

Feeding spectrum of a dominant splash zone enchytraeid, *Mesenchytraeus bungei* Michaelsen, 1901 (Annelida: Oligochaeta), in Lake Baikal (East Siberia)

YU.M. ZVEREVA*, O.A. TIMOSHKIN

Yulia Mikhailovna Zvereva, Oleg Anatolievich Timoshkin, Laboratory of Biology of Water Invertebrates, Limnological Institute SB RAS, Ulan-Batorskaya st., 3, Irkutsk, 664033, Russia. *E-mail: zvereva@lin.irk.ru

Abstract. The first data on feeding spectrum of Baikal enchytraeids are given. Previously we found that *Mesenchytraeus bungei* Michaelsen, 1901 dominates in abundance in splash zone Oligochaeta community of Bolshie Koty Bay, Lake Baikal. Feeding spectrum of *M. bungei* was investigated in summer (partially also in spring and autumn) of 2010–2012 and 2015. Our study is based on pellet content analyses of more than 200 *M. bungei* specimens. Diverse components in different ratio were found during the investigation period, namely green algae, diatoms, higher plants debris, various animal remains, some minor components and sediment particles. All the pellet content was subdivided into phylogenous and animal material, unidentified matter and sediment particles. Phylogenous material appeared to be a dominant component of pellets (up to 87%) in almost all cases. Our analysis showed that *M. bungei* is a saprophage with a preference to phylogenous detritus.

Key words. Feeding, splash zone, Enchytraeidae, *Mesenchytraeus bungei*, Lake Baikal

INTRODUCTION

Aquatic oligochaetes (Annelida: Oligochaeta) are easily found at the bottom of different water bodies and play an essential role in self-purification and organic matter decomposition processes. Investigation of oligochaetes' feeding behavior is necessary in order to assess their significance for food chains; nevertheless, most of facts on it are ambiguous and contradictory. The way of feeding is inseparably related to their life-style. For instance, phytophilic worms living among the aquatic vegetation feed like grazers (Monakov 1998), using periphyton (*e.g.*, diatoms and other unicellular algae) with organic sediment particles as a food. Mostly it concerns representatives of the Family Naididae. They are capable of selective digestion of ingested particles (Timm 1987). Species of the genus *Chaetogaster* can attack and ingest tiny invertebrates (Monakov 1998, Čekanovskaya 1962).

The tubificids, lumbriculids and aquatic enchytraeids belong to the ground-dwelling oligo-

chaetes (Čekanovskaya 1962). It has been considered for a long time that such worms just pass sediment particles through their intestine without any selection, but many studies disproved this point of view (Brinkhurst & Austin 1979, Rodriguez *et al.* 2001, Poddubnaya 1961).

Soil enchytraeids could be considered as well-studied ones in terms of their trophism. But before the work of O'Connor (1967) one could find only scattered data for different species of soil enchytraeids until the above author had surveyed all known facts on their feeding behavior. Soil enchytraeids feed on diverse items: decaying leaf litter, bacteria, fungi, nematodes (Dózsa-Farkas 1976). When cultivated, they can utilize oats, yeast, algae and even dead bodies of lumbriculids and arthropods (Briones & Ineson 2002). Several authors have shown that enchytraeids demonstrated evident preference to microfungi (Dash *et al.* 1980) but, vice versa, others have denied it (Standen & Latter 1977).

On contrary to soil enchytraeids, feeding of the aquatic ones is almost unknown (Timm 1987).

We could find some information on the subject for marine enchytraeids only, since representatives of the family are a dominant component of marine meiobenthos (Giere 2009). Giere (1975) examined a diet of some dominant marine enchytraeid species in details. According to the author, marine enchytraeids can feed on diatoms (*Marionina subterranea* Knöllner, 1935), bacteria [*M. spicula* (Leuckart, 1847), *Lumbricillus lineatus* (Müller, 1774)] and decaying aquatic plants and macrophytes [*L. rivalis* (Levinsen, 1884), *L. lineatus* and *Enchytraeus albidus* Henle, 1837].

There is a marked lack of information on the trophism of freshwater enchytraeid species, despite the fact they are often to be found in lacustrine littoral (Lindegaard *et al.* 1994) and profundal (Timm 1996) zone. The data on the feeding of the Baikalian Enchytraeidae are also lacking. That is one of the reasons why our investigation focuses on the study of feeding of the *Mesenchytraeus bungei* Michaelsen, 1901.

The second reason is that the species is widely distributed for the whole lake splash zone. Recently we have started an investigation of the Lake Baikal splash zone (Timoshkin *et al.* 2012b). This zone is an above-water part of the littoral, which is subject to wave action (an analogue of marine supralittoral). So far there was only one special work focused on the coastal zone (Veinberg & Kamaltynov 1998). Our and previous studies showed Baikal Lake splash zone as unique one with quite specific hydrodynamic and temperature regime. We revealed this zone has some characteristic peculiarities, for instance there is the highest level of detritus accumulation here (Timoshkin *et al.* 2012a).

