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Peculiarities of the Zooperiphyton Succession in Beaver Ponds of a Small River

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Abstract—The increase in the species diversity of the zooperiphyton and intensifying succession due to the increase of the abundance of chironomid larvae (stage I) was observed upstream along the small Latka River (a tributary of Rybinsk Reservoir) during the first year after the appearance of the beaver dam, when the depth increased and the flow velocity decreased. In the beaver pond, which was overgrown by yellow water-lily, the zoocenose succession depended greatly on the abundance of the vegetating and fading plants. During the vegetation period, at high abundance of the yellow water-lily, the species richness of the zoocenose decreased, and then it increased again the next year, when new vegetation was low, and the old plants were decomposing en masse. Directly downstream from one of the beaver dams, the mollusks affected negatively the seasonal succession of the zoocenoses under an instable water level and current regime, when they removed nearly all the fouling from the substrates.

Keywords: small river, beaver ponds, zooperiphyton, succession
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INTRODUCTION

The problem of studying the succession in different ecosystems is complicated, and there is a lack of knowledge available to develop it. When studying the aquatic biogeocenoses, the studies of succession are complicated by the high diversity and many components of the biotopic groups of the hydrobionts, limitations of visual observations, and problems in organizing synchronized studies in the water body, which require a number of different specialists.

On the scale of decades and centuries, and even thousands of years, the structural changes in different biotopic groups of the organisms linked to the development of the ecosystem are realized as seasonal and annual successions, i.e., the evolutionary and ecological adaptation processes are ongoing (Bigon et al., 1989). Taking this into account, the smallest temporal scale of the succession of the ecosystem (seasonal or annual, i.e., repeating each year) has to be applied when searching for the regularities of the formation of the community structure with regard to the environment within the framework of comparative biogeocenology (Skal'skaya et al., 2003).

The succession processes have been studied the least for the different groups of invertebrates in small rivers; in particular, there is insufficient data on the periphyton zoocenose structure for beaver ponds.

This study aims to describe the peculiarities of the seasonal succession of the zooperiphyton in the beaver ponds of a small river (Latka River, a tributary of Rybinsk Reservoir) and to search for the major factors affecting the zoocenose structure forming in different years.

MATERIALS AND METHODS

The zooperiphyton was sampled in 2003–2005 at five stations on Latka River from artificial substrates (wooden beams) and natural substrates (waterlogged wood and stones). Using the artificial substrates permitted us to consider our study as semi-experimental and performed directly after the appearance of new ponds of zoogenous origin in the water stream. In order to analyze the succession, samples were obtained from artificial substrates deployed at three stations: in the upstream area (station no. 3), in the beaver pond located upstream from the discharge of the dairy (station no. 4), and at a station that is located downstream from the highest beaver dam (station no. 6). The sampling site map, the detailed method of deploying the artificial substrate, and the description of the standard sampling and processing methods used for the water reservoirs, lakes, and small rivers have been published before (Skal'skaya, 2002; *Ekosistema maloi reki...*, 2007). In total, 96 quantitative samples have been obtained and analyzed.

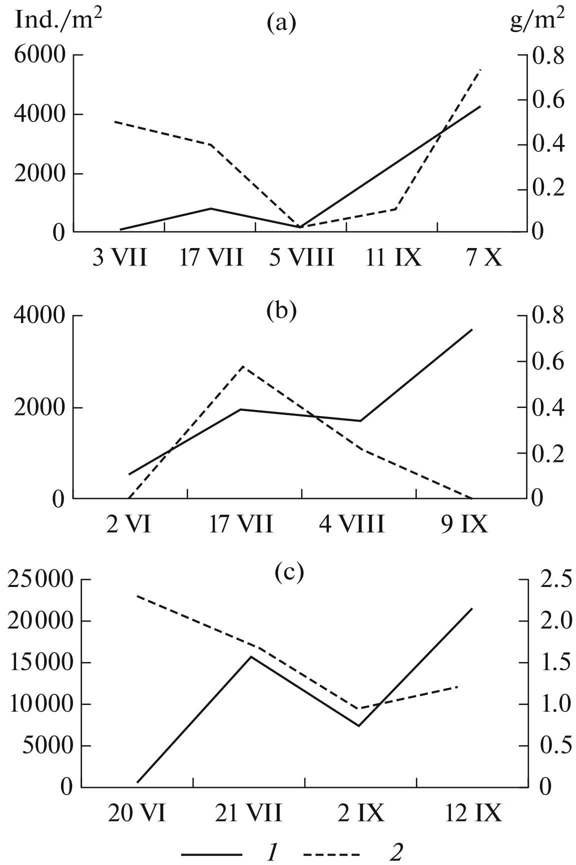

Fig. 1. Abundance and biomass of the zooperiphyton at station no. 3 in the Latka River in 2003 (a), 2004 (b), and 2005 (c): *1*, abundance, *2*, biomass.

