2010, *n*=5						
3,030±919 (909–5,757)	909±271 (303–1,515)	121±121 (0–606)	424±353 (0–1,818)	606±318 (0–1,515)	121±121 (0–606) (Gregarinida?)	5,211±886 (2,727–7,879)

Table 1 (continued)

Density (ind. m^{-2}), mean ± standard error, minimum–maximum

Nematoda	Cyclopoida	Harpacticoida	Ostracoda	Turbellaria	Others	Total
Gorevoy Utes oil seep, 53°18′N, 108°23′E						
St-GU-14, GR, 900 m, oil, bitumen, anoxic silt, 05.08.2009, *n*=2						
625 (417–833)	417 (0–833)	0	0	833 (0–1,667)	0	1,875 (833–2,917)
St-GU-15, GC, 900 m, oxic silt, bitumen, 05.08.2009, *n*=3						
4,219±1,934 (422–6,751)	281±281 (0–844)	141±141 (0–422)	141±141 (0–422)	0	141±141 (0–422) (Hydroacaria)	4,923±2,366 (422–8,439)
St-GU-16, GR, 904 m, oxic silt, bitumen, bacterial threads, 21.08.2009, *n*=4						
2,637±918 (844–5,063)	2,532±1,034 (0–5,063)	105±105 (0–422)	316±202 (0–844)	316±202 (0–844)	0	5,906±1,748 (3,376–10,970)
Reference site 2, 53°19.62′N, 108°19.52′E						
St-17, GR, 1,425 m, oxic silt, diatom aggregations, 20.08.2009, *n*=5						
591±215 (0–1,266)	169±103 (0–422)	253±103 (0–422)	0	0	0	1,013±169 (422–1,266)

The Frolikha vent and the Gorevoy Utes oil seep are located near the eastern shore in the northern and central basins of the lake respectively. These structures are associated with small local faults along the shore, which are clearly expressed in seismic records and incline towards the basin centres. Sediment thickness is about 2 km at the Gorevoy Utes oil seep. Migration of gas-bearing fluid and oil occurs from the central part of the basin along the lower sediment layers, and ascends along the fault (Khlystov et al. 2007).

The Malenky mud volcano and the St. Petersburg methane seep are found in the central parts of the southern and central basins of Lake Baikal respectively, associated with fault scarps visible not only in seismic records but also in the bottom relief. The displacement amplitude reaches some tens of metres. In the southern basin, the fault stretches north-eastwards and inclines north-westwards; in the central basin, the fault inclines south-westwards. Both faults can be traced to the depth of occurrence of a bottom simulating reflector (350–400 m). Seismic profiles of the Malenky mud volcano revealed evidence of an acoustically transparent chimney along which the discharge of gas-saturated fluid has been inferred (Van Rensbergen et al. 2002; Klerkx et al. 2006; Cuylaerts et al. 2012). Sediment thickness at both these study sites reaches 7.5 km (Hutchinson et al. 1992).

Materials and methods

Geochemical analyses

Pore water analyses were conducted on sediment cores (maximum length of 25 cm) collected by the deepwater manned *Mir* submersible. Upon arrival onboard the mother ship and within about 3 h of core retrieval, pore water samples were extracted every 2–3 or 5–10 cm, centrifuged initially at 10,000 and subsequently at 14,000 revolutions per minute, and stored at 4 °C. Anion/cation concentrations were assessed at the Laboratory of Hydrochemistry and Atmosphere Chemistry, Limnological Institute SB RAS, Irkutsk, according to techniques described by Zemskaya et al. (2010). In the present article, data are reported for the upper 25 cm of four cores collected by the *Mir* submersible at the Gorevoy Utes oil seep, the Frolikha vent and the St. Petersburg methane seep, and two cores from the Malenky mud volcano.

The isotopic carbon and nitrogen composition of benthic animals was determined on material collected from aboard the *Mir* submersible by means of a slurp gun device or a benthos net. Whole specimens of invertebrates or the muscle tissue of fish were oven dried at 60 °C and ground to a fine powder using an agate mortar and pestle. After removal of lipids in a chloroform/methanol treatment, isotopic analyses were performed at the Laboratory of Stable Isotopes (Far

Eastern Geological Institute of FEB RAS, Vladivostok). Subsamples of about 0.5 mg were weighed in tin capsules and analysed using a FlashEA-1112 elemental analyser coupled via ConFlo-III interface with a MAT-253 isotope mass spectrometer (ThermoQuest, Frankfurt). The relative contents of the ^{13}C and ^{15}N heavy isotopes in samples are defined as δ deviations (in ‰) from the corresponding standards:

$$\delta X\ (‰) = [(R_{sample} - R_{standard})/R_{standard}] * 1{,}000$$

where X is δ^{13}C or δ^{15}N, and R is the ratio of heavy to light stable isotope contents (^{13}C/^{12}C or ^{15}N/^{14}N). δ^{13}C and δ^{15}N values are expressed relative to the generally adopted international references V-PDB and AIR respectively. Analytical error was 0.1‰ for δ^{13}C and δ^{15}N.

Gases were analysed in gravity cores from all four sites: the Frolikha vent, three cores; the St. Petersburg methane seep, three cores; the Malenky mud volcano, ten cores; the Gorevoy Utes oil seep, 20 cores, including three cores collected from aboard the *Mir* submersible. Concentration and composition of hydrocarbon gases were determined onboard ship by means of a portable EKHO-PID gas chromatograph (Trofimuk Institute of Petroleum Geology and Geophysics, Novosibirsk) equipped with a flame-ionisation detector (2-m packed column of 2-mm inner diameter, Porapak sorbent, isothermal regime, T=100 °C). Measurements of δ^{13}C of hydrocarbon gases were performed at the Laboratory of Isotopic-Analytical Methods, Institute of Geology and Mineralogy SB RAS, Novosibirsk, using a Finnigan MAT253 mass spectrometer with a chromatograph GC Trace (capillary column Agilent Poraplot Q, 30 m, 0.32 mm, constant helium flux, T=30 °C). The error was 0.3‰ for δ^{13}C.