It seems remarkable that taxocenoses of the Baikalian splash zone are dominated by a single or 2–3 species. For example, the Oligochaeta community here is dominated by *M. bungei* (Zvereva *et al.* 2012). It comprised up to 92% of the total number of oligochaetes. Though, the identity of this mass enchytraeid species and the species, which was described by Michaelsen in

1901, one could call into a question. *M. bungei* was mentioned in Čekanovskaya 1962, Veinberg & Kamaltynov 1998, and Semernoy, 2004 without any revision. The only attempt to redescribe it was made by Timm (2003) on a single available specimen differed from the Michaelsen's original description. So now the species evidently needs a revision (Timm 2003). Nevertheless, the authors still believe the species under study is a single mass species. Our supposition is supported by preliminary molecular analyses (unpublished data). Although there is a taxonomic problem, it seems reasonable to investigate such dominant species from ecological point of view to reveal their role for the whole lake ecosystem. Obtained results could be regarded as the first data on feeding habits of Baikal enchytraeids.

MATERIALS AND METHODS

Lake Baikal, located in the central part of Asia (eastern Siberia) on the border of Irkutsk Region and the Republic of Buryatia, Russia. Our investigation was carried out at the Limnological Institute field station in Bolshie Koty Bay. The bay is slightly jutting into the land near the village of the same name, located 20 km north-east of Listvyanka village, South Baikal (Fig. 1).

Investigation was conducted in the different months of 2010–2012 and 2015. There are two routine methods for oligochaetes' feeding pattern study: (1) stomach content analyses (Dash *et al.* 1980, McElhone 1979, Poddubnaya 1961) and (2) pellet content examination (Rodriguez *et al.* 2001). The latter method seemed to us more appropriate after practicing both of these approaches.

The present study was based on pellet content analyses of *M. bungei*, collected on the beach opposite to Limnological Institute field station (Fig. 1). Specimens were sampled in the splash zone, at the area between the water edge and 0.5 m upward. A total of 207 specimens were examined.

We chose worms of the largest size group (3–4 cm long) for our analysis. They were kept in Petri dishes with 3 ml of bottled Baikal water in the

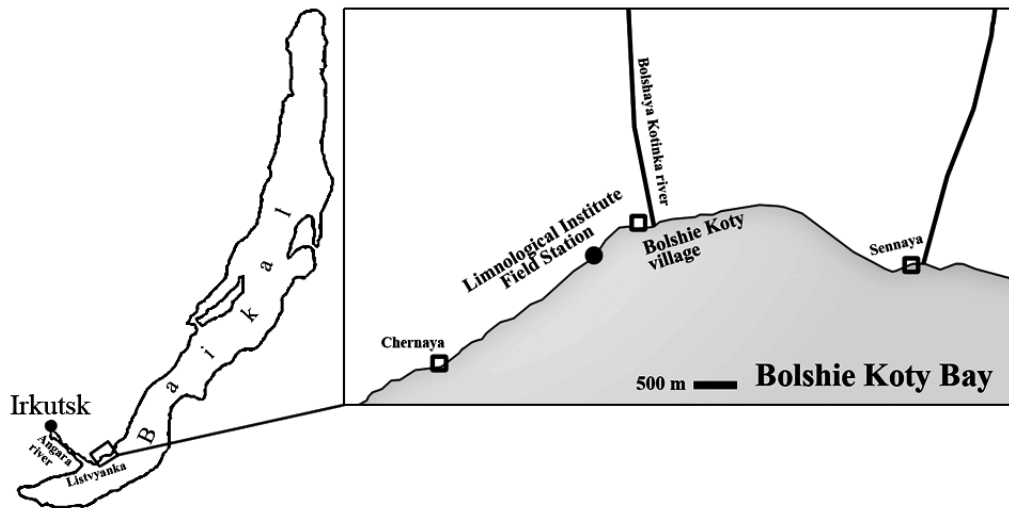


Figure 1. Sampling site location (big black dot) in Bolshie Koty Bay, Lake Baikal

fridge individually for 24 hours. Then pellets from the dishes were mounted on slides. We examined the slides under a microscope and estimated the percentage contribution of each food component in 10–20 microscopic fields per slide. The similar method of estimation was implied by Poddubnaya (1961) for the intestine content of tubificids.

For estimation we subdivided all pellet content into three basic groups: (1) phylogenous material *sensu lato* or pellet phyto-component (it consists of algae, macrophytes and land plant remains), (2) animal material and (3) unidentified matter (Fig. 3). Fungi and Cyanobacteria from pellets were mentioned separately from phylogenous material. Besides the foregoing components we found sediment particles, but they could not be considered as a food item.

Pellet content was analyzed with Olympus CX21FS1 microscope, with 4x, 10x, 20x and 40x magnifications. Photos were made by means of Olympus C-3040 zoom (3.3 MPx) camera and digital camera TouPCam FMA050 with microscope lens adapter.

RESULTS

The earliest season we obtained the data for was **March** of 2012 when the splash zone was yet mostly frozen. At that season diatom algae consti-

tuted the pellets bulk (Fig. 2a). We found both single cells and conglomerates as a mix of sediment particles, diatom cells and their fragments. Diatoms were presented by *Cymbella*, *Navicula*, *Cocconeis*, *Didymosphenia*, *Synedra* (*S. acus* and *S. ulna*), *Diatoma* and other genera. Conifer needles and various filamentous green algae (*e.g.* *Ulothrix zonata* (Web. & Mohr) Kütz., *Mougeotia* spp., *Spirogyra* spp.) occurred in the pellets. Cyanobacteria and fragments of arthropod chitinous exoskeletons were scarce. Unfortunately, such an “early” data were available only for one year.

