

---

---

ZOOPLANKTON, ZOOBENTHOS,  
ZOOPERIPHYTON

---

---

# Effect of Zebra Mussel *Dreissena polymorpha* (Pallas, 1771) (Mollusca, Dreissenidae) and Perch *Perca fluviatilis* (L.) (Pisces, Perciidae) of Different Age Groups on the Structure and Main Characteristics of Macrozoobenthos in Experimental Mesocosms

G. Kh. Shcherbina<sup>a,\*</sup> and V. V. Bezmaternykh<sup>b</sup>

<sup>a</sup>Papanin Institute for Biology of Inland Waters, Russian Academy of Sciences, Borok, Nekouzskii raion, Yaroslavl oblast, 152742 Russia

<sup>b</sup>Berg State Research Institute on Lake and River Fisheries, Perm Branch, Perm, 614002 Russia

\*e-mail: gregory@ibiw.yaroslavl.ru

Received August 30, 2016; revised February 2, 2018; accepted April 5, 2018

**Abstract**—The composition of macrozoobenthos in experimental mesocosms has been studied. A total of 116 invertebrate taxa are found, with chironomids (50 species), mollusks (25), and oligochaetes (21) the most widely represented. Most of the revealed taxa (61%) are common for *Dreissena polymorpha* (Pallas, 1771) biocenoses in the Rybinsk Reservoir; other species have invaded mesocosms during the experiment. The minimal number of invaders is found in mesocosms with perch larvae; the maximal is in both variants with the zebra mussel. It is shown that in the absence of zebra mussels those age groups of perch consuming macrozoobenthos reduce its main structural characteristics. The maximum sum of the main structural characteristics is recorded in mesocosms with yearlings of perch and zebra mussels. This indicates a positive environment-forming role of *Dreissena polymorpha* in benthic communities and the possibility that other invertebrates can use its druses as refuge.

**Keywords:** *Dreissena polymorpha*, *Perca fluviatilis*, experimental mesocosms, macrozoobenthos, biomass, abundance, species richness

**DOI:** 10.1134/S1995082919010188

## INTRODUCTION

Numerous studies have shown that zebra mussel *Dreissena polymorpha* influences benthic communities in freshwater bodies [3, 8, 18, 24, etc.]. However, the information on the combined effect of this mollusk and foraging activity of benthivorous fish on the state of the benthic macroinvertebrate communities is scarce. In 1993, an experiment aimed in the study of the effect of zebra mussel and of perch of various age groups on the species composition and structure of macrozoobenthos in experimental mesocosms was carried out at the Sunoga experimental pond base of the Papanin Institute for Biology of Inland Waters, Russian Academy of Sciences (Borok, Russia). Aspects related to the development and growth of perch studied in course of the above experiment is presented in [27].

The goal of the present paper is to study the combined influence of zebra mussel and perch of various age groups on the main structural characteristics of macrozoobenthos and certain components of it.

## MATERIALS AND METHODS

Experimental mesocosms were created in concrete quadrangle containers (4 × 4 m, volume of 15 m<sup>3</sup>, and bottom area 16 m<sup>2</sup>). The bottom of each container was covered ~3-cm-thick layer of loam and filled with water to the level of 20 cm. Following this, the silt (120 volumes of DAK-250 grab sampler) from the Volzhskii reach of the Rybinsk Reservoir was transferred to the containers and the water level was raised to 90 cm. Five variants of the experiment were set (three containers/replicates for each variant): C, only silt was placed in the containers; PY, silt plus 12 specimens of perch yearlings (mean body weight 3.7 g; body length 6.3 cm); PL, silt plus 1100 perch larvae (mean body weight 3.9 mg; body length, 8.5 mm); PY + ZM, the druses of zebra mussel were evenly distributed (at a density of 0.75 kg/m<sup>2</sup>) over the layer of silt and 12 perch yearlings were stocked in the container; and PL + ZM, silt, druses of zebra mussel (0.75 kg/m<sup>2</sup>) and 1100 perch larvae. Perch was selected as a model fish, because this species is very common

in the coastal areas of the Rybinsk Reservoir and can easily adapt to various ecological conditions. In the open part of the reservoir, perch yearlings are typical benthivores, with their main food consisting of midge larvae *Lipiniella araeicola* Shilova and *Chironomus muratensis* Ryser et al. (>90% of stomach content by weight).

The macrozoobenthos was sampled once a week from May 10 to August 11, 1993. In each container, eight samples were collected using a grab sampler with a sampling area of 1/400 m<sup>2</sup> (grab sampler design by G. Kh. Shcherbina); the sampled sediments were washed through a 210- $\mu$ m-mesh gauze. The invertebrates were collected live from the rest of the sediments; the mollusks were preserved in 70% ethyl alcohol and other invertebrates were preserved in 8% formalin. Following 3-month-long storage in the preservatives to stabilize the weights of the preserved animals [1], the samples were processed in a laboratory. A total of 195 samples of macrozoobenthos were collected and analyzed.

To determine the number of chironomid species that emerged, the exuvia of chironomid pupae were sampled from the water surface on the same dates when the macrozoobenthos was sampled. Sampled exuvia were preserved in Oudemans solution and, following the preparation of the total mounts, their species were determined. To analyze the emergence of chironomids, in addition to the number of individuals that emerged and the intensity of emergence of each species, we calculated the index of chironomid emergence ( $D_x$ ) proposed for the first time. The index is a ratio of the sum of all chironomid imagoes in a certain trial for the whole span of the experiment ( $W$ ) to the total number of the chironomid species that emerged in a certain trial: ( $S$ ):  $D_x = W/S$ .