Benthic faunal communities

Macro- and meiofauna were co-extracted from material collected by means of a 0.25 m^2 Ocean grab sampler (GR), as well as gravity (GC) and short benthos corers (BC) from onboard the RV *Vereshchagin*. Samples were taken also by the manned *Mir* submersible using a benthos net (BN) and benthos corers. This article presents the results for 16 quantitative, one semi-quantitative and 12 qualitative zoobenthic samples covering the four study sites (see Table 1). Only those samples with an intact upper sediment layer were used for quantitative assessments.

For zoobenthos quantitative analysis, the sediment was retrieved from the grabs and benthos corers with tubes of 6.5 and 2.5 cm diameter respectively. Invertebrates were counted in the upper 5 cm layer. The sediment was washed through a gauze of 30 μm for the meiobenthos, and of 0.5 mm for the macrobenthos.

All organisms were identified to family or order levels, and some to species level. To enable comparison with published data (Takhteev et al. 1993), densities are expressed in number of individuals per m^2. Descriptive statistics and analysis of variance between groups (ANOVA) served to check for differences/similarities in both meio- and macrozoobenthos densities at fluid/gas discharge sites and reference sites (F test), and to reveal any influence of bacterial filaments/mats. The latter was assessed by single-factor ANOVA of log-transformed data (to reduce heteroscedasticity), followed by Tukey's test. Statistical analyses were conducted using the STATISTICA-6 software package for Windows 7.0.

Results

Frolikha vent

Geochemical characteristics

Visual observations revealed that Frolikha vent bottom sediments were covered with a thin layer of settled planktonic diatoms that formed suspension clouds at even the slightest movement of the *Mir* submersible. Landscape variability was high, including interspersed anoxic (black and blue) and oxic sediment zones. Large amounts of plant remains were found in some samples of reduced sediments with a strong smell of hydrogen sulphide. Moreover, fields of bacterial mats alternated with fields of grey-blue sediments perforated by small holes (see below). The lake floor showed a striking mosaic of oxic silt and pelite ooze, patches (2–3 m^2) of large black pebbles, light-coloured sand, and pale grey silt and pelite.

Compared with the reference sites, the pore waters of vent-associated sediments were characterised by elevated concentrations of several ions (Fig. 1, combined dataset for four cores from the Frolikha vent site).These included anions such as HCO_3^- (up to 10 mM), SO_4^{-2} (up to 0.2 mM), NO_3^- (up to 0.4 mM) and Cl^- (up to 0.5 mM), as well as cations such as Na^+ (up to 10 mM; data not shown). K+, Ca^2+, and Mg^2+ were also present. Σ ions generally increased with decreasing sediment depth. Ammonium was recorded in the surface pore waters of bacterial mats (up to 1.1 mM), but Fe ions were not detected.

Methane dominated the gas composition at the Frolikha vent. Heavy hydrocarbon gases (HHCGs) were represented by ethane, and heavier homologues were recorded only in trace amounts. The isotopic composition of methane was analysed in three samples from the upper (0–30 cm) sediment layer. In two samples, δ^{13}C-C1 was −63.5 and −65.4‰, and C_1/C_2 was 325 and 288 respectively. In the third sample,

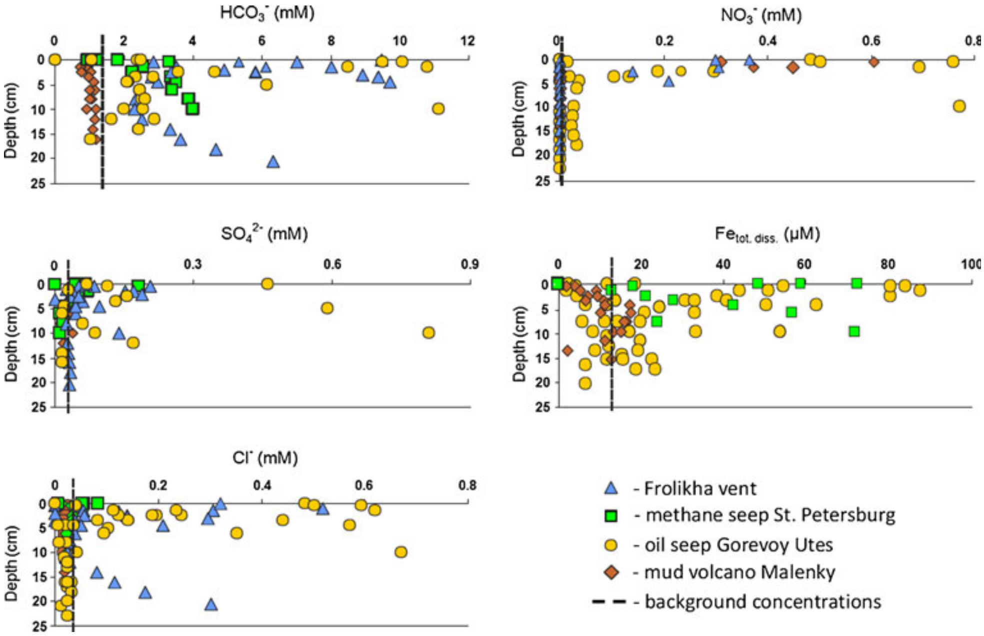

Fig. 1 Subsurface depth profiles of sulphate, bicarbonate, nitrate, chloride and total iron ions in sediment pore waters at the study sites in Lake Baikal

δ^{13}C-C1 was −36.8‰, and C_1/C_2 was 916. Thus, sediments from the Frolikha vent are interpreted to contain methane either of mixed genesis or of thermogenic origin. However, this thermogenic methane had a relatively small ethane admixture as thermocatalytic gas.

Biological community

In all, six taxonomic groups of meiofauna and four groups of macrofauna were identified at five stations at the Frolikha vent (Tables 1 and 2). The meiozoobenthos was represented mostly by nematodes (90 %), followed by cyclops, ostracods, harpacticoids and small turbellarians (mainly Rhabdocoelida). Free-living psammophilous ciliates were found in some samples.