In **June** of 2010–2012 the worms utilized basically filaments of the green macroalga *U. zonata*. In 2010 it was almost the single algal species (Fig. 2b), but in 2011 with the predominance of *Ulothrix* a considerable part was contributed by *Tetraspora* and remains of land plants (Fig. 2c). In **June** of 2012 *Ulothrix* with another green and diatom algae, and unidentified plant remains comprised up to 80% of pellet content (Fig. 2d). Among the diatoms *Cocconeis*, *Hannaea*, *Gomphonema*, *Navicula* were found as well. We also identified pine pollen and sponge spicules in a small amount.

In **July** of 2010–2011 the phyto-component of pellets was more diverse, unless *U. zonata* still played an important role. In 2010 the diatom

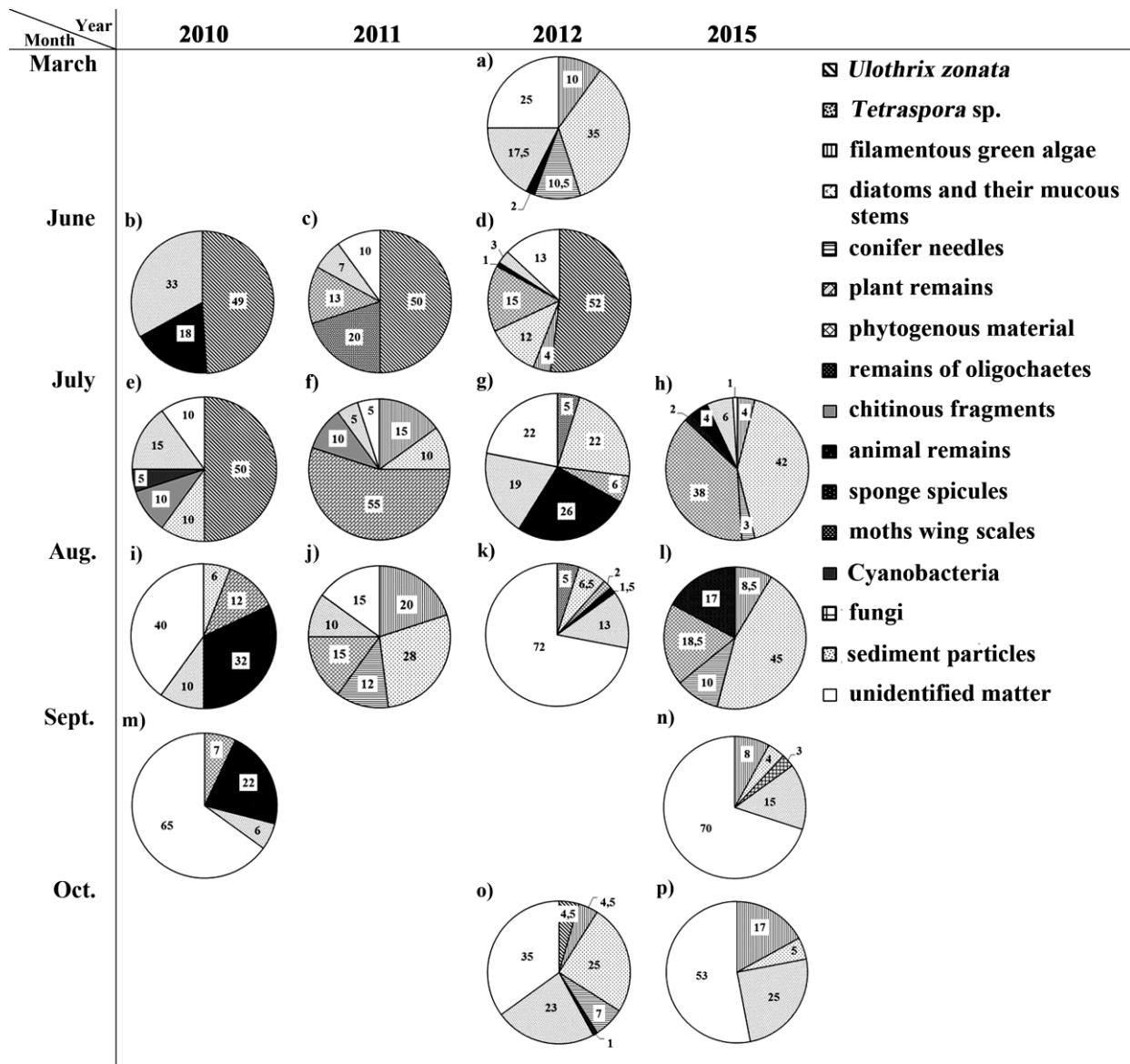


Figure 2. *M. bungei* pellet content in different months of 2010–2012 and 2015. Data are shown as a percentage (%)

