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RESEARCH PAPER

Variation of sponge-inhabiting infauna with the state of health of the sponge *Lubomirskia baikalensis* (Pallas, 1776) in Lake Baikal

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Abstract

Our investigation was conducted during a period of ecological crisis in the coastal zone of Lake Baikal. Mass disease and mortality of the endemic sponges inhabiting the nearshore zone of the lake is one of the characteristics of this crisis. We identified and quantified infaunal organisms associated with *Lubomirskia baikalensis* (Pallas, 1776), which is experiencing mass morbidity and mortality. *L. baikalensis* specimens were subdivided into three groups depending on the degree of body damage they presented: "healthy", diseased, or dead. We found that infauna was almost absent from "healthy" sponges. Infaunal abundance in diseased sponges was 1820 times greater than that in "healthy" sponges, and varied in relation to the type of damage suffered by the sponges. Unaffected fragments of diseased sponges were inhabited by communities that exhibited an average abundance of 13 ind/dm^2, with Oligochaeta, Nematoda, Harpacticoida, and Chironomidae predominating. In the bleached fragments of morbid sponges, the average abundance of infauna was 1303 ind/dm^2, with Harpacticoida, Tardigrada, Cyclopoida, and Oligochaeta dominating. The highest concentration of infaunal animals (18,293 ind/dm^2) was observed in spots that were covered by filamentous cyanobacteria. Diverse and densely populated infaunal communities (4767 ind/dm^2) occurred in the dead sponges, with Nematoda, Tardigrada, Turbellaria, and Oligochaeta particularly abundant.

Keywords Sponge deterioration and mortality · Freshwater sponge consortium · Ecological crisis · Lubomirskiidae · Spongillina · Lake Baikal

Introduction

There are 238 known species of freshwater sponges (Spongillina), and they are widespread in lentic and lotic waters (Manconi and Pronzato 2015). One of the Spongillina families, Lubomirskiidae (4 genera, 15 species), has an extremely restricted geographic distribution (Efremova 2001; Manconi and Pronzato 2008, 2015). Members of the family are found only in Lake Baikal, the most ancient and deepest lake in the world, situated in the central part of Asia. Lake Baikal could be called "the lake of sponges" due to the abundance and species richness of the endemic Lubomirskiidae sponges and the important ecological role they play in the littoral benthic communities (Semiturkina et al. 2009). In the lake, these animals demonstrate an amazing variety of body structures. Their growth forms can be branched, globular, or encrusting, and sizes range from 1.5–2 cm to 1 m. In the recent past, these animals were very abundant and substantially affected the composition of the lake's underwater landscapes. Until mid-2000 (during the so-called pre-crisis period), encrusting sponges covered almost 100% of the bottom area of some coastal zone regions of the lake (Semiturkina et al. 2009).

A sponge is a biogenic substrate that shelters a rich and diverse fauna which presents various types of associations, including commensalism, mutualism, and parasitism (Kharchenko et al. 1989; Kamaltynov et al. 1993; Manconi and Pronzato 2008, 2015; Leite et al. 2016). Healthy freshwater sponges harbor the following animal groups: Cnidaria, Rotifera, Turbellaria, Nematoda, Oligochaeta, Hirudinea, Mollusca, Bryozoa, Hydrachnida, Crustacea, and different

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orders of Insecta (Rezvoy 1936; Konopacka and Siciński 1985; Trylis 1997; Gugel 2001; Gaino et al. 2004; Fusari et al. 2012; Boltruszko and Ejsmont-Karabin 2013; Manconi and Pronzato 2015). Associated animals can live on the sponge surface (epibionts), swim around its body (nectobionts), or live inside the sponge body (infauna).

Kozhov (1931, 1963) was the first to provide a detailed description of the fauna of the lake's stony littoral zone, including some data on the sponges' consortia. Kamaltynov et al. (1993) reported the first quantitative data on the branched sponge consortium in the lake and examined the dependence of the abundance of associated organisms on sponge biomass. Weinberg et al. (2003) investigated the relationships between the Baikalian sponges and their associated organisms, some of which turned out to be obligatory inhabitants. Thus, until now, there have been only two quantitative studies on the healthy consortium within *Lubomirskia baikalensis* (Pallas, 1776).[1]

The endemic sponges of Lake Baikal have recently attracted considerable interest from ecologists. The main reason for this is not their uniqueness but their large-scale demise in the coastal zone of the lake. Within the last 6 years, mass mortality and morbidity of endemic Lubomirskiidae sponges has been reported. According to Timoshkin et al. (2016), 30–100% of branched *L. baikalensis* specimens were found to be diseased, damaged, or dead during the period 2014–2015, depending on the location. Diseased Baikalian sponges are occurring lakewide, and all three growth forms can be affected (Timoshkin et al. 2016; Khanaev et al. 2018).

The deterioration of the sponges is accompanied by the mass development of epizoic cyanobacteria. At present, up to 20 species of cyanobacteria were discovered on the diseased sponges. Interestingly, producers of dangerous microcystins and paralytic shellfish toxins were found among them (Belykh et al. 2016, 2017). Filamentous cyanobacteria, together with diatom algae, tend to form foulings and slimy biofilms on damaged parts of the sponge body (Timoshkin et al. 2016). Such reddish-brown patches on the sponge surface are a main symptom of brown rot syndrome (Kulakova et al. 2017), recently described for Baikalian sponges. Specialists agree that the cyanobacterial films on Baikalian sponges are probably a response to disease, but not its cause (Khanaev et al. 2018).