RESULTS AND DISCUSSION

Long-term studies performed on the small Latka River, which has been polluted for a long time period by the dairy discharge and inhabited by beavers from the 2000s, evidence the complicated pattern of the changes of the zooperiphyton structure at different sites of the river.

Upstream (station no. 3). Before the appearance of the beaver dam, the major ecological conditions at this site were limiting the succession; they included such factors as small depths (limiting the living space for the invertebrates), relatively poor water warming, poor development of the periphyton, and limited food resources. In 2003, the abundance and biomass were low and did not exceed through the season the values of 5000 ind./m^2 and 0.8 g/m^2, respectively (Fig. 1). No absolute dominant has been found except for the settling chironomid larvae of stage I, which might comprise up to 79% of the total zooperiphyton abundance. The young larvae of caddis flies, mayflies, and stone flies did not play a significant role in the zoocenoses. In September, the subdominants by abundance were the chironomid larvae *Diamesa* sp. (17.6%), and in October, *Paratanytarsus confusus* Palmen, 1960 (9.2%). From time to time, a few large larvae of caddis flies, mollusks, and mayflies subdominated by biomass. In early October, the species richness was maximal (14 species).

In 2004, the episodic increase of the water depth and the flow velocity was a result of rainfall and further water level increase; this did not change the overall trend of the succession. The number of species and total abundance in the zoocenoses were similar to those observed in the previous vegetation period, when the leading role belonged to the chironomid larvae of stage I (up to 71%). The community biomass has increased significantly due to the appearance of the few large larvae of the caddis flies *Chaetopteryx* gr. *villosa* Fabricius, 1798, in June and *Potamophylax latipennis* (Curtis, 1834) in July, which comprised 97.2 and 58.7% of the total biomass.

In 2005, new beaver dams changed greatly the hydrological regime at this station, so the water volume increased, and the species richness (19 taxa) and the zooperiphyton abundance (21700 ind./m^2) did also in autumn. These values exceeded significantly the ranges observed during the previous years. As before, the chironomid larvae of stage I dominated and their relative abundance reached 93.3%, so the total abundance has also increased. However, these changes did not result from the biomass increase. In mid-October, the larvae of chironomid *Polypedilum exsectum* (Kieffer, 1916) (46.8%), chironomid larvae of stage I (17.8%), *Tanytarsus verralli* Goetghebuer, 1928 (13.8%), and caddis fly larvae *Lype phaeopa* (Stephens, 1836) (10.6%) were dominating. Therefore, this increase in the water volume and further changes of the hydrological regime promoted the increase of both the species richness in the zoocenose and the abundance of the settling stages of chironomid larvae, but did not result in a significant improvement of the feeding conditions for the invertebrates. If the high water level stays, the environment may change and the succession may become more complicated.

Beaver pond located upstream from the dairy discharge (station no. 4). In 2003–2004, the station depth was quite stable (90–120 cm). The bottom sediments were organized in two layers: gray silt containing many fading and vegetating plants (upper) and black silt (below). Currents were nearly absent. The pond warmed up significantly. In 2003, the water temperature exceeded this parameter at the monitoring station by 3–4°C. In 2004, the difference in the water temperatures nearly disappeared, mostly due to the less favorable meteorological conditions. In autumn, the station was flooded due to the affluent that appeared after a new beaver dam was built. In 2005, the sampling site was shifted approximately 15–20 m downstream, and the new station is located in the zone that was previously polluted by the dairy discharge.