Moreover, this study presents the first report of bdelloid rotifers in Lake Baikal deep waters. These rotifers belong to the family Philodinidae and perhaps are a new species. Bdelloids were found on bacterial mats where they made up more than 80 % of the meiozoobenthos.

Mean meiofaunal abundances varied from 13,270 to 127,168 ind. m^{-2} (Table 1). Abundance was significantly higher ($p<0.05$) than that recorded at reference site 1 (Table 3).

The macrozoobenthos included sponges, planarians, oligochaetes, larvae of chironomids, gastropods and amphipods. The sponge *Baikalospongia intermedia* detected also by Efremova et al. (1995) occurred in colonies of various sizes, sometimes exceeding several square metres and often in close vicinity to bacterial mats. Small light-violet specimens of the amphipod *Eulimnogammarus* sp. (~10–15 ind. 10 cm^{-2}), as well as cyclopoids and ostracods were found on the sponges. Aggregations of other species of amphipods were more often detected in patches of oxic sediments, where numerous "pores" are presumed to be the burrow openings of these amphipods. Similar patches (0.5–3 m in diameter) of amphipods were observed at this site in an earlier survey by Kuznetsov et al. (1991). Light brown-coloured flatworms (Tricladida, Dendrocoelidae, *Bdellocephala* sp.) were concentrated on boulders and pebbles (2–5 ind. ~10 cm^{-2}), together with the limpet *Pseudancylastrum frolikhae*. Another species of gastropods, *Benedictia pumyla* (5–15 ind. 10 cm^{-2}), was found on soft sediments between boulders adjacent to bacterial mats, as well as on boulders and gravel.

Chironomids identified previously as *Sergentia flavodentata* (Proviz 2005) were detected mainly in bacterial mats with reduced black sediments enriched in phytodetritus (Table 2). Here, the oligochaetes were a dominate group. According to Kaygorodova (2011), this would comprise 23 species, including the Baikal-endemic *Rhiacodriloides abyssalis* abundant on bacterial mats. These mats were inhabited also by the sculpin *Neocottus termalis*. The pelagic sculpin *Comephorus baicalensis* was observed near the bottom.

At the Frolikha vent site, macrofaunal abundances varied from ~4,400 to 42,000 ind. m^{-2} (Table 2). Only station St-F-1 differed statistically ($p<0.05$) from reference site 1 (Table 3).

Stable isotope signatures

δ^{13}C of sedimentary organic matter (SOM) ranged from −38.5 to −43.7‰ in bottom sediments and was −47.7‰ in bacterial mats (Fig. 2). These values are much higher than the δ^{13}C for methane of mixed genesis reported above, and are interpreted to reflect the combined signature of methanotrophic bacteria and of less ^{13}C-depleted sulphide-oxidising

Table 2 Density of macrozoobenthos at the study sites (for more information, see Table 1)

Site info.	Density (ind. m^{-2}), mean ± standard error, minimum–maximum				
	Oligochaeta	Amphipoda	Chironomidae	Others	Total
Frolikha vent					
St-F-1, MIR-BC, n=2	23,222 (17,693–28,750)	7,741 (2,112–13,270)	0	0	30,963 (30,962–30,962)
St-F-2, MIR-BC, n=3	6,635±3,378 (2,212–13,270)	14,006±4,834 (4,423–19,904)	0	0	20,641±7,697 (6,635–33,174)
St-F-3, MIR-BN, n=1 (SQ)	29,000	9,000	1,000	3,000 (Gastropoda)	42,000
St-F-4, MIR-BC, n=2	4,423 (4,423–4,423)	0	0	0	4,423 (4,423–4,423)
Reference site 1					
St-6, GR, n=4	5,670±2,270 (1,266–11,392)	0	0	0	5,670±2,270 (1,266–11,392)
St. Petersburg methane seep					
St-SPb-7, MIR-BC, n=1	0	520	0	0	520
St-SPb-8, GC, n=1	1,401	0	0	0	1,401
St-SPb-9, GC, n=5	3,207±510 (2,110–5,063)	1,013±392 (422–2,532)	253±169 (0–844)	0	4,473±819 (2,532–6,751)
St-SPb-10, GC, n=1	256	0	0	0	256
St-SPb-11, MIR-BC, n=3	14,375±6,665 (1,106–22,116)	0	0	0	14,375±6,665 (1,106–22,116)
Malenky mud volcano					
St-M-12, GC, n=6	12,930±2,810 (7,273–26,364)	0	303±192 (0–1,212)	0	13,233±2,085 (7,273–27,576)
St-M-13, GC, n=5	1,288±227 (909–1,818)	76±76 (0–303)	0	454±454 (0–1,818) (Polychaeta)	1,818±643 (909–3,636)
Gorevoy Utes oil seep					
St-GU-14, GC, n=3	972±367 (417–1,667)	0	0	0	972±367 (417–1,667)
St-GU-15, GC, n=3	8,157±2,072 (4,641–11,814)	0	0	0	8,157±2,072 (4,641–11,814)
St-GU-16, GC, n=4	6,329±789 (4,219–8,017)	527±316 (0–1,266)	0	0	6,856±1,039 (4,219–9,283)
Reference site 2					
St-17, GC, n=5	591±169 (0–844)	0	0	0	591±169 (0–844)

bacteria (*Thioploca*) and planktonic organic matter. δ^{15}N SOM ranged between 0.0 and 1.2‰, markedly lower than for planktonic diatoms that form the main source of organic matter in Baikal sediments.

All animals, including benthic fishes, collected from the site of discharge of gas-bearing fluids and from the associated bacterial mats were depleted in the heavy isotopes ^{13}C and ^{15}N (Fig. 2) compared to fauna from the reference sites. At the discharge site, animal δ^{13}C varied from −75.0 to −56.7‰, i.e. within the range of methane of microbial origin. The lowest δ^{13}C values were recorded in limpets (−73.3±2.8‰, n=3), chironomids (−72.5±0.7‰, n=4) and amphipods (−72.7‰). Animal δ^{15}N ranged between −11.2 and +4.0‰.