Although consequences of the ecological crisis in the coastal zone of Lake Baikal are evident, potential causes are still being discussed. One of the most widely supported points of view hypothesizes that nutrient enrichment from human sewage is the main cause of such dramatic changes at many coastal sites of the lake (Kravtsova et al. 2014; Timoshkin et al. 2014, 2016, 2018; Khanaev et al. 2018). The current situation is reminiscent of the cultural eutrophication that occurred in the Laurentian Great Lakes from the late 1950s through the early 1970s. Nonetheless, ecological degradation of the nearshore zone of Lake Baikal may have multiple drivers, including lake level fluctuations (Zohary and Ostrovsky 2011), the input of toxic industrial contaminants (e.g., organochlorine pesticides) (Mamontov et al. 2000), and climate warming (Moore et al. 2009; Izmest'eva et al. 2016).

At present, the cause of the sponges' morbidity and mortality is unknown. An infectious disease agent or unfavorable changes in environmental conditions could be a supposed cause of the disease. For example, it was suggested that an increase in the methane concentration in the water column of Lake Baikal may have caused changes in the algal endosymbionts (zoochlorellae) of the branched sponges, resulting in the mass deterioration and death of the sponges (Denikina et al. 2016). For brevity, we use "diseased" throughout this paper to distinguish healthy from unhealthy sponges.

The purpose of our paper is to determine whether and how invertebrate communities associated with the branched Baikal sponge (*L. baikalensis*) respond to changes in the health status of the sponge. This study is the first to characterize the succession of invertebrates in lubomirskiid sponges transiting from "healthy" through unhealthy to the dead ones. As a first step, our work focused on the meiofauna dwelling inside the sponge body (infauna).

Materials and methods

Sampling was carried out quarterly from December 2015 through September 2016 (December 2015, March, June, September 2016) at two stations located in the southern basin of Lake Baikal (Fig. 1) near Cape Berezovy (51°30′11″N, 104°32′33″E) and Chernaya Bay (51°31′53″N, 105°03′7″E). A total of 31 sponge specimens were collected by SCUBA divers from depths ranging between 5 and 9 m (Table 2). Divers covered each sponge with a cloth bag of 74-μm mesh to prevent the escape of fast-moving associates (mainly crustaceans). Then the sponge was removed from the substratum and the bag was sealed. On the research vessel, each sponge specimen was rinsed in lake water to remove all animals living on the sponge surface (epibionts and nectobionts). This water and the water from each cloth bag were sieved and fixed in 10% formalin (every sponge was treated as a separate sample) and stored for future use. The samples of epi- and nectobionts will be the focus of future study and were not considered in the present paper.

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[1] We use *Lubomirskia baikalensis* (Pallas, 1776) as a valid name for the species in accord with Van Soest et al. (2012).

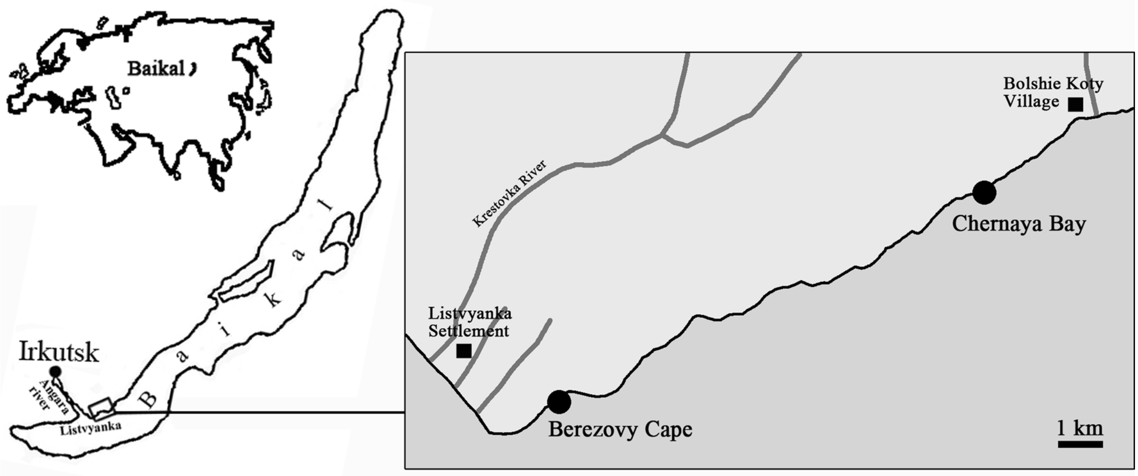

Fig. 1 Locations of sponge sampling sites (*black dots*) in the southern basin of Lake Baikal

