

## Influence of Aquatic Plants of Different Ecological Groups on Zooplankton Distribution and Abundance

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Received June 8, 2017; in final form, July 18, 2017

**Abstract**—The distribution of zooplankton has been studied in a waterbody whose entire area is occupied by phytocenoses with the dominance of plants of different ecological groups. It is shown that, in the phytocoenosis of the submerged hydrophyte *Elodea canadensis*, zooplankton is involved in the classical grazing trophic web. The zooplankton community in this phytocoenosis is mainly made up by algaephagous species. In the habitats occupied by emergent plant *Carex riparia*, zooplankton is more closely associated with the components of the “microbial loop,” where the most abundant groups are predators and bacterio–detritophagous species.

**Keywords:** zooplankton, submerged aquatic plant, emergent aquatic plant, *Carex riparia*, *Elodea canadensis*

**DOI:** 10.1134/S1995425518010080

### INTRODUCTION

Aquatic plants occupy significant areas of littoral and shallow water areas. The impact of higher plants on the cycle of mineral and organic substances in aquatic ecosystems can be considerable. The ability to absorb and accumulate some elements and release them during their life and after their death varies in different species (Dykyjová, 1979). Aquatic plants produce carbohydrates, organic substances, and amino acids and release them in the environment (Lukina, 1990; Ratushnyak, 1993). During their life, aquatic plants do not excrete much phosphorus; the main portion of phosphorus enters the water in the course of hydrophyte decomposition (Granéli and Solander, 1988). Plants from the same ecological group (e.g., submerged, floating or emergent plants) create similar conditions of the environment. Expanding and changing the environment, physicochemical conditions, and relations in food chains, plants impact, on the one hand, the quantity and availability of trophic resources for zooplankton and, on the other hand, the intensity of predator pressure, thus, affecting the distribution and abundance of aquatic organisms.

Zooplankton was studied in a pond without open water sites. Its entire area was occupied by two phytocenoses: the first was dominated by emergent plant sedge *Carex riparia* Curt and the other by submerged plant *Elodea canadensis* Michx.

Nutrition of the sedge is associated more with the ground than the water. In spring, plants grow owing to the accumulation of nutrients by the roots while, in summer, nutrients are absorbed from the soil. The excretion of nitrogen and phosphorus into water by

live propagules is insignificant (Bernard et al., 1988). The nutrients accumulated in the sedge biomass enter the environment during plant decomposition. However, sedge decomposes slowly. In sedge species, biomass loss accounts for only 24–53% per year (Verhoeven and Arts, 1992; Schulz et al., 2011). Emergent plants, in general, are characterized by a lower rate of decomposition than submerged plants (Belova, 1982). During the first 4–7 months, the content of nitrogen and phosphorus in the phytomass of the decomposing plants in the sedge increased relative to the initial levels by 75–100% (Morris and Lajtha, 1986; Bernard et al., 1988). The reduction in nitrogen and phosphorus contents begins after the roots of vegetative plants grow through the plant residues. Hence, sedges can form zones in which N and P are retained in sediments (Morris and Lajtha, 1986; Bernard et al., 1988). Emergent plants were shown to form high production, a small portion of which is utilized by phytophagous species while the greatest part of this production enters to detrital trophic webs or remains unutilized (Longhi et al., 2008). It was noted that, in annual helophytes, nutrients are released faster than in perennial plants (Morris and Lajtha, 1986).

The exchange of mineral and organic substances between elodea and the aquatic environment occurs more actively. The concentrations of phosphorus (phosphates), nitrogen (nitrates and nitrites) (Pokorný et al., 1984), carbohydrates, organic substances, and amino acids (Lukina, 1990; Ratushnyak, 1993; Masachiro and Takuo, 1994) are higher in the sites occupied by elodea than in the open areas. The contents of N, P, and K in the tissues of *Elodea canadensis* is larger