In the present paper we use the terms *aborigines* to define the species that transferred into the mesocosms with the silt from the Volzhskii reach of the Rybinsk Reservoir and *invaders* (in other words, immigrants or colonizers) to define species initially absent from the benthos (in the silt transferred to the containers at the start of the experiment) and unintentionally introduced to the mesocosms and established in them. Most often, invaders were insects that laid egg clusters in the basins during the experiment [24].

The processing of cameral samples followed the commonly accepted routine [1, 9, 19]. To identify bottom macroinvertebrates, relevant identification key books were used [4–7, 10–17, 20–22, 25, 28, 29]. The lists of the species that were found are prepared according to the system and abbreviations given in [26] and in series of identification key books [11–14].

The structure of macrozoobenthos was assessed by the number of taxa, number, biomass, occurrence frequency, and shares of certain taxonomic groups in total number and biomass. The values of domination

index are calculated according to [2]; those of the Shannon index are calculated according to [23].

## RESULTS

The macrozoobenthos of the experimental mesocosms included 116 taxa; chironomids (50 species), mollusks (25), and oligochaetes (21) were most widely represented. Out of all species found, 73 were common for the dreissenid macrozoobenthos communities in the Rybinsk Reservoir (aborigines). The other 43 species appeared in the mesocosms during the experiment (invaders). The vast majority of the species (69) were rare (with an occurrence frequency in the macrozoobenthos of <10%), while only nine species were constantly occurring (with occurrence frequency of  $\geq 50\%$ ): chironomid larvae (7 species) and oligochaetes (2 species) (Table 1). The highest occurrence frequency was characteristic of three species: *Limnodrilus hoffmeisteri* (84.6–97.4%), *Potamothrix moldaviensis* (71.8–92.3%), and *Cladotanytarsus wexionensis* (66.7–79.5%).

During the initial stages of the experiment, the oligochaetes were slightly leading in occurrence frequency. However, following the introduction in the containers of mass polycyclic chironomid species, the latter became a prevailing group until almost the end of the experiment. By the end of the experiment, the roles of two mollusks, *Lymnaea peregra* (Müller) and *Cincina piscinalis* (Müller), became more important.

During the first week of the experiments, the number of species in all variants varied from 13 to 18, with the base comprised of chironomids and oligochaetes. Later on, species diversity rose in all variants. This rise was more pronounced in variants with zebra mussel (PL + ZM and PY + ZM); it was less pronounced in variants with fish (PL and PY). Control mesocosms (C) were intermittent in this aspect. At the same time, the number of species that were revealed was lower in the mesocosms with perch yearlings when compared with the variants with perch larvae. The pattern of dynamics of the number of chironomids larvae was similar. The presence of the zebra mussel in the mesocosms had a less pronounced effect on the number of oligochaetes and mollusks.

For the whole span of the experiment, 29 constant (found in all mesocosms) species were recorded: 19 chironomids, 6 oligochaetes, 3 mollusks, and 3 leeches. The dynamics of the number of constant species did not differ in fact from the dynamics of other structural characteristics. It is worth noting that, in the variants with perch yearlings (PY and PY + ZM), the presence of the zebra mussel facilitated a more pronounced increase in the number of constant species when compared with the variants with perch larvae (PL and PL + ZM).

The analysis of the dynamics of invader species of emerged chironomid imagoes revealed that their max-

**Table 1.** Main structural characteristics of dominant species of bottom macroinvertebrates in various variants of the experimental mesocosms