Oligochaetes feeding in bottom sediments at the Frolikha vent had less depleted δ^{13}C signatures (−62.5±4.7‰, n=5) but lower δ^{15}N signatures (−3.1±4.3‰) than other animals, with the exception of *P. frolikhae* (δ^{15}N of −10.4±0.7‰, n=3). The δ^{13}C and δ^{15}N recorded in flatworms (−63.9±1.0 and 0.3±3.1‰ respectively, n=2) suggest that the upper trophic levels of this benthic community are rooted in methanotroph production. Corresponding to the top of this benthic methanotrophic food web at the Frolikha vent, benthic sculpins had δ^{13}C of −67.5±1.9‰ (n=3) and δ^{15}N of 2.5±0.9‰. At the top of the pelagic food web of Lake Baikal, by contrast, pelagic sculpins had δ^{13}C of −26.6±0.5‰ (n=2) and δ^{15}N of

Table 3 ANOVA results of comparison between zoobenthos density in “hot spots” and reference sites (RS-1 and RS-2), the asterisks indicating statistically significant differences at $p<0.05$

Stations	Meiozoobenthos		Macrozoobenthos	
	F	p	F	p
St-F-1 (RS-1)	35.23	0.019*	387.4	0.000*
St-F-2 (RS-1)	49.00	0.010*	9.14	0.064
St-M-13 (RS-2)	27.53	0.007*	11.61	0.038*
St-M-12 (RS-2)	16.87	0.017*	375.41	0.003*
St-SPb-11 (RS-2)	313.40	0.000*	935.81	0.000*
St-SPb-9 (RS-2)	22.87	0.001*	23.50	0.009*
St-GU-14 (RS-2)	15.24	0.035*	2.84	0.340
St-GU-15 (RS-2)	117.91	0.000*	90.42	0.000*
St-GU-16 (RS-2)	85.83	0.000*	30.31	0.000*

12.9±1.3‰. Filter-feeding sponges (n=4) and small associated amphipods (n=4) had δ^{13}C of −65.0 to −54.6‰ and δ^{15}N of 0.9 to 4.0‰.

St. Petersburg methane seep

Geochemical characteristics

Mounds composed of massive layers of methane hydrates were observed near the St. Petersburg seep from aboard the *Mir* submersible. The lake bottom had patches of both oxic and anoxic surficial sediments consisting of sandy diatom ooze. In all, samples were analysed from four benthos cores and two benthos nets.

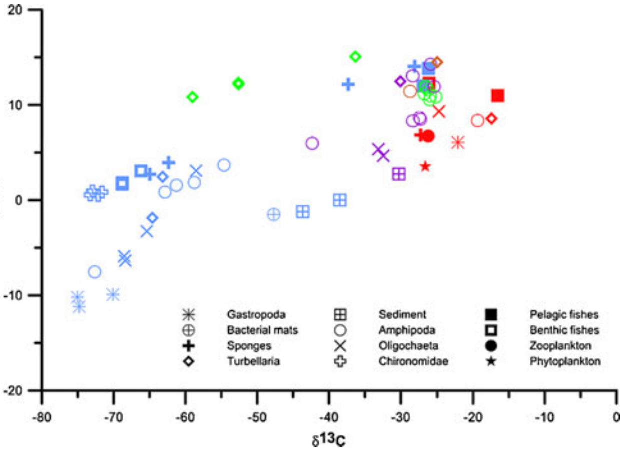

Fig. 2 Cross-plot of stable isotopes of δ^{13}C and δ^{15}N in tissues of benthic invertebrates, and pelagic and benthic fishes at the Frolikha vent (*blue*), St. Petersburg methane seep (*green*), Gorevoy Utes oil seep (*violet*) and Malenky mud volcano (*brown*), compared with corresponding data from Yoshii (1999) and Yoshii et al. (1999) for other sites in Lake Baikal (*red*, averaged data)

Compared with the reference sites, pore waters had elevated concentrations of anions (HCO_3^- up to 5 mM, SO_4^{2-} up to 0.2 mM; Fig. 1), cations (Ca^{2+} up to 3 mM, Na^+, K^+ and Mg^{2+}, data not shown), as well as iron (up to 80 µM; Fig. 1). Chlorine and nitrate were not found in these sediments. Concentrations of some ions (e.g. HCO_3^- and iron) increased with increasing depth in two benthos cores with oxic surface sediments, whereas maximum concentrations were recorded in the anoxic surface sediment layers of the other two cores.

Gases dissolved in pore waters were dominantly methane with a C isotopic composition typical of bacterial origin (δ^{13}C-C1 of −67.3 to −61.7‰), admixed with ethane of thermogenic origin (δ^{13}C-C2 of −30.2 to −28.0‰). Ethane contents were 0.23–0.33 % of the total gas volume, with complete absence of the homologues C_3 and C_4. During a *Mir* submersible dive in 2010, gas bubbles escaping from the lake bottom were sampled. Their δ^{13}C-C1 and δ^{13}C-C2 signatures did not differ markedly from those of gases dissolved in pore waters.

Biological community

In all, five taxonomic groups of meiofauna and three groups of macrofauna were identified at five stations at the St. Petersburg methane seep study site (Tables 1, 2). These groups were the same as those recorded at the Frolikha vent. By contrast, bdelloid rotifers were absent here. Both meio- and macrozoobenthos distributions were rather heterogeneous; maximum density was recorded at the top of a mound. In patches characterised by methane hydrates under a 15-cm layer of diatom ooze, together with surface sediments perforated by small holes and bearing bacterial filaments, the meiofauna was dominated by harpacticoids (up to 40 %).