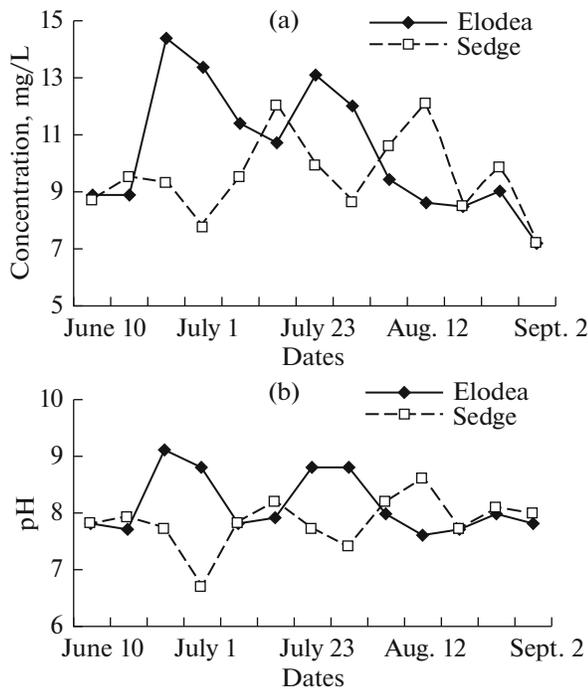


Fig. 1. Dynamics of the dissolved oxygen concentration (a) and pH (b) in the two phytocenoses.

than in *Carex riparia* (Dykyjová, 1979). Since elodea has a higher rate of decomposition (Belova, 1982; Masachi and Takuo, 1994), the nutrient elements enter the water more quickly during plant decomposition in the elodea than in the sedge habitats (Masachi and Takuo, 1994); afterwards they again enter the biotic cycle.

Our goal is to investigate zooplankton distribution in the water body in dependence of the vegetation composition.

## MATERIALS AND METHODS

Studies were carried out in two sites with aquatic vegetation in a pond with an area of 1080 m<sup>2</sup>. The pond is surrounded by low forest cover on three sides and with an uncultivated field on the fourth (southern) side. Phytocenosis with a dominant species *Carex riparia* Curt. (total projective cover of 60%) formed a strip along the southern shore with a length of ~18 m and a width of 2–6 m. Other than the dominant species, this phytocenosis included aquatic moss and solitary plant species *Hydrocharis morsus-ranae* L., *Utricularia vulgaris* L., *Lycopus europaeus* L., *Scutellaria galericulata* L., and *Typha latifolia* L. The water depth in the sampling sites was 0.3–0.7 m. The remaining area of the pond was occupied by a phytocenosis with the dominance of *Elodea canadensis* Michx. (total projective cover of 90%) with small “spots” of *Persicaria amphibia* (L.). Samples were taken from a depth of 1 m. The maximum depth of the pond was 1.9 m. Studies

were conducted during the active vegetating period of aquatic plants from June 10 to September 2 in 2015. By September, elodea occupied the entire water column from the bottom to the surface; its dry mass was 564 g/m<sup>3</sup> (wet mass was 7088 g/m<sup>3</sup>). Sedge stayed in the semisubmerged position throughout the season. In September, the dry mass of the aboveground part of the sedge was 636 g/m<sup>2</sup> (wet mass was 3448 g/m<sup>2</sup>).

Samples were collected weekly in three sites of each phytocenosis. Samples from three sites (2 L) were poured into one bucket; afterwards, the integral sample was taken for the analysis of plant pigments, bacteria, flagellates, and ciliates. Zooplankton samples were taken from different sites which were analyzed separately to study the distribution of zooplankton species in each phytocenosis and compare it between different habitats. Samples of 10 L were filtered through the plankton net with a mesh size of 73 μm and fixed with 70% ethyl alcohol. Then they were processed by the standard methods. Mean values and their confidence intervals were found for each parameter.