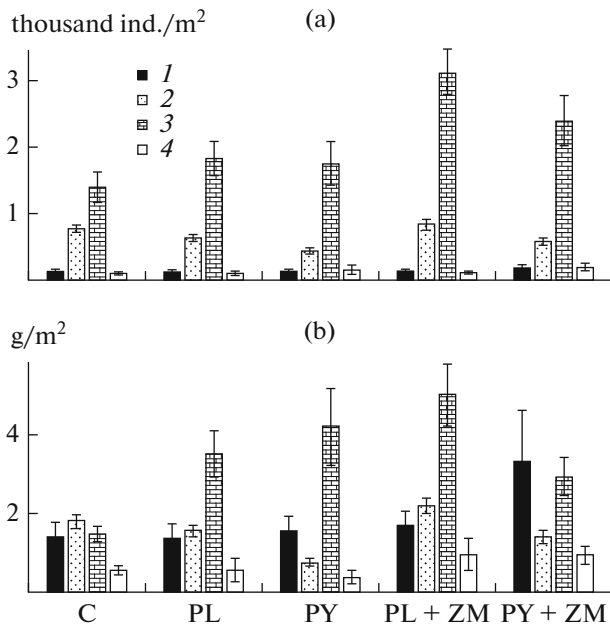
Species	Variant of the experiment				
	C	PL	PL + ZM	PY	PY + ZM
Number, ind./m <sup>2</sup>					
<i>Limnodrilus hoffmeisteri</i> Claparède	<b>362</b>	295	<b>373</b>	206	263
<i>Potamothenix moldaviensis</i> (Vejdovsky et Mrazek)	<b>247</b>	176	<b>264</b>	115	178
<i>Psectrocladius fabricus</i> Zelentsov	108	50	<b>133</b>	27	<b>147</b>
<i>Chironomus cingulatus</i> (Meigen)	41	371	<b>569</b>	206	<b>1063</b>
<i>Cladotanytarsus wexionensis</i> Brundin	410	341	<b>795</b>	333	<b>968</b>
<i>Tanytarsus pallidicornis</i> (Walker)	306	<b>496</b>	<b>699</b>	51	262
<i>T. mendax</i> Kieffer	36	132	<b>219</b>	65	<b>323</b>
<i>Polypedilum nubeculosum</i> (Meigen)	49	<b>59</b>	23	44	<b>71</b>
Biomass, g/m <sup>2</sup>					
<i>Limnodrilus hoffmeisteri</i>	<b>1.05</b>	0.86	<b>1.37</b>	0.38	0.69
<i>Potamothenix moldaviensis</i>	<b>0.52</b>	0.39	<b>0.58</b>	0.21	0.39
<i>Psectrocladius fabricus</i>	0.12	0.06	<b>0.14</b>	0.02	<b>0.14</b>
<i>Chironomus cingulatus</i>	0.23	1.85	<b>2.99</b>	1.25	<b>3.57</b>
<i>Cladotanytarsus wexionensis</i>	0.15	0.11	<b>0.31</b>	0.11	<b>0.36</b>
<i>Tanytarsus pallidicornis</i>	0.17	<b>0.23</b>	<b>0.40</b>	0.03	0.17
<i>T. mendax</i>	0.03	0.08	<b>0.14</b>	0.04	<b>0.24</b>
<i>Polypedilum nubeculosum</i>	0.07	0.10	0.04	0.08	0.11
Occurrence frequency, %					
<i>Limnodrilus hoffmeisteri</i>	97.4	84.6	94.9	82.1	89.7
<i>Potamothenix moldaviensis</i>	89.7	89.7	89.7	71.8	92.3
<i>Psectrocladius fabricus</i>	41.0	35.9	<b>46.2</b>	20.5	35.9
<i>Chironomus cingulatus</i>	25.6	56.4	<b>61.5</b>	46.2	51.3
<i>Cladotanytarsus wexionensis</i>	66.7	69.2	69.2	69.2	<b>79.5</b>
<i>Tanytarsus pallidicornis</i>	69.2	74.4	76.9	35.9	69.2
<i>T. mendax</i>	30.8	56.4	<b>69.2</b>	43.6	<b>71.8</b>
<i>Polypedilum nubeculosum</i>	43.6	41.0	30.8	38.5	48.7
Domination index					
<i>Limnodrilus hoffmeisteri</i>	<b>7.37</b>	5.29	5.24	3.57	4.23
<i>Potamothenix moldaviensis</i>	<b>5.00</b>	3.51	3.44	2.29	3.10
<i>Psectrocladius fabricus</i>	1.77	0.88	1.37	0.42	1.50
<i>Chironomus cingulatus</i>	1.37	<b>6.44</b>	<b>6.78</b>	3.96	<b>10.70</b>
<i>Cladotanytarsus wexionensis</i>	3.53	2.65	3.69	2.59	<b>5.07</b>
<i>Tanytarsus pallidicornis</i>	<b>3.42</b>	<b>3.89</b>	<b>4.01</b>	0.70	2.44
<i>T. mendax</i>	0.68	1.63	1.83	0.94	<b>2.98</b>
<i>Polypedilum nubeculosum</i>	1.19	1.17	0.42	0.97	1.19

Here and in Table 2, boldface letters denote significant differences between the quantitative characteristics.

imal numbers were recorded in the mesocosms with perch yearlings and zebra mussel; the numbers in the mesocosms with perch larvae and zebra mussel were slightly lower. The maximal for the whole span of the experimental values of number and biomass of macro-

invertebrates were observed in both variants with zebra mussel; the lowest was in the mesocosms with perch yearlings and in the control (Fig. 1; Table 2).

An analysis of the dynamics of number and biomass of the main groups of macrozoobenthos revealed



**Fig. 1.** Mean number, thousand ind./m<sup>2</sup> (a), and biomass, g/m<sup>2</sup> (b), of main groups of macrozoobenthos in various variants of the experimental mesocosms: (1) mollusks, (2) oligochaetes, (3) chironomids, and (4) other.

the considerable predominance of invader chironomids by number. These invertebrates dominated during the whole span of the experiment (similarly in all five variants). The role of aboriginal species (the base comprised of oligochaetes, leeches, and mollusks) was inconsiderable. Initially, the total number of aborigines in all variants increased, but it decreased upon reaching the maximum. The fluctuations of the number of aborigines in various variants was inconsiderable, and most pronounced changes were closely related to the appearance of juvenile invader chironomids in macrozoobenthos and the emergence of their imagoes (Fig. 2).

The number of macrozoobenthos changed inconsiderably in the control, exhibiting rather small maxima in the end of June and middle of July, followed by decrease down to the initial value.

In the variant with perch yearlings sans zebra mussel, the number of invaders gradually increased, reaching the maximum by the day 62 of the experiment, after which it gradually decreased (Fig. 2). The fluctuations in number were most pronounced in the mesocosms with perch yearlings plus zebra mussel (two maxima). Already by day 20 the number of bottom invertebrates in these variants reached 3.5 thous. ind./m<sup>2</sup>. The second maximum of number (9.4 thous. ind./m<sup>2</sup>) was much more pronounced than the first one.

The pattern of the number dynamics in the mesocosms with perch larvae sans zebra mussel was similar to that with perch yearlings, but the peak of the number was recorded almost 1 month later. By the 40th day

of the experiment, when perch larvae turned to feeding on bottom invertebrates [27], the number decreased. In the variant with perch larvae plus zebra mussel, the pattern of the number dynamics differed considerably from the previously described variants: a sharp increase was recorded 10 days after the experiment started, although bottom invertebrates comprised 70% of stomach content in perch larvae [27]. Later, the fluctuations in macrozoobenthos number were inconsiderable and sharply decreased 1 week before the end of the experiment (Fig. 2).