Oligochaetes were a dominant group among the macrofauna; chironomids (*Sergentia* sp.) were recorded only at one station (St-SPb-9) with anoxic sediments (Table 2). Large white solitary flatworms (Tricladida, Dendrocoelidae) about 20 cm in length inhabited the tops and slopes of mounds. In 2009 (albeit not in 2010), aggregations of the amphipod *Polyacanthisca calceolat*a were recorded in near-bottom waters above thick layers of methane hydrates.

Mean densities of meiozoobenthos varied from ~1,000 to 94,000 ind. m^{-2}, and of macrozoobenthos from ~250 to 14,000 ind. m^{-2} (Tables 1, 2). In both cases, the values were significantly higher than at reference site 2 (Table 3).

Stable isotope signatures

Values of δ^{13}C for the large white flatworms (planarians) varied from −59.0 to −36.3‰ (n=4). Their δ^{15}N values varied between 10.8 and 15.1‰; these are much higher than in flatworms from the Frolikha vent but characteristic of other carnivorous animals of Lake Baikal (Fig. 2). The isotopic signature of these flatworms feeding on smaller animals can be attributed to an ingestion of methanotrophic bacteria by the meiozoobenthos of the St. Petersburg seep site. The amphipod *P. calceolata* had δ^{13}C and δ^{15}N values (−26.2±0.5 and 3±0.5‰ respectively, n=9) characteristic of the phytoplankton food web of Lake Baikal (e.g. Yoshii 1999; Yoshii et al. 1999).

Malenky mud volcano

Geochemical characteristics

The lithology and chemical composition of pore waters in earlier cores from the Malenky mud volcano have been reported in detail by Zemskaya et al. (2010). Consistent with these published findings, corresponding data for short cores of the present study indicated decreased concentrations of several major ions in the so-called zone 3 of Zemskaya et al. (2010) relative to background values (Fig. 1). As showed in that earlier study, this zone is characterised by the presence of methane hydrates of different morphology (laminated or lenticular) in subsurface sediments, which cause freshening of pore water at decomposition. Thus, concentrations of HCO_3^- reached only 0.8 mM, of SO_4^{2-} only 0.04 mM and of Cl^- only 0.01 mM. By contrast, values of NO_3^- (up to 0.6 mM) were higher than background (Fig. 1).

Methane of biogenic origin was identified in sediments of the Malenky mud volcano (δ^{13}C-C1 of −68.6 to −61.3‰, n=13). δ^{13}C-C2 data are not available. Based on Hachikubo et al. (2010), however, an admixture of minor amounts of thermogenically sourced ethane is possible at this site.

Biological community

In all, six taxonomic groups of meiofauna and four groups of macrofauna were identified at the two stations of the Malenky mud volcano (Tables 1, 2). However, the zoobenthos of these two stations differed in terms of density and group characteristics. The meiozoobenthos was dominated by nematodes (45–69 %) and the macrozoobenthos by oligochaetes (up to 98 %).

The meiofauna included tentatively identified gregarines, which have not been reported in Lake Baikal before. Polychaetes of the genus *Manayunkia* (Sabellidae) were detected at this site.

Abundance of zoobenthos was not high (~2,400–5,000 ind. m^{-2} for meiozoobenthos and ~1,800–13,000 ind. m^{-2} for macrozoobenthos; Tables 1, 2). Nevertheless, the values were significantly higher ($p<0.05$) than those of reference site 2 (Table 3).

Stable isotope signatures

Abnormally low values of δ^{13}C (−52 to −62‰) were found in chironomid tissues from the Malenky mud volcano, suggesting that this carbon originated from methanotrophic bacteria and that it was involved in the benthic food web of this site (Fig. 2). The isotopic composition of amphipods (δ^{13}C of −28.7‰, δ^{15}N of 11.4‰) and flatworms (δ^{13}C of −25.0‰, δ^{15}N of 14.5‰) was characteristic of the phytoplankton-based food web identified by, for example, Yoshii (1999) and Yoshii et al. (1999) for Lake Baikal.

Gorevoy Utes oil seep

Geochemical characteristics

Gas-saturated clay, silt, sand, and oil-impregnated sediments were detected at the Gorevoy Utes oil seep. Compared with the reference sites, pore waters had elevated concentrations of the anions HCO_3^- (up to 11 mM), SO_4^{2-}, NO_3^- and Cl^- (up to 0.9 mM; Fig. 1), as well as of the cations Ca^{2+} (up to 40 mM), K^+, Na^+ and Mg^{2+} (data not shown), and iron (up to 70 µM; Fig. 1). Such an abnormal composition of pore waters may result from a mixing of host pore waters and ascending oil/gas-bearing fluids, as well as microbial processes occurring in the sediments.

δ^{13}C-C1 values range from −77.7 to −38.5‰, and δ^{13}C-C2 values from −23.4 to −33.3‰. The data suggest an overall thermogenic origin of methane at this site. Nevertheless, the wide range of δ^{13}C-C1 values suggests some admixture of bacterially sourced methane. Indeed, δ^{13}C of −77.7 to −64.2‰ were detected at some distance from the site of oil and gas discharge. Admixture of HHCGs was low in most samples (C_1/C_{2+} values of 37.5 to 2,300). Such low C_2–C_4 contents can be attributed to (1) a mixing of thermogenically sourced gas with bacterially sourced gas formed more intensely in subsurface sediment layers and (2) a segregation of C_{2+} during gas migration from a deeper source towards the upper sediment layers.

Biological community

At the Gorevoy Utes oil seep site, aggregations of invertebrates were confined to inactive and active bitumen mounds (where oil discharged through “droppers”), and their close proximity. These mounds (up to 50 m high) were discovered from aboard the *Mir* submersible in 2008 (Khlystov et al. 2009). In all, six meiozoobenthos groups were identified at three stations at this site.