algae *Gomphonema* and *Didymosphenia* were added to *Ulothrix*, while their mucous stems occurred even more frequently than diatom cells themselves (Fig. 2e). We also marked presence of attached infusoria *Vorticella* sp. (or solely their stems) and Cyanobacteria in a small amount. In 2011 phyto-component dominated in the pellets: *U. zonata*, land plant remains, diatoms (*Gomphonema*, *Cymbella* and *Fragilaria*) and their mucous stems (Fig. 2f). In **July** of 2012 we observed a rare case, when animal material in pellets was

comparable with phyto-material in percentage (Fig. 3c). The most substantial contribution among animal material was made by chitinous remains of arthropods and scales of moth wings (Fig. 2g). The phyto-component was represented by mixture of diatoms (*Hannaea*, *Cocconeis*, *Aulacoseira*, *Synedra*, *Didymosphenia*, *Navicula*), *Tetraspora*, and semidigested plant cells matrix. In **July** of 2015 there was a strong predominance of phyto-component (87%) in the pellet content (Figs. 2h, 3d). Mucous stems of diatoms were a

biggest part of pellet masses (42%). We observed a significant amount of semidigested plant cell matrix (38%), remains of green filamentous algae, conifers needles. Among the animal component moth wing scales played a significant role. The minor components included sponge spicules, pine pollen, Cyanobacteria.

Interestingly, besides semidigested *U. zonata* in **July** of 2010–2012 and 2015 we found in the worm pellets lots of «newborn» *Ulothrix* filaments, which began to grow up and had a size of a few cells. In 2015 one third of *M. bungei* specimens had growing few-celled *Ulothrix* zoospores in their pellets.

M. bungei food spectrum in **August** was highly variable. In 2010 the enchytraeids fed on animal material (Fig. 3a). We found fragments of oligochaete bodies with chaetae of the own

species, *M. bungei*, in the pellets (Fig. 2i). In the pellets collected in **August** of 2011, phyto-material dominated (70% – Fig. 3b). Mucous stems of *Didymosphenia* spp. comprised about 26% of the pellet content (Fig. 2j). Diatoms of the genera *Cymbella* and *Cocconeis* were permanent components of the pellet mass. Also we found remains of oligochaete bodies. In **August** of 2012 there was an uncharacteristic case (Figs. 2k, 3c): the biggest part of the pellets was formed by unidentifiable detritus (72%) and sediment particles (13%). The rest of pellet content consisted of phyto-material, namely diatoms and their mucous stems and various plant remains; animal material and fungal hyphae (1.5%). Also we noticed in average 2 germinating *Ulothrix* zoospores with the length of 3–12 cells per every analyzed *M. bungei* specimen. As minor components were identified pine pollen and sponge spicules.

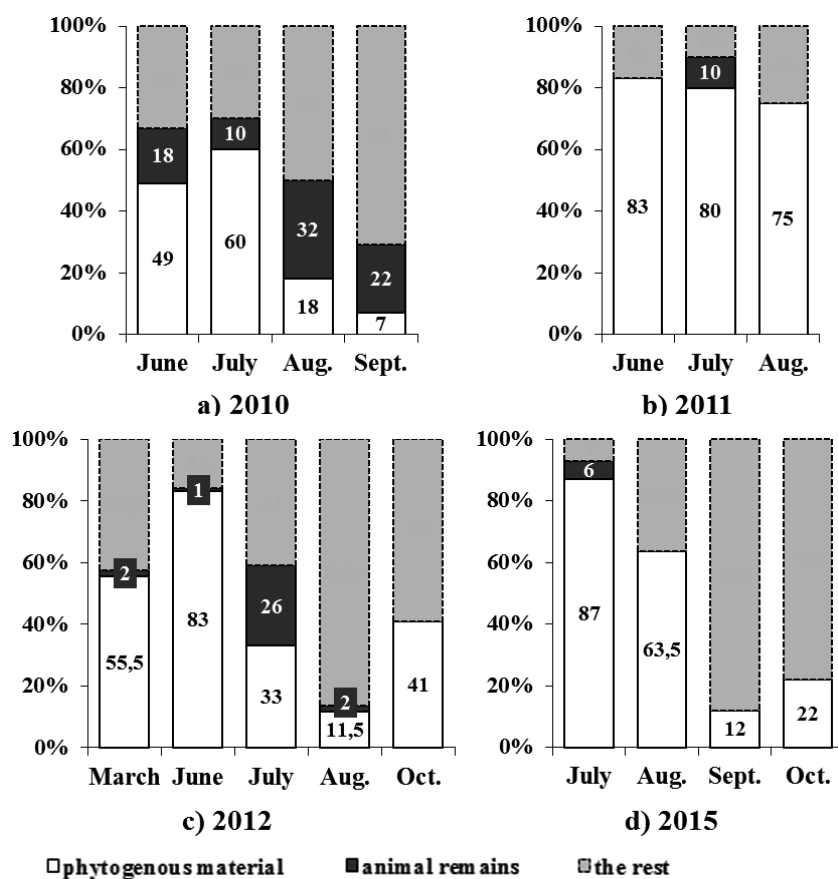


Figure 3. The change in plant and animal material contribution in *M. bungei* pellet content in 2010–2012 and 2015. Such scarce components as Fungi and Cyanobacteria were included into “the rest” category

In **August** of 2015 phyto-component prevailed in pellet content (Fig. 3d). Mainly it was mucous stems of *Didymosphenia*, green filamentous algae (*Spirogyra* spp.) and other algal and plant remains (Fig. 2l). Additionally, we found fungal hyphae, sponge spicules, moth scales, sedentary infusoria *Vorticella* (1–2 specimens per worm), colonial algae *Volvox*, and pine pollen.