Throughout the entire span of the experiment, macrozoobenthos biomass did not change considerably in the control. The base of the biomass consisted of oligochaetes; chironomids; and, in some periods, mollusks. In general, the biomass was about 4 g/m<sup>2</sup>, with peaks of an accidental rather than regular character. It is worth noting that the share of the aborigines was slightly higher than of invaders (Fig. 2).

In both variants with perch yearlings, the patterns of the biomass dynamics of aborigines and invaders were similar. During first 5 weeks of the experiment, the biomass of invader chironomids was inconsiderable (Fig. 2). Later on, the biomass of macrozoobenthos increased and, by weeks 8–10 in the mesocosms with perch yearling, reached 10–15 g/m<sup>2</sup>; with perch yearlings and zebra mussel, it reached 11–12 g/m<sup>2</sup>.

In both variants with perch larvae, the patterns of the biomass dynamics of aboriginal and invader species were similar but differed strongly from other variants. The biomass reached maximal values in the beginning of August, followed by sharp drop (Fig. 2).

The minimal shares of chironomids number (58%) and biomass (28%) were recorded in control; maximal values of these parameters (71 and 61%, respectively) were in the mesocosms with perch yearlings (Fig. 1).

In the experimental mesocosms, 33 species of imago chironomids emerged. The minimal number of species emerged from the mesocosms with perch yearlings (10); in the variant with perch larvae + zebra mussel and in the control, the number was considerably higher (23 and 22 species, respectively) (Table 2). Of 33 species of chironomid imagoes that emerged during the experiment, 13 laid eggs again and 11 of these species emerged at least twice by the end of the experiment.

During the experiment, the maximal number of species was recorded in the mesocosms with zebra mussel; the minimal was recorded with fish; control mesocosms were intermediate in this respect. In the variants with zebra mussel, the increase in species richness was determined mostly by the group of "other" species, with the base comprised of dayflies, caddisflies, chaoborides, etc., while the numbers of species of chironomids, oligochaetes, and mollusks in the compared mesocosms differed only slightly. It is worth noting that in the variants with zebra mussel, the contribution of invaders to the increase in species

**Table 2.** Structural characteristics of macrozoobenthos in various variants of experimental mesocosms

Structural characteristics	Variant				
	C	PL	PL + ZM	PY	PY + ZM
Total number of found species:	69	65	<b>79</b>	61	<b>75</b>
Chironomids	36	30	38	29	33
Oligochaetes	14	15	15	12	15
Mollusks	15	16	15	13	15
other	4	4	<b>11</b>	7	<b>12</b>
Number of aboriginal species*	48	48	48	40	46
Number of invading species*	21	17	<b>31</b>	21	<b>29</b>
Mean number of species*	21 ± 1	21 ± 1	<b>26 ± 1</b>	18 ± 1	<b>25 ± 1</b>
Number of chironomid species that emerged*	<b>22</b>	15	17	10	<b>23</b>
Chironomid emergence index, $D_x^*$	3.4	<b>5.5</b>	<b>7.1</b>	3.0	<b>4.6</b>
Number of constant species, $P \geq 50\%^*$	15	14	17	9	<b>22</b>
Mean number, thousand ind./m <sup>2</sup> *	2.4 ± 0.2	2.7 ± 0.3	<b>4.2 ± 0.4</b>	2.5 ± 0.3	<b>3.4 ± 0.4</b>
Mean biomass, g/m <sup>2</sup> *	5.2 ± 0.4	7.0 ± 0.8	<b>9.9 ± 1.1</b>	6.9 ± 1	<b>8.6 ± 0.9</b>
Sum of main structural characteristics	138	130.2	<b>160.2</b>	110.4	<b>161.6</b>

\*Main structural characteristics that were summed.

number was most important, while the numbers of aborigines differed inconsiderably. The calculations of the mean number of totally recorded species and the number of constant species also revealed that, in the variants with zebra mussel, these numbers are significantly higher than in three other variants (Table 2).