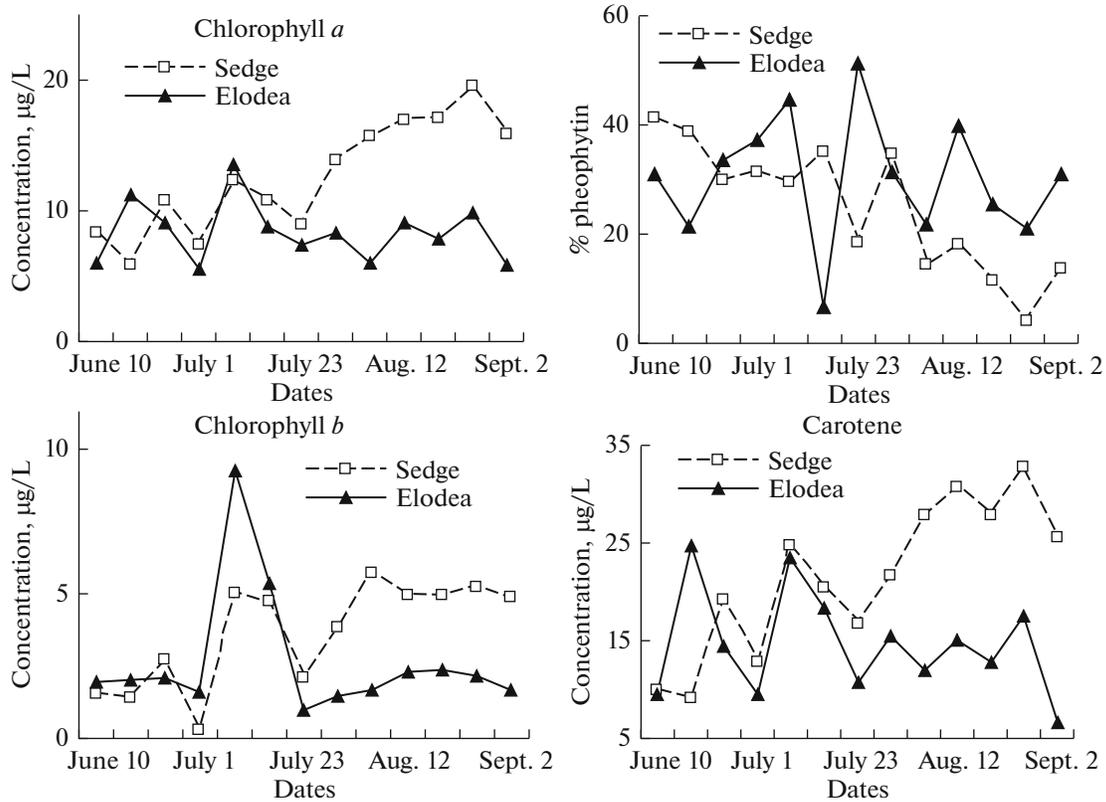
The content of phytoplankton pigments was measured using the spectrophotometric method in an acetone extract (Sirenko and Kureishevich, 1982). Bacteria were precipitated on nuclear filters with a pore diameter of 0.17 μm, stained with DAPI fluorochrome (Porter and Feig, 1980), and counted under an epifluorescence microscope. The number of flagellates was counted in “live” water samples using light microscopy. The biomass was found using its relationships with the size and geometric shape of the cells, assuming that the specific density is equal to one. Ciliates were identified in freshwater samples in Bogorov’s chamber under a MBS-10 light microscope (Russia); small forms were identified under a Ergaval microscope (Germany). The total biomass was calculated using individual masses of ciliates taken from published data (Chorik, 1968; Mamaeva, 1979; Zharikov, 1996). Species were identified according to the Identification Guide (Kahl, 1930–1935; Mamaeva, 1979; Carey, 1991; Foissner and Berker, 1996).

Water temperature, pH, and biological samples were taken in the morning at the time interval 09:00–10:30 am. The dissolved oxygen concentration was measured by the iodometric method (ISO 5813-83, 2010).

The relationships between the quantitative characteristics of the aquatic species were found using Spearman’s rank correlation coefficient. The calculations were performed using the PAST program (Hammer et al., 2001).

## RESULTS

In the water of the elodea phytocenosis, oxygen concentrations and pH were higher than in the sedge phytocenosis until late July (Fig. 1). The water temperature in the morning was  $19.2 \pm 2.4^\circ\text{C}$ .



**Fig. 2.** Dynamics of the concentrations of pigments and the content of pheophytin in phytoplankton in the elodea and sedge thickets.

Concentrations of phytoplankton pigments and their dynamics in two types of vegetation thickets were similar until late July. Later in the sedge thickets, the concentrations of chlorophylls *a* and *b* and carotenoids were twofold higher than the corresponding concentrations in the elodea thickets (Fig. 2). The concentrations of chlorophyll *c*, which is typical of diatom algae, were low (on average, 0.6 µg/L) in both types of thickets. Since the end of July, the concentration of pheophytin decreased in the sedge phytoceenosis, averaging 16% of the total chlorophyll concentration, while in phytoplankton from the elodea thickets, the concentration of pheophytin remained at the level of 30% of the total chlorophyll concentration throughout the summer. Since the end of July, the pigment index  $E_{480}/E_{665}$  indicated a greater proportion of yellow pigments in the phytoplankton in the elodea than in the sedge thickets.