In **September** of 2010 the pellet content was performed by oligochaete bodies' remains with *M. bungei* chaeta along with a larger part of unidentified matter (Fig. 2m). In **September** of 2015 unidentified matter dominated (70%) in *M. bungei* pellets (Fig. 2n). Various filamentous algae (including *Spirogyra* spp.) and diatom mucous stems were as a phyto-component with a small percentage contribution. We found a little amount of fungi (3%), sponge spicules, pine pollen.

In **October** of 2012 besides unidentified matter and sediment particles there was almost solely phylogenous material (40% – Fig. 3c). Such components as mucous stems of *Didymosphenia*, other diatoms (*Cocconeis*, *Cymbella*, *Hannaea*, *Navicula*, *Synedra*), green filamentous algae (*Ulothrix*, Cladophoraceae), conifer needles remains contributed a biggest part in pellet content (Fig. 2o). We observed Cyanobacteria presumably of the genus *Phormidium* in a small amount (1%). In **October** of 2015 we marked only phylogenous material (22%) together with sediment particles and unidentified matter in the enchytraeids' pellets. The phylogenous material was represented by different green filamentous algae remains and mucous stems of diatoms (Fig. 2p). As minor components were found moth scales, sponge spicules, pollen, animal remains (chitinous exoskeletons), and *Eudorina*-like colonial algae.

DISCUSSION

All the non-predatory oligochaetes could be roughly subdivided into three groups: (1) “detritus feeders”, (2) “sand swallows”, and (3) “diatom eaters” (Giere 1975). The enchytraeid *M. bungei* apparently could be attributed to a detritophage with phylogenous detritus preference. This Baikal

oligochaete occupies an ecological niche, which is similar with enchytraeids *L. lineatus*, *L. rivalis* and *E. albidus*. These enchytraeids also prefer to gather in high numbers around or inside of detritus masses (O'Connor 1967). In laboratory cultures they are able to transform fresh *Fucus* spp. and *Zostera marina* Linnaeus into dark-brown amorphous fecal masses in a short time (O'Connor 1967).

Dózsa-Farkas (1998) carried out a special investigation of enchytraeid fauna in detritus accumulations on the shallow Lake Balaton shores (Hungary). She found that the detritus accumulation biotope is poor in terms of enchytraeid species number in comparison with soil. Although species richness was less in the shore detritus than in soil, enchytraeids yielded there a maximum value of $217,900 \pm 10,872$ inds. m^{-2} . In the case of Lake Baikal detritus accumulations we can assume a maximum number about $40,000$ inds. m^{-2} (Timoshkin *et al.* 2012a). Such species of enchytraeids evidently have to play a significant ecological role in consuming and transforming a tremendous mass of organic matter thrown on the shores of lakes (Dózsa-Farkas 1998) and seas (O'Connor 1967).

Researchers' opinions concerning the detritus as a food item is rather contradictory. In the former studies detritus and algae were considered as a primary food source for oligochaetes (Giere 1975). The previous (Giere 1975) and our original detritus attractiveness tests showed that the overwhelming majority of enchytraeids concentrated in detritus layer and surrounding ground layers.

With the exception of mineral sediment particles, which may comprise up to 33%, the rest of *M. bungei* pellet content is detritus of different origin. In the present study we subdivided pellet content into three basic groups: (1) phylogenous material *s. l.* (algae, macrophytes, and plant remains), (2) animal material and (3) unidentified matter (Fig. 3). Additionally, sometimes we found fungal hyphae and Cyanobacteria, but in a quite small amounts. It should be emphasized that it is rather difficult to judge about fresh plant material

in enchytraeids feeding, because often it is hard to separate it from already decaying material. Although, such widespread enchytraeid species as *L. lineatus* and *E. albidus* are supposed to prefer exactly thin-walled inner plant cells (Giere 1975). For example, in July of 2015 we observed lots of semidigested matrix of fresh algal cells.

Phytogenous material has been quantitatively predominating in comparison with the other types of detritus during all investigation period (Fig. 3); its percentage varied in the range of 7–87%. Also phytogenous detritus appeared to be more diverse. It was performed by green algae (i.e., *U. zonata*, *Tetraspora*, unidentified Cladophoraceae, *Spirogyra*). *Ulothrix* should be mentioned especially, as it was a permanent component of the oligochaete pellet content in June and July. Sometimes it made up to 100% of *M. bungei* pellet content. Even when there was *Ulothrix* in the shore detritus accumulations just in a small amount, it was certainly found in the pellets of *M. bungei*. In this case we can state that the latter species demonstrates some kind of nutritional selectivity. The fact of *Ulothrix* zoospores germination in the enchytraeid pellets undoubtedly requires a special study to reveal the role of *M. bungei* in *U. zonata* distribution.