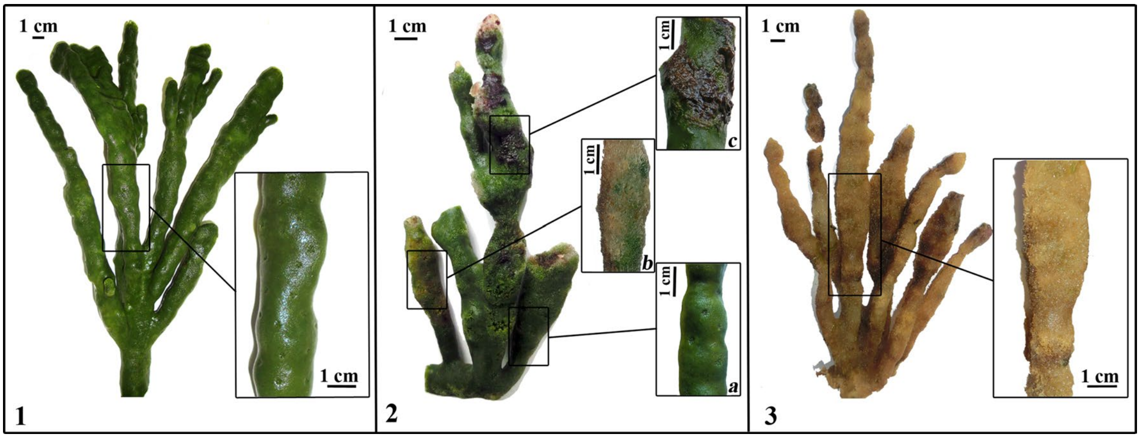

Fig. 2 Different states of health of branched sponge *L. baikalensis* individuals. **1** A "healthy" sponge. **2** A diseased sponge (*a* unaffected fragments, *b* bleached fragments, *c* fragments covered by a fouling or biofilm). **3** A dead sponge

Soon after sampling, we chose small fragments of sponge body that we would use to study the infauna. Chosen fragments were removed, photographed, weighed, and fixed in 70% ethanol. Before estimating the abundance of infauna in the sponges, we first classified each *L. baikalensis* specimen as "healthy", diseased, or dead. The typical color of healthy *L. baikalensis* is bright green (Rezvoy 1936; Kozhov 1963). Therefore, a sponge was considered "healthy" if it had a bright green body and the absence of any damage, tissue bleaching, patches, cyanobacterial foulings, or other atypical films (Fig. 2.1). If the sponge color differed from green and the features above were present, the sponge was considered to be diseased (Fig. 2.2). If we observed necrotic areas on the sponge body and it had a brownish color (signs of decay) or foulings/biofilms on the surface, the sponge was considered dead (Fig. 2.3). It should be noted that, at present, even sponges that look green and vigorous cannot be considered to be truly healthy, so we considered them to be relatively "healthy".

We chose random fragments on different parts of the branches (apical, middle, and basal) of "healthy" and dead sponges. From diseased sponges, we cut off fragments and classified them as either (a) unaffected, (b) bleached (sponge fragments with destroyed tissue and without colorful endosymbionts), or (c) covered by a fouling or biofilm (Fig. 2.2). Biofilms were classified as one- or two-layered coverings formed by diatom algae and cyanobacteria. Foulings consisted of mats of filamentous cyanobacteria. In the laboratory, we carefully macerated sponge fragments and collected all the meiobenthic animals under a stereomicroscope. In this work, the term "meiobenthos" denotes an assemblage of motile bottom aquatic animals (small metazoans and large protozoans) with body lengths ranging from 0.3 mm up to 4 mm (after Kurashov 1994). Organisms were identified to the lowest practical taxonomic level and stored in 70% ethanol. To identify animal species and cyanobacteria, we used a compound microscope (4×, 10×, 40× magnification) and up-to-date guides and keys (Semernoy 2004; Komárek and Anagnostidis 2005). Sörensen's distance was used to compare the degree of similarity of species assemblages inhabiting sponges in different states of health (Shitikov et al. 2003). A taxonomic group or species was characterized as dominant if its contribution to the total abundance was higher than 5% (Lazareva 1997). The number of individuals was standardized to 1 dm^2 of sponge surface (mean ± standard error of mean), as most of the animals inhabited near-surface layers of the sponge body. The area of the sponge surface was computed from photos using the program Image-Pro Plus 7.0. Only part of the data (33 samples) were calculated for 100 g of wet sponge (Table 2) to permit comparison with the results of Kamaltynov et al. (1993), who quantified the fauna associated with absolutely healthy *L. baikalensis* during the pre-crisis period.

Results and discussion

Biodiversity

The sponge body acts as a fairly stable biotope, providing its inhabitants with favorable conditions for their development and reproduction. Fauna associated with freshwater sponges includes many taxa (Manconi and Pronzato 2015). The same is true for the Baikalian branched sponge, *L. baikalensis* (Kamaltynov et al. 1993; Weinberg et al. 2003). In the case of infauna, only scarce oligochaetes *Nais* sp. and a cyclopoid copepod, *A. spongicola* (found exclusively in sponge oscula) were noted previously inside healthy individuals of *L. baikalensis* (Kamaltynov et al. 1993).

Infaunal associates of *L. baikalensis* in different states of health belonged to 12 taxonomic groups (Table 1). We only found representatives of Nematoda and Oligochaeta in the bodies of "healthy" sponges. In contrast, infaunal communities of diseased and dead sponges were taxonomically richer, and they included all 12 taxa, with Nematoda, Tardigrada, Oligochaeta, and Crustacea dominating in terms of abundance. Interestingly, the groups Rotifera and Tardigrada were observed among associated fauna (including epi- and nectofauna) for the first time.

In our study, 53 taxa in total were recorded for *L. baikalensis* infauna (Table 1). More infaunal taxa were observed in diseased (40 taxa) than in dead (31 taxa) sponges. The fauna of "healthy" *L. baikalensis* was distinctly different from those of diseased and dead sponges (5 and 6% similarity, respectively, using Sörensen's index). In contrast, the faunas of diseased and dead sponges had a high value of similarity (58% with Sörensen's index). "Diseased sponges" was quite a heterogeneous group, as each diseased sponge specimen exhibited different types of damage (Figs. 2.2, 4). That is why we also compared the taxonomic compositions of unaffected fragments, bleached fragments, and fouling-covered fragments of diseased sponges. Sörensen's index showed that the fauna of the unaffected fragments was most similar to that of "healthy" sponges' (25% similarity), but the faunas of bleached fragments and fouling-covered fragments were most similar to each other (50% similarity). We also found that faunas of dead sponges and the bleached fragments of diseased sponges (54%) were the most similar according to Sörensen's index.