Numerous amphipods of different sizes and large white flatworms (Tricladida) inhabited these mounds. Oligochaetes, solitary "bushes" of small, whitish sponges and two species of small (shell<4 mm) gastropods (*Pseudancylastrum frolikhae* and *Choanomphalus bathybius*) were found on bitumen pieces broken off by *Mir* manipulators and lifted to the surface. Two new species of nematodes (Gagarin and Naumova 2010, 2011) occurred in large numbers inside small aggregations of bacteria, fungi and diatom detritus on the bitumen pieces. Ostracods (*Candona* sp.) were also detected there.

The bottom areas adjacent to the bitumen mounds were inhabited mostly by nematodes and cyclopoids (Tables 1, 2). Solitary large gastropods (*Benedicita fragilis*, 25 mm in size), three species of flatworms (Prolecithophora and Tricladida), at least 25 species of amphipods and at least 20 species of oligochaetes have been identified.

Animal abundance varied strongly at the Gorevoy Utes oil seep site (~2,000–6,000 ind. m^{-2} for the meiofauna, and ~1,000–8,000 ind. m^{-2} for the macrofauna). Nevertheless, abundance was significantly higher ($p<0.05$) than that recorded at reference site 2, with the exception of macrofaunal abundance at station ST-GU-14 (Table 3).

Stable isotope signatures

Compared to the Frolikha vent, SOM carbon in bottom sediments of the Gorevoy Utes oil seep site had heavier isotopic signatures (δ^{13}C of −30.8 to −33.5‰). These values are similar to those of oil and bitumoid (−30.5‰) present at the Gorevoy Utes site (Strizhev et al. 1990; Kontorovich et al. 2007). Bottom sediments collected near bitumen mounds had δ^{15}N values of 2.8‰ (Fig. 2). Oligochaetes associated with bitumen mounds had δ^{13}C and δ^{15}N values of −32.8±0.5‰ ($n=2$) and 5.0±0.5‰ ($n=2$) respectively, i.e. similar to the isotopic compositions of bottom sediments and oil hydrocarbons. This finding is attributable to microorganisms feeding on oil hydrocarbons.

The amphipod *Macropereiopus* sp. was ^{13}C-depleted (δ^{13}C of −42.3‰). This can be explained by a contribution of methane-derived carbon to some components of this benthic food web. Other commonly occurring species of amphipods (*Parapallasea lagowskii* and *Ommatogammarus* sp.) and flatworms had C and N isotopic compositions characteristic of the Baikal phytoplankton-based food web (see above for references).

General trends for zoobenthos

Combining the data described above, eight groups of meiobenthic and five groups of macrobenthic invertebrates were recorded at 17 stations at six distinct sites in Lake Baikal: compared to the two stations at the two reference sites, 15 stations at the Frolikha vent, St. Petersburg methane seep, Gorevoy Utes oil seep and Malenky mud volcano can be interpreted as "hot spots" in terms of faunal abundance (Tables 1, 2). Pairwise comparison showed that meiozoobenthos abundances at these hot spots significantly exceeded that of the reference sites. This was the case for macrozoobenthos abundances, too, except for the Frolikha station St-F-2 and the Gorevoy Utes station St-GU-14 (Table 3).

Single-factor analysis revealed a significant statistical dependence of meiozoobenthic abundance on the availability of bacterial filaments and mats at the sediment surface ($F=4.155$, $p=0.038$; Fig. 3a). This was not the case for macrozoobenthic abundance ($F=1.86$, $p=0.192$). Nevertheless, macrofaunal abundance on sediments devoid of bacterial filaments and mats was significantly lower than that for sediments bearing bacterial mats (Tukey's test, $p=0.043$; Fig. 3b).

Discussion

Lake Baikal is of tectonic origin and characterised by strikingly heterogeneous physicochemical conditions involving increased heat fluxes (e.g. Frolikha), discharges of mineralised and oil- and gas-bearing fluids (e.g. Gorevoy Utes), methane seeps (e.g. St. Petersburg) and mud volcanoes (e.g. Malenky). In 2008–2010, surveys aboard the deepwater manned *Mir* submersible helped detect bitumen mounds discharging methane-saturated oil, massive fields of methane hydrates and sites of bubble discharge (Khlystov et al. 2009; personal observations). At the present study sites—the Frolikha vent, St. Petersburg methane seep, Gorevoy Utes oil seep and Malenky mud volcano—analyses of pore water samples obtained by the *Mir* revealed that variations in major ion concentrations reached two orders of magnitude at the Gorevoy Utes oil seep and that, compared to background reference sites, iron concentrations were one order of magnitude higher at the Gorevoy Utes oil seep and St. Petersburg methane seep. This is consistent with earlier findings of considerable spatiotemporal variations in bicarbonate, nitrate, sulphate and chloride within and among specific Lake Baikal regions (Granina 2008; Zemskaya et al. 2001, 2010).

The results also revealed high heterogeneity in total zoobenthos abundance—from 100 s to 100,000 s of specimens per square metre, with maximum meio- and macrofaunal density at the Frolikha vent, minimum density at the Gorevoy Utes oil seep, and intermediate density at the Malenky mud volcano and the St. Petersburg methane seep. Moreover, benthic invertebrate abundance was overall higher than at the reference sites of the present study and other presumably discharge-free deepwater sites investigated by Takhteev et al. (1993; <3,000 ind. m^{-2}). Abundance