The massive overgrowth by the yellow water-lily (*Nuphar lutea*) was a specific feature of this site of the stream. The aquatic plants take part in the trophic cycle of all the components of the food chain both during vegetating and after fading. Many groups of invertebrates are linked with the aquatic plants directly or indirectly. The presence of aquatic plants and low water exchange preconditioned greatly the species composition of the major groups of the fouling species, including chironomid larvae, mollusks, the waterlouse *Asellus aquaticus*, etc. In 2003, the dense beds of the yellow water-lily did not promote the development of the fouling communities (Fig. 2), but inhibited it, probably by excreting phytoncides by the living plants; these compounds prevented the presence of invertebrates. The oxygen regime in the bottom water layer was, probably, also unfavorable. An extremely low abundance has been observed for the chironomid larvae of stage I (<360 ind./m^2, or 26.5% of total abundance). There were no dominants (invertebrates) throughout the season. In summer, the mollusks dominated in the poor-species zoocenoses (young specimens of Planorbidae, *Acroloxus lacustris* (Linnaeus, 1758), and *Physa fontinalis* (Linnaeus, 1758); they comprised up to 58.8% by abundance and up to 90.3% by biomass (540 ind./m^2 and 1.1 g/m^2, respectively). From time to time, the waterlouse, leeches *Erpobdella octoculata* (Linnaeus, 1758) and *Glossiphonia complanata* (Linnaeus, 1758), and large larvae of the caddis fly *Phryganea bipunctata* Retzius, 1783 played a significant role in the community. During the vegetation period, only six to eight species were registered in the zoocenoses; and their number increased up to fourteen only in September.

In early June 2004, the decomposing leaves and stalks of the yellow water-lily vegetating during the previous season were found in the near-bottom layer. The newly vegetating plants grew slowly and poorly, and they faded in early September. These environmental changes affected greatly the enrichment of the species composition at all the depths, so the number of species during succession increased from 8 up to 38. The reproduction activity of the fouling species intensified, so the total abundance also increased compared to the previous season by an order of magnitude and even more (Fig. 2). The chironomid larvae dominated among the numerous groups of invertebrates. Their ratio decreased from early summer to autumn from 87.9 down to 54.9%, and the larvae of stage I had the greatest contribution to the total abundance. The composition of the dominant species (the larvae of the more advanced stages, by abundance) changed through the summer (early dates of the month) as follows: no dominants in June; *Chironomus* gr. *plumosus* (15.0%) and *Cricotopus* gr. *sylvestris* (5.0%) in July; *Tanytarsus verralli* (9.2%) and *Paratanytarsus confuses* (4.8%) in August; *Ablabesmyia* gr. *monilis* (Linnaeus, 1758) (11.1%) and *Chironomus* f.l. *plumosus* (10.3%) in September. In autumn, oligochaetes, mostly *Dero*