Lubomirskia baikalensis infauna appears to be less diverse than that of Spongillidae representatives belonging to the other family of freshwater sponges, which is cosmopolitan. Konopacka and Siciński (1985) found 17 taxonomic groups represented by 74 species of macrofauna associated with Spongillidae in the River Gać. Such rich biodiversity of faunal associates in Spongillidae is largely the result of the presence of different orders of Insecta (Gugel 2001; Gaino et al. 2004; Sokolova and Palatov 2014) in these sponges. The same authors also noted that "dead" colonies (i.e., colonies in a state of anabiosis) of these sponges contained more taxonomic groups than did living colonies. Such a situation is similar to that which we have reported for the infauna of dead *L. baikalensis*. The main difference is that dead colonies are a natural part of the life cycle of Spongillidae, but not for Lubomirskiidae.

Infauna of "healthy" *L. baikalensis*: density and composition

The occurrence of invertebrates inside the sponge body is common for freshwater Spongillidae. Some typical infaunal associates of *Spongilla* have been known for a long time (e.g., neuropterans *Sisyra*, trichopterans *Leptocerus* and *Ceraclea*, chironomids, and hydrachnids *Unionicola*) (Rezvoy 1936). In contrast, only a few specimens of Nematoda and Oligochaeta were found inside the bodies of "healthy" *L. baikalensis* sponges (Table 2, Fig. 3).

Differences in body structure between lubomirskiid and spongillid sponges may explain the disparity between their infaunal assemblages. The body of a healthy *L. baikalensis* is firm and rubbery with a well-developed dermal membrane and a strong skeleton (Rezvoy 1936). Only certain amphipods of the genus *Eulimnogammarus* are able to gnaw holes into the body of *L. baikalensis* (Rezvoy 1936; Kamaltynov et al. 1993; Weinberg et al. 2003). For Spongillidae, oligochaetes and various insect larvae can easily carve their way inside the sponge body and use it as a food source and building material (Rezvoy 1936; Gaino et al. 2004).

Therefore, the present study confirms that there is a very low abundance of infaunal invertebrates inside "healthy"

Table 1 List of dominant infaunal species within endemic *L. baikalensis* sponges in different states of health: “healthy”, diseased (a: unaffected fragments of the diseased sponges; b: bleached fragments; c: fragments covered by foulings/biofilms), and dead

Taxa	“Healthy”	Diseased			Dead
		a	b	c	
Ciliophora	–	–	–	–	+
Turbellaria					
Macrostomum sp.	–	–	–	+	++
Baikalobia copulatrix (Korotneff, 1912)	–	–	–	+	–
Geocentrophora sp.	–	–	+	–	–
Opisthocystis angarensis (Sibirjakova, 1929)	–	–	–	–	+
Opisthocystis sp. (*sabussovi* ?)	–	–	–	–	+
Gyratrix hermaphroditus Ehrenberg, 1831	–	–	–	+	++
Dalyellioida sp.	–	–	–	–	+
Kalyptorhynchia sp.	–	–	–	+	+
Nematoda					
Tobrilus saprophagus Naumova et Gagarin, 2017	–	–	+	–	++
Tobrilus sp.1	–	–	–	+	–
Tobrilus sp.2	+	–	–	–	–
Eutobrilus sp.	–	++	+	++	–
Tripyla sp.	+	–	–	–	–
Monhystera paludicola de Man, 1881	–	–	+	–	+
Eumonhystera filiformis (Bastian, 1865)	–	–	–	–	+
Ethmolaimus pratensis de Man, 1880	–	–	–	+	–
E. pilosus Shoshin, 1998	–	–	–	–	+
Allodiplogaster mordax (Shoshin, 1989)	–	–	–	–	++
Allodiplogaster sp.	–	–	–	–	+
Oligochaeta					
Machetna koshovi (Sokolskaya, 1962)	–	–	+	–	–
Machetna sp.	–	+	+	–	+
Nais baicalensis Sokolskaja, 1962	–	–	+	–	+
N. similis Semernoy, 1984	–	–	++	–	++
N. tatijanae Semernoy, 1984	–	–	++	–	++
Chaetogaster diaphanus litoralis Semernoy, 1985	–	–	++	–	+
Ch. paucus Semernoy, 1985	–	–	+	–	+
Ch. cf. *crocodilus*, Semernoy, 1985	–	–	+	–	–
Ch. gavrilovi Semernoy, 1985	+	++	+	+	+
Tubificidae gen. sp. juv.	–	–	–	+[a]	–
Enchytraeidae gen. sp. juv.	–	+[a]	–	–	–
Rotifera					
Filinia terminalis (Plate, 1886)	–	–	–	–	+
Lecane bulla (Gosse, 1886)	–	–	+	+	–
L. lunaris (Ehrenberg, 1832)	–	–	+	–	–
Euchlanis ligulata Kutikova et Vassiljeva, 1982	–	–	+	–	–
Dicranophorus sp.	–	–	+	+	–
Bdelloidae gen. sp.	–	–	+	+	+
Harpacticoida					
Harpacticella inopinata Sars, 1908	–	–	++	–	–
Bryocamptus (*Rheocamptus*) *rylovi* Borutzky, 1931	–	–	+	+	+
B. (*Rh.*) *baikalensis* Borutzky, 1931	–	++	++	+	–
B. (*Rh.*) *denticulatus* Borutzky et Okuneva, 1972	–	–	–	++	+
Attheyella (*Ryloviella*) *baikalensis* Borutzky, 1931	–	–	–	+	–
Moraria schmeily van Douwe, 1903	–	–	+	–	–
Canthocamptus (*Canthocamptus*) *gibba* Okuneva, 1983	–	–	+	++	–