Remains of land plants play also an essential role in the nutrition of this oligochaete species. Fragments of leaf external tissue and conifer needle remains can often be found in *M. bungei* pellets. Diatom algae could be indicated as an important part of the pellet phyto-component. It should be marked, that they are characteristic component of gut content of oligochaetes from various families. For instance, widespread *Stylaria lacustris* (Linnaeus, 1767) assimilates diatoms *Asterionella*, but does not consume green algae *Scenedesmus* (Streit 1978). *Chaetogaster diastrophus* (Gruithuisen, 1828) prefers certain diatom genera among the other food items (McElhone 1979). Some authors noted, that tubificids also use diatom algae as a food, and *Lumbriculus variegatus* (Müller, 1774) may digest diatoms but not green algae (Timm 1987). Analyses of gut content of dominant marine

interstitial enchytraeid *M. subterranea* showed that it exclusively fed on pennate diatoms (Giere 1975).

Diatoms' thecae are a regular component in pellets of *M. bungei*. The genera *Didymosphenia*, *Gomphonema*, *Cocconeis*, *Hannaea*, *Cymbella*, *Navicula*, *Fragelaria*, *Synedra*, and *Aulacoseira* were found most frequently. We often observed *Cocconeis* in quite large amounts in pellet content as it is an epiphyte of filamentous green algae. Mucous stems of diatoms should be mentioned specifically. These stems permanently occur in the pellet content of splash zone enchytraeids. Due to the high number of *Didymosphenia* in detritus accumulation in 2015 the mucous stems were observed during July–October and contributed 4–45% of *M. bungei* pellet content (Fig. 2 h, l, n, p).

As for animal material, it rarely constituted more than 30% in *M. bungei* pellet content (Fig. 3). The biggest contribution was made by large fragments of arthropod (crustaceans and insects) chitinous exoskeleton. Remains of oligochaetes (with *M. bungei* chaetae) also were a significant component among animal material of pellets. Finding of *M. bungei* remains in their own pellets is rather intriguing phenomena, which is hard to explain by their possible predatory behavior. Although, authors noted that necrophaging is not unknown among enchytraeids (O'Connor 1967, Čekanovskaya 1962).

During the whole period of studying we found various minor components of the pellet content: Cyanobacteria, pine pollen, moth scales, sponge spicules, colonial green algae (*Volvox* and *Eudorina*), attached infusoria *Vorticella*, and fungal hyphae. Besides, we observed parasitic rotifers at a resting (cyst-like) stage. More often they were noticed being dead, but in some cases we watched them alive and rarely free-floating. In this paper we do not discuss this fact in details.

It is known that a rich microflora grows on the particles of decaying organic matter (Monakov 1998). Certainly feeding on microorganisms could

explain the preference of rotten phylogenous material such as “ripe” coastal detritus accumulations (Timoshkin *et al.* 2012a). Hence the question appears: do enchytraeids utilize larger detritus particles themselves as a food, or the primary source of their feeding are microorganisms.

In literature there are arguments both for (Dash *et al.* 1980, 1981, O'Connor 1967), and against (Latter 1977, Latter & Howson 1978, Standen & Latter 1977, Toutain *et al.* 1982) the statement that detritus debris in the majority of cases serves only like a substratum for microorganisms and stays more or less untransformed, but bacteria and fungi are main food source to be directly consumed. Detritus was not recorded in the alimentary tracts of marine enchytraeid *M. spicula*. There was only brownish amorphous mass, which appears to be an agglomeration of bacteria (Giere 1975). Bacterial food is available to oligochaetes even in sand biotopes. Not only small, but also large oligochaete specimens can partially or entirely live on bacteria. That was shown in experiments with lacustrine and soil species (Giere 1975).

On the other hand, could a bacterial biomass serve as sufficient food source to sustain oligochaete populations? Even despite the great rates of bacterial growth, it seems to be doubtful that oligochaetes are able to get required energy with feeding on bacteria exclusively (Giere 1975). Nielsen (1961) has calculated that population of soil enchytraeids with density of 50,000 inds. m⁻² for surviving for 1 year need to utilize 30–40 g m⁻² of bacteria.

Latter (1977) demonstrated, that *Cognettia sphagnetorum* (Vejdovský, 1878) grew better in axenic cultures, rather than in cultures with microorganisms. Studies of Toutain *et al.* (1982) indicated that soil enchytraeids were feeding on plant remains like saprotrophs. Giere & Hauschildt (1979, cited in Gelder 1984) experimentally proved that a suitable food source for *L. lineatus* was algae, but not bacterial films. Additionally, investigation of digestive enzymes of some tropic soil enchytraeids revealed the presence of cellulase, which theoretically gives them an ability to consume a phylogenous material

(Dash *et al.* 1981). Thus mixed diet (microorganisms, living/dead plants) seems to be more expectable at least for oligochaete macrofauna (Giere 1975).

We can conclude that to solve the complicated question on a real food source for oligochaetes, one would need to combine traditional techniques of feeding examination with analyses of stable isotopes. Such analyses are commonly implied in feeding biology, but not yet on enchytraeids (Briones & Ineson 2002). Unfortunately, in literature we can find only a few cases of investigation of the feeding of Enchytraeidae with stable isotopes and mostly it is considered only in the context of a large soil ecosystem trophic net (Schmidt *et al.* 2004). There is only one special work devoted to soil enchytraeids feeding using radiocarbon techniques (Briones & Ineson 2002). The results of ¹⁴C carbon dating showed that enchytraeids mainly assimilated organic matter (leaf litter), about 5–10 years old (Briones & Ineson 2002).