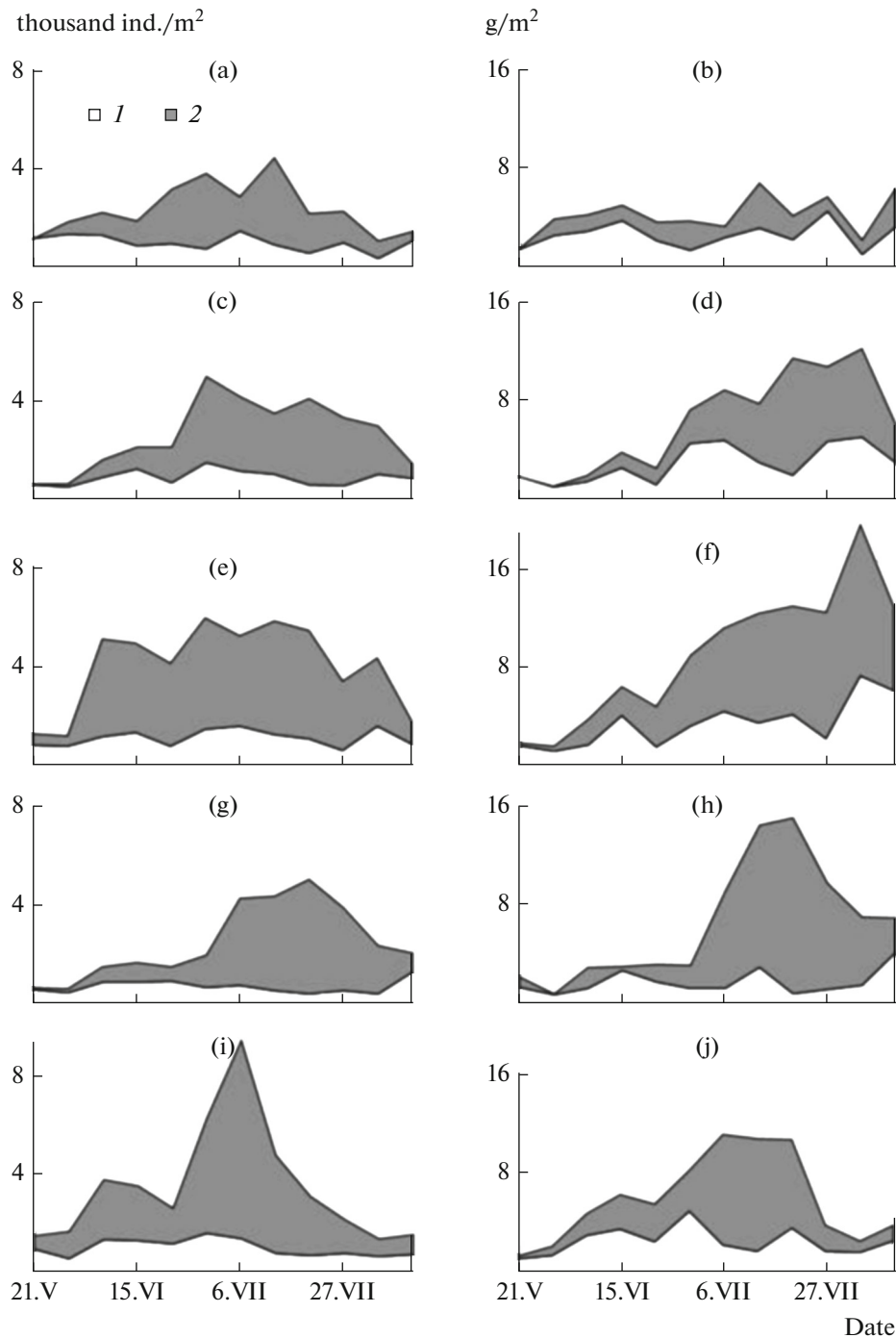
The values of the emergence index were also higher in the variants with *Dreissena polymorpha*: both in the mesocosms with perch larvae and yearlings these values increased in the presence of the mollusk by factor of 1.6. At the same time, in the variants with perch yearlings, the values were 2.5 times lower than in the variants with perch larvae (Table 2).

## DISCUSSION

An analysis of the dynamics of the number of species revealed that their maximal values were recorded in the variants with zebra mussel; the minimal was with perch yearlings (Table 2). At the same time, in the mesocosms with perch yearlings, the number of recorded species was lower than in the containers with larvae. Such a difference in the dynamics patterns is quite understandable: perch yearlings are benthivores while perch larvae consumed mainly zooplankton during the first month of the experiment [27]. The higher species richness recorded in the mesocosms with zebra mussel relates to the vital activity of the mollusks, as a result of which feces and agglutinates settle to the bottom and serve as a food for the many gatherers and swallows which make up the base of macrozoobenthos species composition in the experimental mesocosms.

Out of all the recorded species, 73 are common in the macrozoobenthos of dreissenid biocenoses in the Rybinsk Reservoir, while the other 43 species established in the mesocosms during the experiment (25 species are chironomids). Of all invaders, 30 species occurred very seldom and in small numbers. Species such as mollusk *Lymnaea peregra* (Müller) and chironomids larvae *Chironomus cingulatus*, *Ch. obtusidens* Goetghebuer, *Microtendipes pedellus* (De Geer), *Polypedilum nubeculosum*, *Tanytarsus pallidicornis*, and *Paratanytarsus confusus* Palmén were recorded in all five types of mesocosms, being relatively numerous in certain periods. The vast majority of invaders are heterotopic species reaching mass development in the adjacent ponds and ephemeral waterbodies. The dynamics patterns of invaders differ slightly from those of all previous characteristics. The smallest number of invaders was observed in the mesocosms with perch larvae, a slightly higher number was seen with perch yearlings and in the control, and a much higher number was found in both variants with zebra mussel (Table 2). The base of the invaders was comprised of chironomid larvae of tribe Tanytarsini, the majority of which are gatherers in terms of feeding mode. The filtration activity of the zebra mussel formed favorable conditions for this group of invertebrates, determining their high species richness.

As it was noted above, the fluctuations in the number of aborigines in various variants were inconsiderable, and the main changes were closely related to the appearance in macrozoobenthos of juvenile invader chironomids and the emergence of their imagoes (Fig. 2). The strongest fluctuations in number were



**Fig. 2.** Dynamics of number (thousand ind. /m<sup>2</sup>) and biomass (g/m<sup>2</sup>) of aboriginal (1) and invader (2) species in various variants of the experimental mesocosms: C (a, b), PL (c, d), PL + ZM (e, f), PY (g, h), and PY + ZM (i, j).

observed in the variants with the zebra mussel, where in the PY + ZM variant two maxima were recorded; in the PL + ZM variant there were four maxima.