Table 1 (continued)

Taxa	"Healthy"	Diseased			Dead
		a	b	c	
Echinocamptus (*Limocamptus*) *baicalensis* Borutzky, 1931	–	–	+	–	–
Cyclopoida					
Acanthocyclops galbinus Mazepova, 1962	–	–	++	+	+
A. spongicola Mazepova, 1962	–	–	–	+[a]	–
Cladocera					
Alona labrosa Vasiljeva et Smirnov, 1969	–	–	+	–	+
Amphipoda	–	–	+	+	+
Ostracoda	–	–	+	+	+
Chironomidae	–	+	+	++	+
Tardigrada					
Mixibius sp.	–	–	++	++	++
Isohypsibius cf. *baicalensis*	–	–	–	–	+

Nematodes were identified mostly to genus level because of the predominance of juvenile specimens and the lack of mature nematodes

Two "+" symbols indicate a dominant taxon

[a] Rare specimen

Table 2 Average abundance of infauna for *L. baikalensis* sponges in different states of health

	No. of sponge specimens	Average infaunal abundance			
		ind/dm^2	No. of samples	ind/100 g	No. of samples
"Healthy"	5	3 ± 2	16	8 ± 4	16
Diseased	22	5461 ± 1496	58	167 ± 85	15
Dead	4	4767 ± 2174	9	5442 ± 1608	2

L. baikalensis sponges (5 ± 4 ind. per 100 g wet sponge weight). This is similar to previous data obtained for Baikalian sponges during the pre-crisis period (Kamaltynov et al. 1993). It is likely that a few nematodes and oligochaetes inhabit the *L. baikalensis* body where the sponge surface experiences normal, low-level damage (scratches, cracks, cavities). Consequently, rich and abundant infauna is uncharacteristic of absolutely healthy *L. baikalensis*.

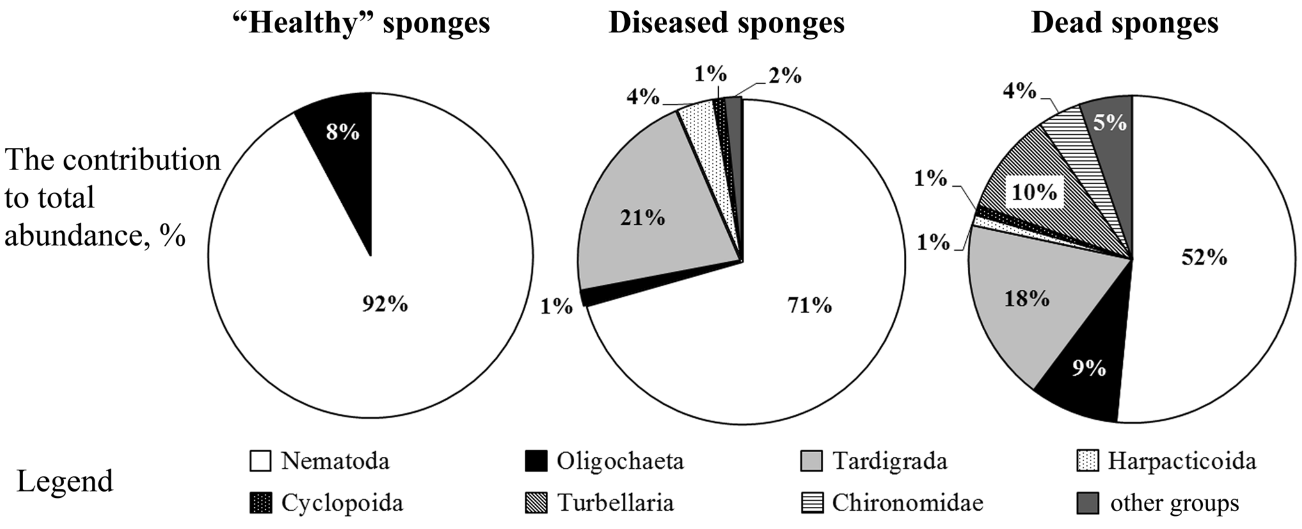

Fig. 3 The contributions of different taxonomic groups to the total infaunal abundances in "healthy", diseased, and dead *L. baikalensis* sponges