To summarize, we could state that *M. bungei* is a saprophage like many soil enchytraeids (Toutain *et al.* 1982). Our results demonstrate that it feeds on phylogenous detritus, what is also characteristic to soil representatives of the Family Enchytraeidae (Briones & Ineson 2002). We also suppose that the species has a feeding preference to filamentous green algae, especially to *U. zonata*. Our research supposed to be logically continued with stable isotopes analyses of *M. bungei* to specify its trophic status and establish what kind of material it assimilates primarily. Usually it is difficult to interpret stable isotopes data without information on ecology of feeding. Our results can be regarded as the first data on feeding of the Baikalian enchytraeids.

Acknowledgements – We thank V.V. Vishnyakov (IBIW RAS) and E.A. Volkova for the help with green and diatom algae genera identification. Authors gratefully thank N.A. Rozhkova for reviewing of the paper and valuable remarks. Also we are sincerely thankful to the anonymous reviewers for a great contribution to the manuscript. Funding of this work was generally provided by the State Project of SB RAS No. 0345-2016-0009 (O.A. Timoshkin is a supervisor), partially by the grant of RFBR No. 16-34-00074 and the Grants-in-Aid for Scientific Research (KAKENHI) No. 15H05112.

REFERENCES

- BRINKHURST, R.O. & AUSTIN, M.J. (1979): Assimilation by aquatic Oligochaeta. *Internationale Revue der gesamten Hydrobiologie und Hydrographie*, 64(2): 245–250. doi: [10.1002/iroh.19790640209](https://doi.org/10.1002/iroh.19790640209)
- BRIONES, M.J.I. & INESON, P. (2002): Use of ¹⁴C carbon dating to determine feeding behaviour of enchytraeids. *Soil Biology and Biochemistry*, 34(6): 881–884. doi: [10.1016/S0038-0717\(02\)00010-X](https://doi.org/10.1016/S0038-0717(02)00010-X)
- ČEKANOVSKAYA, O.V. (1962): *Vodnye maloschetinkovye chervi fauny SSSR*. AN SSSR, Leningrad, 411 pp.
- DASH, M.C., NANDA, B. & BEHERA, N. (1980): Fungal feeding by Enchytraeidae (Oligochaeta) in a tropical woodland in Orissa, India. *Oikos*, 34(2): 202–205. doi: [10.2307/3544183](https://doi.org/10.2307/3544183)
- DASH, M.C., NANDA, B. & MISHRA, P.C. (1981): Digestive enzymes in three species of Enchytraeidae (Oligochaeta). *Oikos*, 36(3): 316–318. doi: [10.2307/3544628](https://doi.org/10.2307/3544628)
- DÓZSA-FARKAS, K. (1976): Über die Nahrungswahl zweier Enchytraeidenarten (Oligochaeta: Enchytraeidae). *Acta Zoologica Academiae Scientiarum Hungaricae*, 22: 5–28.
- DÓZSA-FARKAS, K. (1998): The enchytraeid fauna (Annelida, Oligochaeta) of accumulated debris along the shore of Lake Balaton, and seasonal dynamics of the species. *Opuscula Zoologica Budapest*, 31: 33–42.
- GELDER, S.R. (1984): Diet and histophysiology of the alimentary canal of *Lumbricillus lineatus* (Oligochaeta, Enchytraeidae). *Hydrobiologia*, 115(1): 71–81. doi: [10.1007/978-94-009-6563-8_12](https://doi.org/10.1007/978-94-009-6563-8_12)
- GIERE, O. (1975): Population structure, food relations and ecological role of marine oligochaetes, with special reference to meiobenthic species. *Marine Biology*, 31(2): 139–156. doi: [10.1007/BF00391626](https://doi.org/10.1007/BF00391626)
- GIERE, O. (2009): *Meiobenthology: the microscopic motile fauna in aquatic sediments*. 2nd ed. Springer Science & Business Media, 527 pp.
- LATTER, P.M. (1977): Axenic cultivation of an enchytraeid worm, *Cognettia sphagnetorum*. *Oecologia*, 31(2): 251–254. doi: [10.1007/BF00346925](https://doi.org/10.1007/BF00346925)
- Latter, P.M. & Howson, G. (1978): Studies on the microfauna of blanket bog with particular reference to Enchytraeidae. *Journal of Animal Ecology*, 47(2): 425–48. doi: [10.2307/3792](https://doi.org/10.2307/3792)
- LINDEGAARD, C., HAMBURGER, K. & DALL P.C. (1994): Population dynamics and energy budget of *Marionina southerni* (Cernosvitov) (Enchytraeidae, Oligochaeta) in the shallow littoral of Lake Esrom, Denmark. In: REYNOLDS, T.B. & COATES, K.A. (Eds.) Aquatic Oligochaete Biology 5, *Hydrobiologia*, 278: 291–301.
- MCÉLHONE, M.J. (1979): A comparison of the gut contents of two co-existing lake-dwelling Naididae (Oligochaeta), *Nais pseudobtusa* and *Chaetogaster diastrophus*. *Freshwater Biology*, 9(3): 199–204. doi: [10.1111/j.1365-2427.1979.tb01503.x](https://doi.org/10.1111/j.1365-2427.1979.tb01503.x)
- MONAKOV, A.V. (1998): *Pitanie presnovodnykh bespozvonochnykh*. RAS, Moskva, 320 pp.
- NIELSEN, C.O. (1961): Respiratory metabolism of some populations of enchytraeid worms and free-living nematodes. *Oikos*, 12(1): 17–35. doi: [10.2307/3565169](https://doi.org/10.2307/3565169)
- O'CONNOR, F.B. (1967): *The Enchytraeidae*. In: BURGESS, A. & RAW, F. (Eds.) Soil biology. Academic Press, London & New York, p. 213–258.
- PODDUBNAYA, T.L. (1961): Materialy po pitaniyu massovykh vidov tubificid Rybinskogo vodokhranilisha. *Trudy Instituta Biologii Vodokhranilishch*, 4: 219–231.
- RODRIGUEZ, P., MARTINEZ-MADRID, M., ARRATE, J.A. & NAVARRO, E. (2001): Selective feeding by the aquatic oligochaete *Tubifex tubifex* (Tubificidae, Clitellata). *Hydrobiologia*, 463(1–3): 133–140. doi: [10.1007/978-94-010-0597-5_15](https://doi.org/10.1007/978-94-010-0597-5_15)
- SCHMIDT, O., CURRY, J.P., DYCKMANS, J., ROTA, E. & SCRIMGEOUR, C.M. (2004): Dual stable isotope analysis ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of soil invertebrates and their food sources. *Pedobiologia*, 48(2): 171–180. doi: [10.1016/j.pedobi.2003.12.003](https://doi.org/10.1016/j.pedobi.2003.12.003)
- SEMERNOY, V.P. (2004): *Oligochaeta of Lake Baikal*. Nauka, Novosibirsk, 528 pp.
- STANDEN, V. & LATTER, P.M. (1977): Distribution of a population of *Cognettia sphagnetorum* (Enchytraeidae) in relation to microhabitats in a blanket bog. *Journal of Animal Ecology*, 46(1): 213–29. doi: [10.2307/3957](https://doi.org/10.2307/3957)
- STREIT, B. (1978): A note on the nutrition of *Stylaria lacustris* (Oligochaeta: Naididae). *Hydrobiologia*, 61(3): 273–276. doi: [10.1007/BF00044453](https://doi.org/10.1007/BF00044453)
- TIMM, T. (1987): *Maloschetinkovye chervi (Oligochaeta) vodoemov Severo-Zapada SSSR*. Valgus, Tallinn, 277 pp.