The decrease in the number in the PY + ZM variant noted in the second half of June was related to the peak of emergence of chironomid imagoes. The second maximum was correlated with the mass appear-

ance of the second generation of chironomid larvae (90% of total macrozoobenthos) and especially of their small representatives of the tribe Tanytarsini. A sharp drop in the number during the further stage of the experiment was most likely determined by two reasons: first, in the end of June to beginning of July, the second peak of emergence of chironomid imagoes was

observed; second, chironomid larvae were subject to double pressure of predators—perch yearlings and predatory bottom invertebrates, the number and biomass of which by the end of the experiment comprised more than 20% of the total macrozoobenthos. The noticeably higher number of macroinvertebrates (especially chironomids in the PY + ZM variant when compared to the PY variant) relates to the fact that numerous small larvae of chironomids found shelter in the zebra mussel druses, while in the containers devoid of the mollusk they were more vulnerable to predation by innumerable perch yearlings.

As was noted above, the pattern dynamics of biomass in aborigines and invaders were similar in both variants with perch yearlings. A slightly higher biomass of aborigines in the mesocosms with the zebra mussel relates to the filtration activity of the latter. It is likely that a relatively weak rise in the biomass of chironomid larvae during the first 5 weeks of the experiment was determined by the presence of a large number of leeches feeding predominantly of these larvae [6]. Upon the decline in leeches, the biomass of chironomid larvae became faster and peaked in July. After the appearance in the macrozoobenthos of large larvae of *Chironomus cingulatus*, the biomass increased sharply. Its further decrease was presumably caused by the following two factors. First, on July 20 the emergence of *Ch. cingulatus* began being most intensive in the mesocosms with the zebra mussel, where the chironomid population reached the prepupa stage after 3 weeks. Second, in the mesocosms devoid of the zebra mussel, perch yearlings consumed, first and foremost, larger specimens of this chironomid species, as was indicated by inconsiderable rise in the mean individual weight of the midge larvae noted in this variant (Fig. 3). In the mesocosms with the zebra mussel, large larvae found shelter in the mollusk druses, the vitality products of which facilitated the fast growth rate of midge larvae.

It is likely that the sharp decrease in the biomass noted at the end of July was due to several reasons. First, the biomass of leeches rose considerably. Second, trophic resources of planktic communities were severely exhausted, making filtration feeding energetically disadvantageous for the zebra mussel, and this hampered the inflow of food for gatherers and swallows to the bottom sediments. Third, these mesocosms were most overgrown by filamentous algae that covered large part of the mussel druses, thus likely affecting development of the aboriginal species.

In both variants with perch larvae, the patterns of the biomass dynamics in the aborigines and invaders were similar, significantly differing from other variants. The maximal values of biomass were recorded in the beginning of August, followed by sharp drop (Fig. 2). In the mesocosms with the zebra mussel, the rate of biomass increase was higher until the end of the experiment, although, in this case particularly, already by day 10 of the experiment, chironomids comprised 70%

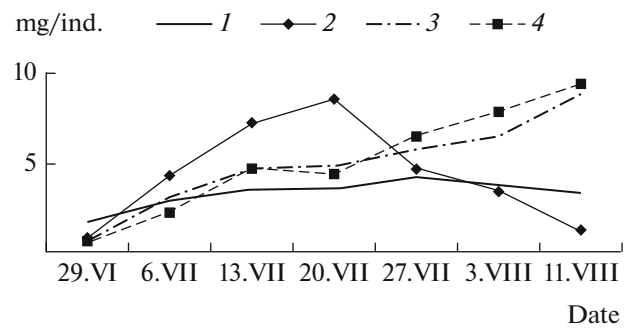


Fig. 3. Mean individual weight of *Chironomus cingulatus* larvae in various variants of the experimental mesocosms: 1—PY, 2—PY + ZM, 3—PL, 4—PL + ZM.

of stomach content in the perch larvae [27]. Although in the mesocosms with perch larvae the number of macrozoobenthos decreased during the second half of the experimental period, its biomass increased significantly (Fig. 2). This relates to *Ch. cingulatus* larvae, the species that was main dominant during the second half of the experiment. In mesocosms with perch larvae, when they turned to feeding on bottom invertebrates, II and III instar midge larvae became the main prey for the fish (mean individual weight rose from 0.61–0.62 mg by the end of June to 8.61–9.32 mg by the end of the experiment) (Fig. 3). The average values of number, biomass, and Shannon index for the whole span of the experiment were highest in the mesocosms with perch larvae plus zebra mussel; they were minimal in the control. The role of chironomid larvae was especially important in all variants except for the control, where the mollusks dominated (Fig. 1; Table 2).

As was noted above, the emergence index in chironomids is the most interesting structural characteristic. In both variants, the presence of *Dreissena polymorpha* increases the index value by a factor of 1.6 owing to the improvement of trophic conditions for chironomids; for the age of perch it is by a factor of 2.5 (Table 2). This was because perch larvae are unable to feed on pupae upon the emergence of chironomid imagoes owing to their large sizes. Even in the wild, perch yearlings prefer to feed on chironomid pupae that need to spend some time before emergence in the water column, where they become easily available prey not only for benthivorous, but also for planktivorous fish.