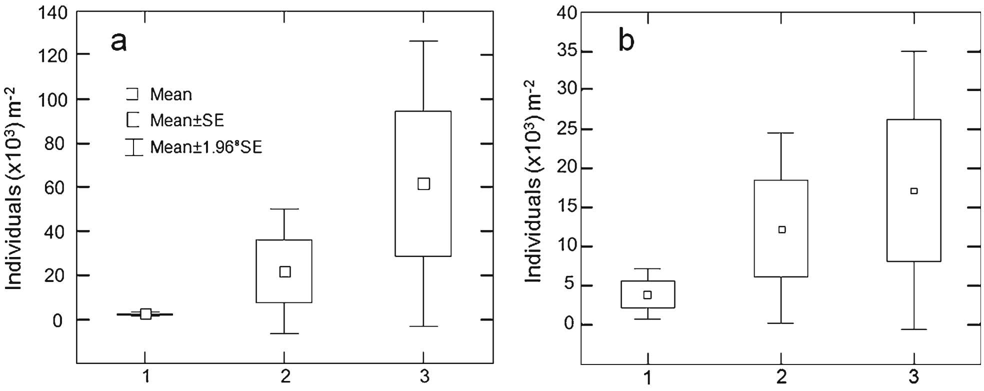

Fig. 3 Boxplots of mean abundance of **a** meiozoobenthos and **b** macrozoobenthos in sediments (1) devoid of bacterial filaments and mats, and (2) bearing white-coloured sulphur bacteria filaments or (3) white- to silvery-coloured bacterial mats

was highest on bacterial mats—characteristic also of marine seep ecosystems (e.g. Tarasov 2006)—and lowest in sediments devoid of bacterial filaments and mats. It should be noted that the highest heat fluxes and vast fields of bacterial mats were recorded only near the Frolikha vent (Golubev 1993; Namsaraev et al. 1994; Zemskaya et al. 2001; present study), whereas at other sites the sulphide-oxidising bacteria *Thioploca* occurs in smaller amounts as individual filaments. These data imply that differentiated interactions between discharge fluids and microorganism activity form the key driving force controlling benthic community structure at such Lake Baikal "hot spots". Spot discharges of mineralised and oil- and gas-bearing fluids in Lake Baikal deep waters would at least partly explain the patchy distribution of zoobenthic organisms.

High heterogeneity in zoobenthic abundance and community structure has also been observed in marine deep-water vents and seeps (e.g. Steichen et al. 1996; Gebruk et al. 2003; Cordes et al. 2010; Vanreusel et al. 2010). Similarly to marine seeps, the Baikal seep meiofauna were dominated by nematodes, cyclops, harpacticoids and ostracods. In the former, however, rotifers detected on the sulphide-oxidising bacteria *Thioploca* belong to the order Monogononta (Sommer et al. 2003), whereas those found on the bacterial mats of the Frolikha vent belong to the order Bdelloida. Again contrasting with marine seep ecosystems, the macrofauna of Lake Baikal seeps was dominated only by amphipods, giant planarians and oligochaetes, whereas bivalves were absent.

Another unique feature of Baikal seeps involves the chironomid larvae of the genus *Sergentia* inhabiting the 300 to >1,000 m depth zone, mainly in anoxic sediments associated with phytodetritus and on bacterial filaments or mats. Their patchy distribution in Baikal deep waters has been reported by Proviz (2008), and their high density in discharge areas by Klerkx et al. (2003). High abundances of chironomid larvae have been recorded also in some freshwater ecosystems with low oxygen concentrations (Malinin et al. 1992) and in reduced sediments with elevated concentrations of organic carbon and bacteria (Vinogradov et al. 2002). Chironomid larvae probably feeding on bacteria have light isotopic carbon composition (−62 to −73‰), suggesting the consumption of methane-derived carbon (Kuznetsov et al. 1991; Klerkx et al. 2003; present study). In addition to discharge areas serving as food source for the larvae, it can be speculated that ascending gas bubbles could act as a vector enabling the imago to reach the lake surface from greater depths.

Combining the results of the present study with data from earlier publications (Namsaraev et al. 1994; Klerkx et al. 2003; Kalmychkov et al. 2006; Krylov et al. 2010) shows that the Frolikha vent (northern basin) and St. Petersburg methane seep (central basin) are characterised by methane of mixed genesis (thermogenic+biogenic), whereas the methane source is mainly thermogenic at the Gorevoy Utes oil seep (central basin) and biogenic at the Malenky mud volcano (southern basin). Gases with δ^{13}C signatures similar to those of methane and ethane have been found also in, for example, the Caspian Sea (e.g. Ginsburg and Soloviev 1994), the Gulf of Mexico (e.g. Sassen et al. 2003), the Bay of Cadiz (e.g. Stadnitskaia et al. 2006), as well as in terrestrial mud volcanoes of Azerbaijan (e.g. Mazzini et al. 2009). Methane of biogenic origin was recorded at all study sites of the present article.

Methane of different genesis is involved in food webs of many lacustrine ecosystems, notably when chironomid larvae consume methane-oxidising bacteria, as demonstrated by Kiyashko et al. (2001) and Jones and Grey (2011). According to the latter authors, methane carbon can make up 60 % of total carbon in chironomid biomass. Earlier works by Kuznetsov et al. (1991), Gebruk et al. (1993) and Grachev et al. (1995) showed that carbon from biogenic methane was involved in the food web of the entire animal community inhabiting the Frolikha vent, including chironomid larvae, oligochaetes, sponges, planarians and amphipods, but those authors did not analyse nitrogen stable isotope signatures. The isotopic compositions of carbon and nitrogen can serve to link the pelagic and benthic phytoplankton-based food webs of Lake Baikal; previous studies reported δ^{13}C of −29 to −5‰, and δ^{15}N of 2 to 16‰

(Yoshii 1999; Yoshii et al. 1999). These values differ markedly from those recorded in most benthic organisms at hot spots in the present study.

The food webs of marine seep fauna, including interrelations with symbionts, have been widely discussed in the scientific literature. Studying three Pacific methane seeps, Levin and Michener (2002) revealed that, although most of the macrofauna appeared to be heterotrophic, light δ^{15}N (−2.73 to 3.00‰) and δ^{13}C (−60.96 to −32.20‰) values together provided evidence for chemoautotrophic symbioses in some animals. Those authors mentioned that the fauna likely consumed a variety of food sources, involving both photosynthetic- and methane-derived carbon. Similar results were obtained by Demopoulos et al. (2010) for seep fauna from the Gulf of Mexico. They also reported a broad range of infaunal δ^{15}N and δ^{13}C values, and argued that the infauna was largely heterotrophic with the exception of several taxa (nematodes and gastropods) having very light δ^{15}N (−6.1 and −1.1‰ respectively) and δ^{13}C (about −54‰ in both cases), indicating possible reliance on chemoautotrophic symbioses. Levin and Michener (2002) and Demopoulos et al. (2010) considered free-living bacteria (both chemosynthetic and heterotrophic) on seeps as a significant source of nutrients to the zoobenthos. Thurber et al. (2010), investigating heterotrophic and symbiont-bearing taxa of mega- and macrofauna from a New Zealand cold seep, suggested that sulphide oxidation supports symbiont-bearing taxa and methanotrophic symbionts. Moreover, they discussed some instances of co-occurring heterotrophic species with very light signatures, and their possible consumption of free-living bacteria. Based on these earlier findings, it is possible to put forward some hypotheses explaining the wide spectrum of stable isotope signatures recorded in benthic animals from the discharge sites of the present study.