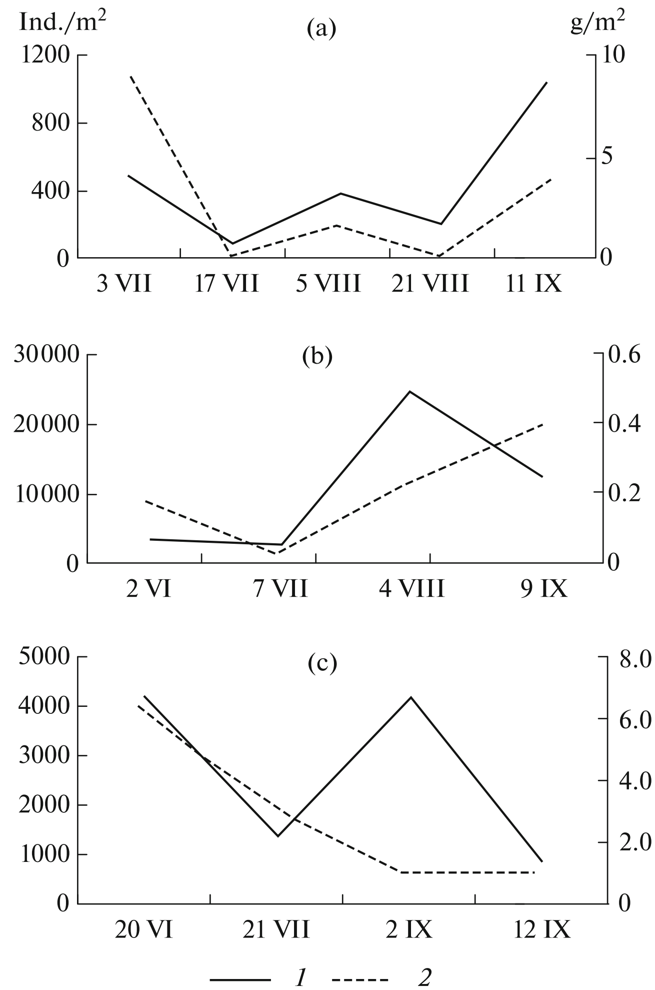

Fig. 2. Abundance and biomass of the zooperiphyton at station no. 4 in the Latka River in 2003 (a), 2004 (b), and 2005 (c): *1*, abundance, *2*, biomass.

obtuse d'Udekem, 1855 (32.5%), were the dominant species. Large invertebrates (mollusks, larvae of caddis flies, and leeches) were found in the zoocenoses, but they played a secondary role, so no biomass increase was been observed compared to the previous year.

In 2005, the changing of the sampling site affected the observed structure of the forming zoocenoses. Another environment resulted from the respective interchanging of the zoocenose composition; this proved the theory of the highly mosaic pattern of the forming communities along the whole river (Skal'skaya, 2007). In this zone, despite the stoppage of the dairy discharge, the bottom sediments rich in organic compounds still affected the hydrobionts. During the season, the chironomid larvae dominated and were represented by a variety of species of the genus *Chironomus*: *Chironomus pseudothummi* Strenzke prevailed in June by the abundance (27.4%), accompanied by *Ch. melanotus* Keyl (11.8%) and

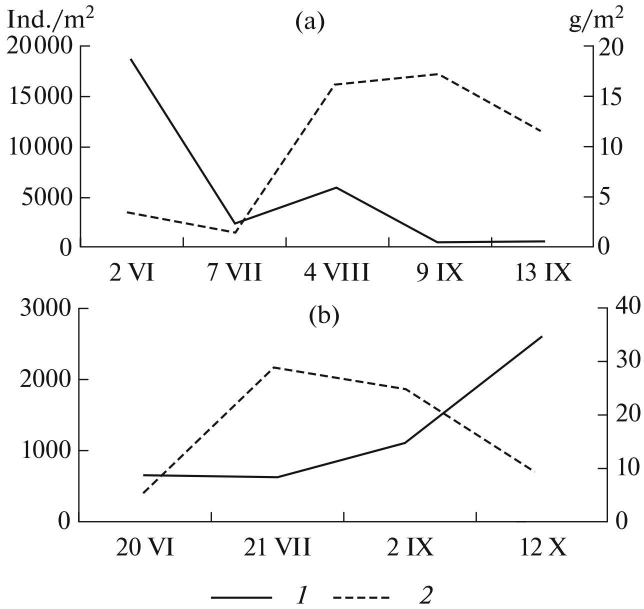

Fig. 3. Abundance and biomass of the zooperiphyton at station no. 3 in the Latka River in 2004 (a) and 2005 (b): *1*, abundance, *2*, biomass.

Ch. piger Strenzke (10.4%); in July, *Ch. parathummi* Keyl (22.2%); in early September, *Ch. pseudothummi* (23.8%); in mid-October, *Ch. pseudothummi* (44.1%) and *Ch. parathummi* (23.5%). Despite the presence of these chironomid larvae, which are the indicator species of a saprobic environment, their low relative abundance evidences the trace amount of the organic load at this riverine site.

Beaver pond located downstream from the dairy discharge site (station no. 6). The station is located approximately 1-km downstream from the dairy discharge site and at a level lower than the highest beaver dam, which was ruined from time to time by road workers. This site was characterized by an unstable flow velocity (from 0 up to 20–30 cm/s), which depended on the state of the beaver dam located upstream and the appearance of another beaver dam downstream. The water depth varied accordingly from 22 to 70 cm. There were no aquatic plants, and the bottom sediments were silty sands.