It is also worth noting that, as a rule in the mesocosms with perch yearlings devoid of zebra mussels, the majority of structural parameters are lower than those in the containers with perch larvae. This phenomenon is quite understandable: perch yearlings turn to feeding on benthos by the beginning of the experiment, while perch larvae during the first month of the experiment consumed mainly zooplankton and only later bottom invertebrates dominated their ration by biomass [27]. On the contrary, in the mesocosms with

perch yearlings plus the zebra mussel, the maximal values of emerged chironomids species and of number of constant species were noted (Table 2). This relates to the fact that many large invertebrates (the main food for perch yearlings) may successfully hide in zebra mussel druses, thus becoming less vulnerable for predation by the fish.

The increase in number and biomass of the dominant larvae of *Chironomus cingulatus* indirectly confirms the above suggestion. In both variants with perch larvae (PL and PL + ZM), the rates of increase in the mean individual weight of *Ch. cingulatus* population during the period from June 29 to August 11, 1993, did not in fact differ and, by the end of the experiment, the IV instar larvae were at the stage of prepupae (Fig. 3). This may be explained by the fact that only younger (I and II) populations of chironomids are available for perch larvae; consuming these larvae perch promoted the growth of the mean individual weight of *Ch. cingulatus* larvae. In the mesocosms with perch yearlings, the rise in the mean individual weight of *Ch. cingulatus* population significantly differed in different variants. In the containers devoid of *Dreissena polymorpha* (PY), some rise of mean individual weight was observed, but it was inconsiderable. On average, by the end of the experiment, the chironomid population did not reach the stage of prepupae, because perch yearlings consumed first and foremost larger IV instar larvae, decreasing mean individual weight of the whole population. In the containers with zebra mussels, the larvae grew very fast and reached the stage of prepupae after 3 weeks. Certainly, good trophic conditions and the possibility of using mollusk druses as shelters are the main reasons for the fast growth exhibited by the larvae in the mesocosms with zebra mussels. The repeated egg laying in the population of *Ch. cingulatus* noted in the mesocosms with perch yearlings and zebra mussel (PY + ZM) indicates good trophic conditions in these conditions. As a result, the mean individual weight of the larvae continued to decline by the end of the experiment (Fig. 3).

The highest values of number and biomass of macroinvertebrates average for the period of the experiment were noted in both variants with zebra mussels; the least values were in the mesocosms with perch yearlings and in the control (Fig. 1; Table 2).

## CONCLUSIONS

A total of 116 taxa were found in the experimental mesocosms; 61% of these taxa are common for *Dreissena polymorpha* biocenoses in the Rybinsk Reservoir; the rest of the species were established over the period of the experiment. The minimal number of invader species was noted in the mesocosms with perch larvae; the maximal was in the mesocosms with zebra mussels. The study revealed that the combination of studied factors (presence and age of perch and of zebra mussel) affects the number, biomass, and diversity of

both macrozoobenthos as a whole and of its main components. In the mesocosms with perch yearlings devoid of zebra mussels, the biomass, number, and species diversity of macrozoobenthos were lower than in the variants with perch larvae. This indicates that, upon the absence of zebra mussels, the age groups of perch consuming benthos decrease its main structural characteristics. On the other hand, in the containers with perch plus zebra mussels, the values of main structural characteristics were maximal, which indicates a positive environment-forming role of *D. polymorpha* in the benthic communities and the possibility for some benthic invertebrates to use its druses as shelters.

## COMPLIANCE WITH ETHICAL STANDARDS

*Conflict of interests.* The authors declare that they have no conflict of interest.

*Statement on the welfare of animals.* All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

## REFERENCES

1. Borutskii, E.V., The technique of quantitative account of benthic fauna. A method for treatment of quantitative samples of lacustrine benthos. Methods for determining raw weight, *Tr. Limnol. St. Kosine*, 1934, no. 17, pp. 119–136.
2. Brotskaya, V.A. and Zenkevich, L.A., Quantitative account of the benthic fauna of the Barents Sea, *Tr., Vses. Nauchno-Issled. Inst. Mor. Rybn. Khoz. Okeanogr.*, 1939, vol. 4, pp. 5–98.
3. *Dreissena Dreissena polymorpha* (Pallas) (Bivalvia, Dreissenidae): *Sistematika, ekologiya, prakticheskoe znachenie* (Zebra Mussel *Dreissena polymorpha* (Pallas) (Bivalvia, Dreissenidae): Systematics, Ecology, and Practical Significance), Moscow: Nauka, 1994.
4. Zhadin, V.I., *Mollyuski presnykh vod SSSR* (Mollusks of Fresh Waters of the USSR), Moscow: Akad. Nauk SSSR, 1952, no. 46.
5. Kiknadze, I.I., Shilova, A.I., Kerkis, I.E., et al., *Kariotipy i morfologiya lichinok triby Chironomini. Atlas* (Karyotypes and Morphology of the Chironomini Tribe Larvae: Atlas), Novosibirsk: Nauka, 1991.
6. Lipina, A.N., *Presnye vody i ikh zhizn'* (Freshwaters and Their Life), Moscow: Uchpedgiz, 1950.
7. Lukin, E.I., *Fauna SSSR* (The Fauna of the USSR), vol. 109: *Piyavki* (Leeches), part 1: *Piyavki presnykh i solonovatykh vodoemov* (Leeches of Fresh and Brackish Waters), Moscow: Nauka, 1976.
8. Lyakhnovich, V.P., Karataev, A.Yu., and Mitrakhovich, P.A., *Effect of Dreissena polymorpha Pallas on the ecosystem of an eutrophic lake*, *Biol. Vnutr. Vod. Inf. Byul.*, Leningrad, 1983, vol. 60, pp. 25–28.
9. *Metodika izucheniya biogeotsenozov vnutrennikh vodoemov* (A Method to Study Biogeocenoses of Inland Water Bodies), Moscow: Nauka, 1975.