As in marine seep communities, the Frolikha vent in Lake Baikal is inhabited by animals with a broad range of carbon and nitrogen isotopes. Heavy δ^{13}C values were identified in the pelagic sculpin *Comephorus baicalensis* (golomyanka), which is known to feed mainly on the pelagic amphipod *Macrohectopus branickii* (Kozhov 1963; Yoshii et al. 1999). Both golomyankas and amphipods were observed in the water column at the Frolikha vent from aboard the *Mir* submersible. Values of δ^{13}C (−26.6±0.5‰) and δ^{15}N (12.9±1.3‰) suggest that the golomyanka occupies the third trophic level in the lake pelagic phytoplankton food web, which is in agreement with the data obtained by Yoshii et al. (1999). Lighter δ^{13}C signatures (up to −75‰) were recorded in eight groups of invertebrates from the Frolikha vent. Judging by the carbon (less than −44‰) and nitrogen (<3‰) isotope values, sponges, planarians, limpets, chironomids, oligochaetes and benthic sculpins constitute the basis of chemosynthetic trophic pathways. Benthic animals from the Frolikha vent may be classified into three groups associated with different bottom substrates and different trophic pathways.

The first group includes the gastropod *Pseudancylastrum frolikhae* (δ^{13}C of −73.3±2.8‰, δ^{15}N of −10.4±0.7‰), which feeds on diatom detritus and free-living bacteria (including probably chemosynthetic bacteria) on hard substrates (pebbles and boulders), and is likely to be consumed by the predatory planarian *Bdellocoephala* sp. (δ^{15}N of 0.3±3.1‰). It should be noted that limpets and planarians coexisted on hard substrates with some species of amphipods, the latter being another potential food item for planarians.

The second group consists of amphipods (δ^{13}C of −72.7, δ^{15}N of −7.5‰) feeding on phytodetritus and bacteria, and in turn being consumed by the benthic sculpin *Neocottus termalis* (δ^{13}C of −67.9±1.5‰, δ^{15}N of 2.2± 0.7‰). According to Sideleva (2003), this benthic sculpin is an endemic species of the Frolikha vent. Amphipods and sculpins of this group were collected from bacterial mats. This second group also has oligochaetes (δ^{13}C of −65.3±4.5‰, δ^{15}N of −3.1±4.3‰) and chironomid larvae (δ^{13}C of −72.5±0.7‰, δ^{15}N of 0.73±0.2‰).

Interactions within the third group of invertebrates, including the sponge *Baikalospongia intermedia* (δ^{13}C of −63.7±1.8‰, δ^{15}N of 3.4±0.9‰) and amphipods of the genus *Eulimnogammarus* inhabiting these sponges (δ^{13}C of −59.4±3.6‰, δ^{15}N of 2.0±1.2‰), are unlikely to be trophic. Thus, amphipods concentrate on the sponge surface where they find food (detritus and bacteria accumulating on sponges), and a refuge from predators. Interestingly, two unique biotic assemblages discovered by Thurber et al. (2010) to be fuelled largely by methane are a hard-substrate, multi-phyla sponge-associated community and a soft-sediment assemblage dominated by ampharetid polychaetes.

Very light C and N isotopic signatures in animals of different trophic levels at the Frolikha vent are here attributed to consumption not only of methanotroph organic matter but also of chemotrophic bacteria that accumulate dissolved ^{13}C-depleted inorganic carbon formed via methane oxidation. As shown by Brooks et al. (1987) in their seminal paper on deep-sea hydrocarbon seep communities, light δ^{15}N values in various animals testify to interactions with chemoautotrophic symbionts of similar signatures. More recently, Olu-Le Roy et al. (2004) demonstrated that some species of bivalves from cold seeps of the Mediterranean Sea with light δ^{13}C (−23.6 to −44.6‰) and δ^{15}N (1.9 to −1.6‰) signatures bore symbionts in their gill filaments. Possible association with symbionts is currently being investigated in Lake Baikal seep macroinvertebrates, with preliminary evidence of ectosymbionts in, for example, nematodes.

In contrast to the Frolikha vent benthic community, the present data proved insufficient to trace trophic interrelations at the other discharge sites examined in Lake Baikal, where fauna at the Malenky mud volcano and the St. Petersburg methane seep is associated mainly with soft sediments, whereas that at the Gorevoy Utes oil seep occupies both soft and hard substrates (young and older bitumen mounds). Nevertheless, animals with light C isotopic values were identified there, too: planarians at the St. Petersburg methane seep, the amphipod *Macroperiopus* sp. and oligochaetes at the Gorevoy Utes oil seep, and chironomid larvae at the Malenky mud volcano. Moreover, mobile amphipods with heavy C signatures recorded at these three sites likely belong to the phytoplankton-based food web.

In conclusion, there is evidence of similarities and differences between Lake Baikal vent/seep ecosystems and their counterparts in the marine realm. Although more detailed understanding of the exact mechanisms of Baikal vent/seep functioning awaits further investigation, the present findings suffice to at least partly explain why Lake Baikal is a notable outlier in global temperature–biodiversity patterns, exhibiting the highest biodiversity of any lake worldwide but at an extremely cold average temperature (see Allen et al. 2002; Moore et al. 2009; Hovland et al. 2012).

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