- TIMM, T. (1996): Enchytraeids (Oligochaeta, Enchytraeidae) as lake-dwellers. *Newsletter on Enchytraeidae*, 5: 47–55.
- TIMM, T. (2003): Some Enchytraeidae from the shore of Lake Baikal. *Newsletter on Enchytraeidae*, 8: 1–9.
- TIMOSHKIN, O.A., VISHNYAKOV, V.S., VOLKOVA, E.A., SHIROKAYA, A.A., KULIKOVA, N.N., ZAITSEVA, E.P., LUKHNEV, A.G. *et al.* (2012): Biologiya pribrezhnoy zony ozera Baikal. Soobschenie 2. Beregovye skopleniya zapleskovoy zony: klassifikatsiya, sezonnaya dinamika kolichestvennykh i kachestvennykh pokazateley ih sostava. *The Bulletin of Irkutsk State University, Biology, Ecology*, 5(1): 40–91.
- TIMOSHKIN, O.A., SUTURIN, A., BONDARENKO, N.A., KULIKOVA, N.N., ROZHKOVA, N.A., SHEVELEVA, N.G., OBOLKINA, L.A. *et al.* (2012): Introduction into biology of the coastal zone of Lake Baikal. 1. Splash zone: first results of interdisciplinary investigations and its role for the lake ecosystem monitoring. *The Bulletin of Irkutsk State University, Biology, Ecology*, 5(3): 33–46.
- TOUTAIN, F., VILLEMIN, G., ALBRECHT, A. & REISINGER, O. (1982): Étude ultrastructurale des processus de biodégradation. II. Modèle enchytraeides-litière de feuillus. *Pedobiologia*, 23: 145–156.
- VEINBERG, I.V. & KAMALTYNOV, R.M. (1998): Soobshchestva macrozoobentosa kamenistogo plyazha ozera Baikal. 1. Fauna. *Zoologicheskiy zhurnal*, 77 (3): 259–265.
- ZVEREVA, YU.M., TIMOSHKIN, O.A., ZAITSEVA, E.P., POPOVA, O.V., LUKHNEV, A.G., TOMBERG, I.V., KULIKOVA, N.N. & VISHNYAKOV, V.S. (2012): Osobennosti ekologii *Mesenchytraeus bungei* Michaelsen (Annelida, Oligochaeta) – massovogo vida oligohet zony zapleska ozera Baikal. *The Bulletin of Irkutsk State University, Biology, Ecology*, 5(3): 123–135.