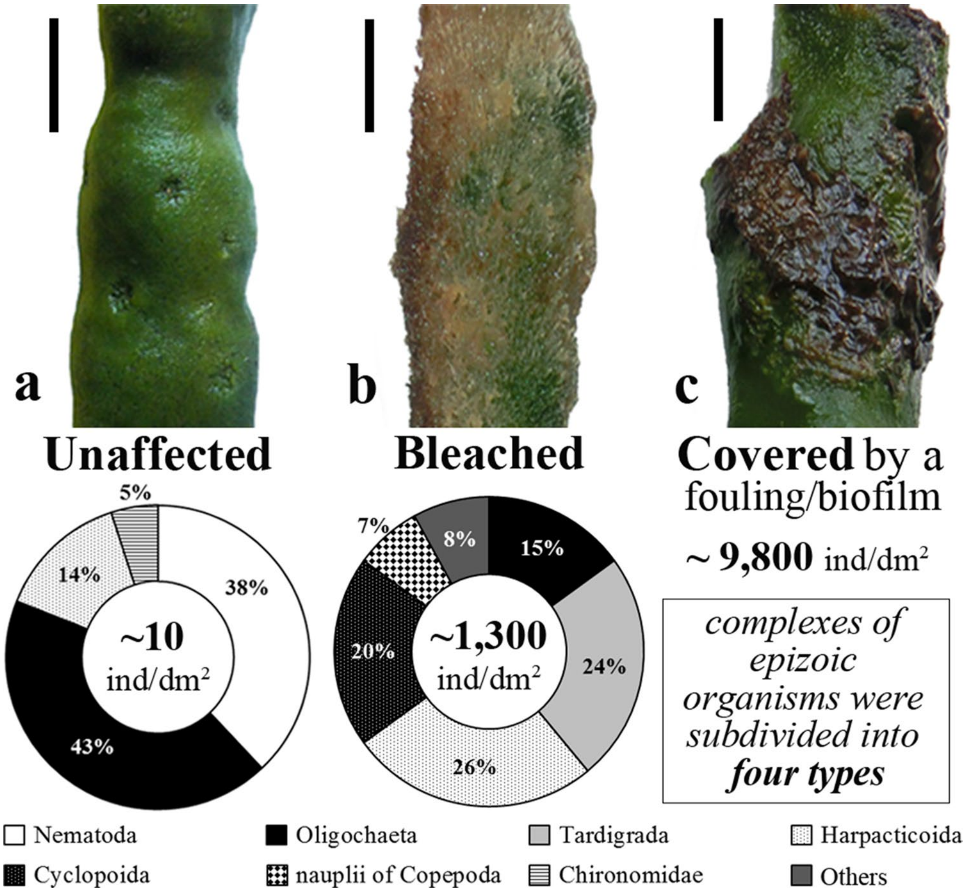

Fig. 4 The average abundances and percentages of infaunal animals residing in diseased *L. baikalensis* sponges presenting different damage types: **a** unaffected fragments, **b** bleached fragments, **c** fragments covered by a fouling or biofilm. The *scale bars* equal 1 cm

Infauna of diseased and dead *L. baikalensis:* density and composition

Disease initially leads to a deterioration of the sponge body (decreased firmness due to tissue destruction), which presents an opportunity for a diverse and dense infaunal community to develop (Fig. 3). We assessed infaunal composition and abundance separately for each of three types of tissue damage in diseased sponges (Fig. 4). Unaffected fragments of diseased sponges harbored a small quantity of invertebrates (10 ind/dm^2). Besides oligochaetes and nematodes, which dominated there, we also found Harpacticoida and Chironomidae (Table 1, Fig. 4a). In bleached fragments, the total number of invertebrates was 1303 ± 441 ind/dm^2. Dominant infaunal groups in sponges with that type of damage were Harpacticoida, Tardigrada, Cyclopoida, and Oligochaeta (Table 1, Fig. 4b). Additionally, nauplii of Copepoda (7%), Rotifera, Nematoda, Chironomidae, Ostracoda, Cladocera, Turbellaria, and Amphipoda (juveniles ~ 3 mm long) contributed up to 15% of the infaunal abundance in total.

As a result, we observed that the spatial distribution of infauna in the diseased sponges was erratic and variable. Two factors contributed to this: (1) the heterogeneity of the surfaces of diseased sponge specimens, and (2) gradual decomposition of the sponge body. Therefore, in the unaffected fragments of diseased sponges, the density of infaunal organisms was minimal, just as it was in “healthy” *L. baikalensis*. In the bleached fragments, empty space appeared between the skeletal elements, along with a bulk of consumable food sources. This resulted in a 130-fold increase in the density of infauna present in the bleached tissue in comparison to that of “healthy” *L. baikalensis*. Thus, decay processes contributed to the development of rich communities of saprophages in the affected areas of the sponge body.

In fragments of diseased sponges covered with cyanobacterial/diatom foulings and biofilms, there were numerous animals within the damaged sponge body, but there were even more in the fouling matrix. The highest infaunal density (9791 ± 2732 ind/dm^2) occurred in these fragments (Fig. 4c). We subdivided these complexes of epizoic organisms into four types (Fig. 5). Distinct faunal assemblages varying in abundance and structure inhabited these complexes (Table 3). The invertebrate communities with the largest abundance (18,293 ± 5958 ind/dm^2) occurred in three complexes containing cyanobacteria, and were dominated numerically by nematodes. In biofilms formed mostly by diatom algae, however, the animal community was poorer in