This site of the river was greatly affected by the diluted dairy discharge, which was partly bioremediated by the saprobic invertebrates developing en masse upstream in the highly polluted area. In early June 2004, a rich zoocenose characterized by high abundance (18800 ind./m^2) and biomass (3.3 g/m^2) was observed; it comprised the chironomid larvae, oligochaetes, nematodes, larvae of caddis flies, and mayflies; the chironomid larvae and oligochaetes comprised 96.9% of the total abundance and 11.9% of the total biomass (Fig. 3). The chironomid larvae of stage I comprised 69.3% of the total abundance; their contribution decreased later. Large, but few larvae of caddis flies *Limnephilus decipiens* (Kolenati, 1848) and the larvae of mayflies *Cloen dipterum* (Linnaeus, 1758) comprised 87.9% of the total biomass. A month later, the total abundance of zooperiphyton had decreased dramatically, with a small increase later on in August and the minimal values observed in autumn. The opposite pattern was observed for the biomass dynamics. In early July, small numbers of *Anisus contortus* (Linnaeus, 1758) and *A. acronicus* (Ferussac, 1807) appeared, and then the mollusks dominated by biomass.

The maximal species richness of zooperiphyton (26 species) was registered in August. The most abundant mollusk was *Planorbis planorbis* (Linnaeus, 1758); this group comprised in total 5.2% of abundance and 76.5% of biomass. Chironomid larvae were also a very diverse group. *Chironomus parathummi*, *Ch. piger*, and young larvae, comprising together 61.2% of the total abundance and 19.8% of biomass, dominated in the *Chironomus* genus. *Cricotopus* gr. *sylvestris* (13.4% of total abundance) was the subdominant species among chironomids, and the abundances of the other chironomid species were insignificant.

In early September, large mollusks *Limnaea stagnalis* (Linnaeus, 1758) and *Planorbis planorbis* comprised almost all the small invertebrates and so cleaned the substrates. The number of species (including mollusks) decreased down to five. In October, nine species were registered due to the appearance of the chironomid larvae and oligochaetes onto the substrates.

In 2005, the pollution of the river by the dairy discharge was stopped; this promoted a more favorable environment in the stream and minimized the contribution of *Chironomus* larvae in thte zooperiphyton. The leading role in biomass belonged to mollusks. From time to time, they dominated also by abundance. The dominating species were *Planorbis planorbis, Physa fontinalis* (Linnaeus, 1758), and *Lymnaea lagotis* (Schranck, 1803). Through summer and autumn, when the predator pressure of large mollusks on the small invertebrates was decreasing, the species richness of the zooperiphyton increased from eight species (late June) up to 22 species (mid-October). In this season, the chironomid larvae dominated by abundance (74.3%), with the maximal contribution of larvae of stage I (51.3%).

CONCLUSIONS

In the small Latka River, structural changes in the zoocenoses are tightly linked to the hydrological and hydrochemical peculiarities of the water stream. The major factors are the depth (the volume of the living space for the hydrobionts), flow velocity, presence of the shallow nearshore refuge zones, weediness, anthopogenic and zoogenic pollution, and the degree of food provision for the hydrobionts. Small-scale (or local) successions take place even in a changing water level regime in the presence of beaver ponds. The succession processes in the river may be intermittently interrupted by high water from rainfall, so the already formed communities may be partly ruined, the biotopes may be cleaned from the old inhabitants, and a place for the new communities appears. The limited volume of the living space for the invertebrates and the pronounced dynamics of the environment in Latka River are accompanied by formation of ephemeral communities that include species characterized by a short life cycle and high renewing potential (due to the new generations), so no stabilization has been observed in the communities studied.

The natural factors limiting the succession of the periphyton zoocenoses in the upstream area were the low water and the food deficit. The increase of the invertebrate species richness and increase of the chironomid larvae of stage I were observed at the early stages after an increase in the water volume due to the appearance of beaver dams, but the biomass was still low.

In the beaver pond (station no. 4) overgrown by the yellow water-lily, the seasonal dynamics and the structure of the forming communities were linked to the abundance of vegetating and fading plants. In the years favorable for the aquatic plant vegetation, the zooperiphyton succession was suppressed; the opposite pattern was observed when the weed density was low, and the plants of vegetation of the previous year faded, rich and various zoocenoses were formed.

Diverse zoocenoses referring to the pollution level formed at the river site located downstream from the beaver dam (station no. 6) and characterized by an instable water level and current regime, and under an anthropogenic load. The succession could be interrupted by the gastropods that consumed almost all the fouling communities onto the substrates. The decrease in the pressure of the omnivorous invertebrates in autumn resulted as an increase of the species richness and domination of the chironomid larvae in the zooperiphyton.

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