The number of bacteria in the water gradually increased during the growing season. The mean values of the microorganism abundances averaged over the growing season were close in the elodea and sedge thickets (Table 1). In the phytoceenosis of elodea, the dynamics of the number of bacteria had a pronounced sawtooth character owing to abrupt jumps in the number of bacteria. In the sedge thickets during the last 4 weeks of the study period (August to early Septem-

ber), the number of bacteria was relatively stable, ranging from  $16.8 \pm 1.1$  million cells/mL. In thickets of both types, the number of bacteria correlated with the concentration of chlorophyll *a*. In the sedge thickets, bacteria correlated, in addition, with the number of their consumers: ciliates, rotifers, and crustaceans of the family Chydoridae (Table 2).

The abundance and biomass of the flagellates in the elodea and sedge thickets changed in a similar pattern. However, in late July and mid-August, biomasses of flagellates were higher in the sedge thickets. In the sedge thickets, the correlation coefficient between the number of flagellates and the biomass of ciliates was statistically significant (Table 2).

In the sedge phytoceenosis, the number of testate amoebae (Testacea) of the genera *Arcella* and *Diffugia* were higher by an order of magnitude than in the elodea thickets (Table 1).

In general, 37 species of ciliates were recorded. Among them, 31 species were found in the sedge and 21 species in the elodea thickets. In both phytoceenoses, *Strombidium viride* Stein and *Halteria grandinella* (O.F. Müller) were commonly present, while *Coleps hirtus* (Ehrenberg) were common only in the sedge. The highest abundance of *Strombidium viride* was recorded in June: 594000 ind./m<sup>3</sup> in the elodea

**Table 1.** Abundance and biomass of plankton taxa in the phytocenoses of elodea and sedge (minimum–maximum (average))

Parameters		Elodea	Sedge
Abundance	Bacteria, mln cells/mL	3.5–19.8 (11.2)	7.1–18.1 (12.3)
	Flagellates, cells/mL	95–323 (198)	29–455 (222)
	Testacea, thou. ind./m <sup>3</sup>	0.4–3.9 (2.1)	4.3–45.9 (21.6)
	Ciliates, thou. ind./m <sup>3</sup>	297–759 (492.5)	231–1221 (657.5)
	Rotifera, thou. ind./m <sup>3</sup>	0.9–4.9 (2.5)	2.7–24.8 (12)
	Cladocera, thou. ind./m <sup>3</sup>	1.2–7.3 (2.9)	4.3–29.2 (16.9)
	Copepoda, thou. ind./m <sup>3</sup>	39.5–126.6 (82.8)	26.6–122.6 (70.8)
Biomass, mg/m <sup>3</sup>	Flagellates	320–3500 (1350)	210–3370 (1660)
	Ciliates	30.9–237.3 (97.7)	9.24–553.2 (120)
	Rotifera	1.3–13.3 (4.8)	3.3–21.6 (11.2)
	Cladocera	8.4–34 (13.9)	17.4–96.5 (57.5)
	Copepoda	216.4–1134.4 (502.3)	394.9–1047.4 (697)

**Table 2.** Statistically significant relationships between the quantitative parameters of planktonic organisms in the phytocenoses of elodea and sedge

Parameters	<i>R</i>	<i>p</i>
Elodea		
Chlorophyll <i>a</i> & N bacteria	–0.57	<0.05
Chlorophyll <i>a</i> & B ciliates	–0.64	<0.05
Sedge		
Chlorophyll <i>a</i> & N bacteria	0.87	<0.001
Chlorophyll <i>a</i> & N algaephagous ciliates	–0.63	<0.05
Chlorophyll <i>a</i> & B bacterio–detritophagous ciliates	0.74	<0.01
Chlorophyll <i>a</i> & B Chydoridae	0.57	<0.05
Chlorophyll <i>a</i> & N Rotifera	0.66	<0.05
Chlorophyll <i>a</i> & B Rotifera	0.57	<0.05
N bacteria & B ciliates	0.64	<0.05
N bacteria & B bacterio–detritophagous ciliates	0.73	<0.01
N bacteria & N Chydoridae	0.55	<0.05
N bacteria & B Chydoridae	0.68	<0.05
N bacteria & N Rotifera	0.59	<0.05
N flagellates & B ciliates	0.70	<0.01
N flagellates & B algaephagous ciliates	0.67	<0.05
B bacterio–detritophagous ciliates & N Chydoridae	0.63	<0.05
B bacterio–detritophagous ciliates & B Chydoridae	0.69	<0.01
B bacterio–detritophagous ciliates & N Rotifera	0.70	<0.01
B bacterio–detritophagous ciliates & B Rotifera	0.58	<0.05