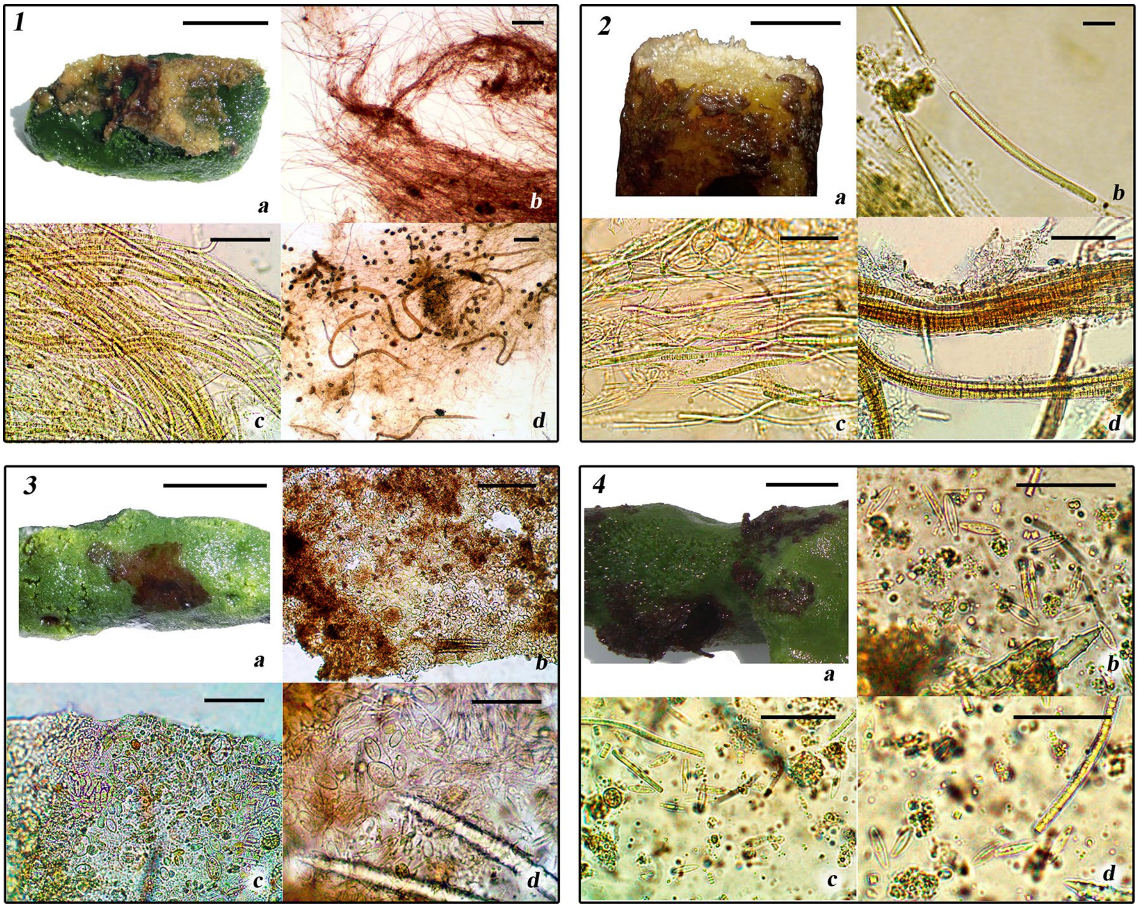

Fig. 5 Epizoic complexes of diseased sponges (*L. baikalensis*). **1** Filamentous cyanobacteria *Tychonema* sp. and a mixture of other cyanobacterial species (*a* sponge body covered by a fouling, *b* filaments of *Tychonema* at 4× magnification, *c* the same at 40× magnification, *d* nematodes, their eggs, and tardigrades between the filaments at 4× magnification). **2** Filamentous cyanobacteria *Phormidium aerugineo-caeruleum* (Gomont) Anagnostidis & Komárek and *Pseudanabaena galeata* Böcher, *Symplocastrum* sp. (*a* sponge body covered by a fouling, *b* filaments of *Ph. aerugineo-caeruleum* at 40× magnification, *c* the same, *d* filaments of *Symplocastrum* sp. at 40× magnification). **3** Diatom algae *Cocconeis* sp. and cyanobacteria *Chamaesiphon fuscus* (Rostafinski) Hansgirg (*a* sponge body covered by a biofilm, *b* the biofilm at 4× magnification, *c* the same at 40× magnification, *d* the same). **4** Diatom algae and filamentous cyanobacteria *Tychonema* sp. (*a* sponge body covered by a biofilm, *b* the biofilm at 40× magnification, *c*, *d* the same). *Scale bars*: **1***a*, **2***a*, **3***a*, **4***a*: 1 cm; **1***b*, **1***d*, **3***b*: 200 µm; **1***c*, **2***c*, **2***d*, **3***c*, **3***d*, **4***b*, **4***c*, **4***d*: 50 µm; **2***b*: 20 µm

Table 3 Invertebrate faunal assemblages and abundances in four different epizoic complexes on the surfaces of diseased sponges (*L. baikalensis*) collected from Lake Baikal in December 2015 through September 2016

Complex type	Dominant algal species of epizoic complex	Fauna of complex	Total faunal abundance
Fouling	Filamentous cyanobacteria *Tychonema* sp. and mixture of other cyanobacterial species	Nematoda (95% of the total abundance), Tardigrada (5%), Oligochaeta, and Harpacticoida (less than 1%)	1200–54,414 ind/dm^2 ($N=6$)
Fouling	Filamentous cyanobacteria *Ph. aerugineo-caeruleum* and *P. galeata*, *Symplocastrum* sp.	Nematoda (95%), Rotifera, Tardigrada, Cyclopoida, Oligochaeta (5%)	9942 ind/dm^2 ($N=1$)
Biofilm	Diatom algae *Cocconeis* sp. (less often *Gomphonema* sp., *Navicula* sp.), and cyanobacteria *Ch. fuscus*	Harpacticoida (45%), Tardigrada (45%), Chironomidae (7%), Rotifera, Nematoda, Oligochaeta, Turbellaria, Cyclopoida, Amphipoda, Ostracoda (3%)	303–11,386 ind/dm^2 ($N=3$)
Biofilm	Diatom algae and filamentous cyanobacteria *Tychonema* sp.	Nematoda (100%)	9362–16,067 ind/dm^2 ($N=2$)

number (4502 ± 2833 ind/dm^2) but consisted of more taxa, including tardigrades, harpacticoids, and chironomids.