10. *Opredelitel' presnovodnykh bespozvonochnykh Evropeiskoi chasti SSSR* (Identification Guide to Freshwater Invertebrates of the European part of the USSR), Leningrad: Gidrometeoizdat, 1977.
11. *Opredelitel' presnovodnykh bespozvonochnykh Rossii i sopredel'nykh territorii* (Identification Guide to Freshwater Invertebrates in Russia and Adjacent Countries), vol. 1: *Nizshie bespozvonochnye (Lower Invertebrates)*, St. Petersburg: Nauka, 1994.
12. *Opredelitel' presnovodnykh bespozvonochnykh Rossii i sopredel'nykh territorii* (Identification Guide to Freshwater Invertebrates in Russia and Adjacent Countries), vol. 2: *Rakoobraznye (Crustaceans)*, St. Petersburg: Nauka, 1995.
13. *Opredelitel' presnovodnykh bespozvonochnykh Rossii i sopredel'nykh territorii* (Identification Guide to Freshwater Invertebrates in Russia and Adjacent Countries), vol. 4: *Vysshie nasekomye, dvukrylye (Higher Insects, Dipteras)*, St. Petersburg: Nauka, 1999.
14. *Opredelitel' presnovodnykh bespozvonochnykh Rossii i sopredel'nykh territorii* (Identification Guide to Freshwater Invertebrates in Russia and Adjacent Countries), vol. 6: *Mollyuski, polikhety, nemertiny (Mollusks, Polychaetes, and Nemertean)*, St. Petersburg: Nauka, 2004.
15. Pankratova, V.Ya., *Lichinki i kukolki komarov podsem. Orthoclaadiinae fauny SSSR (Diptera, Chironomidae)* (Larvae and Pupae of Mosquitoes of the Subfamily Orthoclaadiinae of the Fauna of the USSR (Diptera, Chironomidae)), Leningrad: Nauka, 1970.
16. Pankratova, V.Ya., *Lichinki i kukolki komarov podsem. Podonominae i Tanypodinae fauny SSSR (Diptera, Chironomidae)* (Larvae and Pupae of Mosquitoes of the Subfamilies Podonominae and Tanypodinae of the Fauna of the USSR (Diptera, Chironomidae)), Leningrad: Nauka, 1977.
17. Pankratova, V.Ya., *Lichinki i kukolki komarov podsemeistva Chironomidae fauny SSSR (Diptera, Chironomidae)* (Larvae and Pupae of Mosquitoes of the Subfamily Chironomidae of the Fauna of the USSR (Diptera, Chironomidae)), Leningrad: Nauka, 1983.
18. Perova, S.N. and Shcherbina, G.Kh., Effect of massive invasive species on the macrozoobenthos productivity in the Gorky Reservoir, in *Invazii chuzherodnykh vidov v Golarktike* (Invasions of Alien Species in the Holarctic), Borok: Rybinskii Pechatnyi Dvor, 2003, pp. 148–152.
19. Sokolova, N.Yu. and Bakanov, A.I., A method for quantitative account and identification of the spatial distribution of benthos (chironomids), in *Metodicheskoe posobie po izucheniyu khironomid* (A Methodological Guide for the Study of Chironomids), Dushanbe: Donish, 1982, pp. 3–19.
20. Chekanovskaya, O.V., *Vodnye maloshchetinkovye chervi fauny SSSR* (Aquatic Oligochaetes of the Fauna of the USSR), Moscow: Akad. Nauk SSSR, 1962.
21. Chernovskii, A.A., *Opredelitel' lichinok komarov semeistva Tendipedidae* (Identification Guide to Larvae of Mosquitoes of the Family Tendipedidae), Moscow: Akad. Nauk SSSR, 1949.
22. Shilova, A.I., *Khironomidy Rybinskogo vodokhranilishcha* (Chironomids of the Rybinsk Reservoir), Leningrad: Nauka, 1976.
23. Shannon, K., Mathematical theory of communication, in *Raboty po teorii informatiki i kibernetiki* (Works on the Theory of Information Science and Cybernetics), Moscow: Inostrannaya Literatura, 1963, pp. 243–332.
24. Shcherbina, G.Kh., Effect of the mollusk *Dreissena polymorpha* (Pall.) on the structure of macrozoobenthos of experimental mesocosms, *Biol. Vnutr. Vod*, 2001, no. 1, pp. 63–70.
25. Cranston, P.S., A key to the larvae of British Orthoclaadiinae (Chironomidae), *Freshwater Biol. Assoc.*, 1982, no. 45, p. 152.
26. *Limnofauna Europaea*, Stuttgart: Gustav Fischer Verlag; Swets and Zeitlinger B.V., 1978.
27. Mavrin, A.S. and Strel'nikova, A.P., Feeding, development, and growth of juvenile perch *Perca fluviatilis* in mesocosms in the presence of filter-feeding zebra mussel *Dreissena polymorpha* Pallas, *Inland Water Biol.*, 2011, vol. 4, no. 2, pp. 232–241. <https://doi.org/10.1134/S1995082911020143>
28. Wiederholm, T., Chironomidae of the Holarctic region. Keys and diagnoses. Part 1: Larvae, *Entomol. Scand. Suppl.*, 1983, no. 19.
29. Wiederholm, T., Chironomidae of the Holarctic region. Keys and diagnoses. Part 2: Pupae, *Entomol. Scand. Suppl.*, 1986, no. 28.

*Translated by D. Pavlov*