The highest density of invertebrates was observed in epizoic complex I formed by *Tychonema* sp. and other cyanobacterial species, which covered the apical fragment of the sponge branch (September 2016, Chernaya Bay, see Fig. 5.1). Many nematodes (49,296 ind/dm^2), along with their eggs, and tardigrades (5075 ind/dm^2) were observed within the dense interlacing of cyanobacterial filaments. We found that areas with cyanobacterial foulings of *Tychonema* sp. were preferred by infauna to biofilms consisting of the diatoms *Cocconeis* sp. and *Ch. fuscus.* We suggest that the highest density of nematodes occurs in foulings consisting of filamentous cyanobacteria. Omnivorous nematode genera (*Tobrilus* and *Eutobrilus*) dominated here, and they consume protozoans, diatoms, and fungal hyphae, with some species being carnivorous. The detritus-consuming (selective and nonselective) nematodes of the genera *Monhystera* and *Ethmolaimus* (Gagarin 2001) occurred more rarely.

It is noteworthy that biofilm complex III (Fig. 5.3) was present on sponges in Lake Baikal before their mass disease. Also, such biofilms were observed for epiphyton of *Elodea canadensis* Michx. and in experiments with steel plates in the littoral zone of Lake Baikal (Pomazkina et al. 2012; Sorokovikova et al. 2013). The diatom biofilms mentioned above develop in places where sponge branches touch a substrate or each other, forming a chitin-like crust on the sponge surface. Therefore, their development could be considered a natural process and not related to the mass disease of Baikalian sponges. Invertebrate communities inhabiting this complex could be regarded as common for healthy sponges.

Dead sponge fragments exhibited the highest grade of tissue degradation and had skeletal elements of a brownish color. In the dead sponges, animals inhabited the entire body of the decaying sponge, and they were able to penetrate from the surface deep into the sponge body. Invertebrate abundances in dead sponges ranged from 638 to 16,556 ind/dm^2 (4767 ind/dm^2 on average). In dead *L. baikalensis* sponges, such taxonomic groups as nematodes, tardigrades, microturbellarians, and oligochaetes dominated (Table 1, Fig. 3). The remaining 12% of the total abundance was contributed by chironomids, large infusoria (~ 300 µm), cyclopoids, rotiferans, ostracods, cladocerans, and amphipods (juveniles) (Fig. 3). The invertebrate community in the dead sponge was distinguished by marked increases in the abundances of turbellarians and chironomids and the appearance of large infusoria. The latter group was not observed in the infauna of the "healthy" or diseased sponges.

The decaying body of a dead sponge becomes a "grand feast" for various saprophagous animals and bacteria, which play an active role in the sponge's decomposition. It is well known that bacterioflora, microdetritus particles (up to 15 µm), and tiny periphytic algae (green algae and diatoms) are primary food objects for the bdelloid rotiferans (Kutikova 2005) that were observed in diseased and dead sponges (Table 1). A large number of small multicellular organisms such as rotiferans may, in turn, attract carnivorous invertebrates (e.g., turbellarians, *Chaetogaster* oligochaetes). The bodies of the dead sponges were massively occupied by saprobic nematodes (genus *Allodiplogaster*), which inhabit any biotope characterized by a high concentration of decaying organic matter (Gagarin 2008). Also, omnivorous *T. saprophagus* was found in dead sponges along with the other bacterivorous nematodes *Monhystera paludicola*, *Eumonhystera filiformis*, and *Ethmolaimus pilosus*.

Conclusions

Deterioration and mass mortality of the endemic Lubomirskiidae sponges is ongoing in Lake Baikal. Ecologically, the Lubomirskiidae sponges play an essential role in the functioning of the Lake Baikal ecosystem. These filter feeders actively and efficiently clean large amounts of water, pumping it throughout their bodies. Baikalian sponges are highly important consumers of microplankton, especially bacteria. Clearly, the loss of endemic Baikalian sponges is an major conservation problem, but the loss of the natural filter these sponges provide will also greatly affect lake water quality and other endemic organisms.

Results of this study show that infauna is normally absent inside the bodies of "healthy" *L. baikalensis* sponges. The disease may make a large amount of food resources available for infaunal organisms, resulting in invertebrate communities that develop in affected sponge tissue. The subsequent death of *L. baikalensis* stimulates the formation of abundant saprophagous communities throughout the sponge. With the deterioration of the sponge body, the number of taxonomic groups increased sixfold, and invertebrate abundance increased 1000-fold. All these organisms are directly or indirectly processing organic matter. Some animals inhabit cyanobacteria or diatom foulings and biofilms, which tend to develop profusely on the surfaces of diseased sponges. Moreover, filamentous cyanobacteria harbor the most abundant infaunal communities, which are dominated by nematodes (up to 18,000 ind/dm^2).

The striking increase in saprophagous invertebrates inhabiting diseased and dead sponges may also change the community structure of higher trophic levels such as macrobenthic invertebrates and fish in the nearshore zone, which may, in turn, alter the functioning of the coastal ecosystem of the entire lake.

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