*R*, Spearman correlation coefficient; *p*, probability value; N, abundance, and B, biomass.

and 660000 ind./m<sup>3</sup> in the sedge thickets. The maximum of *Halteria grandinella* was observed in the elodea in late July (165000 ind./m<sup>3</sup>) and in the sedge in late August (627000 ind./m<sup>3</sup>). *Coleps hirtus* in the

sedge reached its peak in September (297000 ind./m<sup>3</sup>). In the phytocenosis of the elodea, algaephagous species prevailed, averaging 68% of the total abundance of ciliates. In the phytocenosis of the sedge, bacterio–

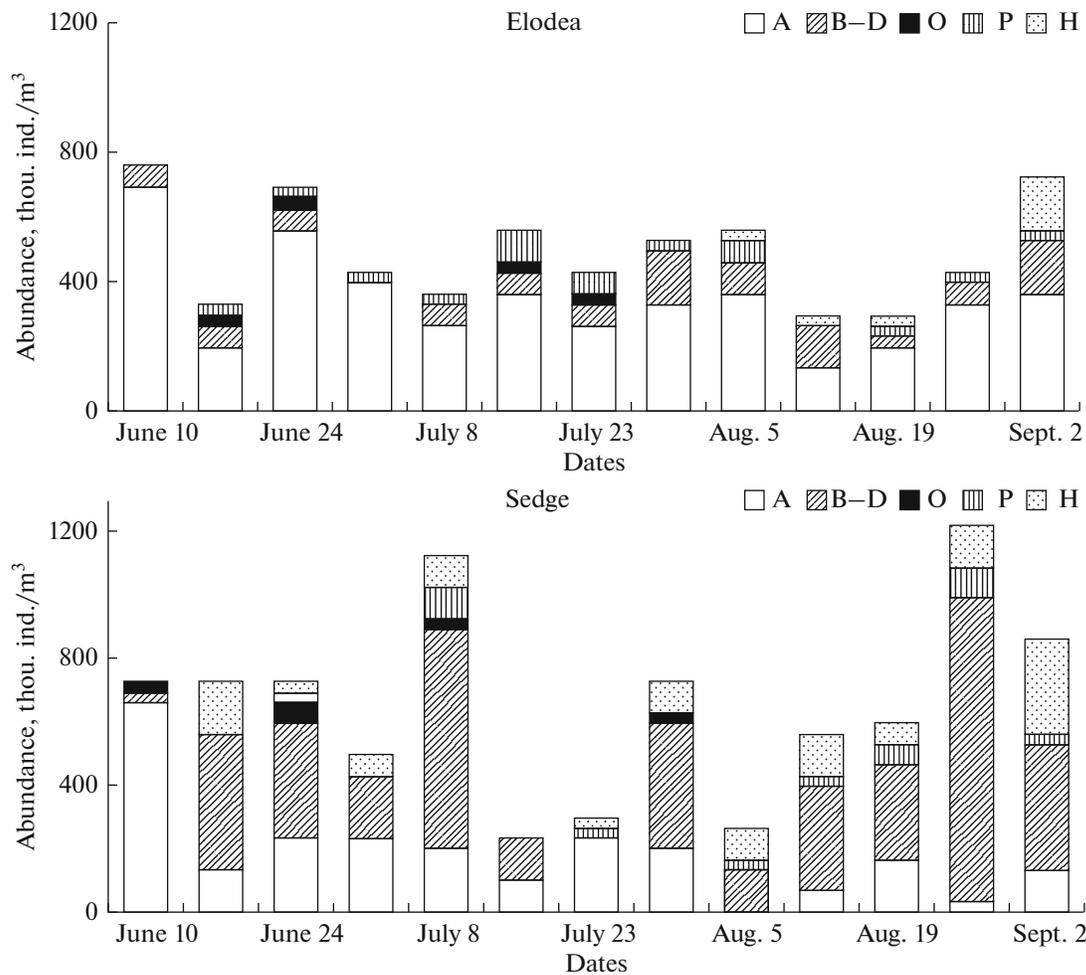


Fig. 3. Distribution of ciliates along the trophic groups: (A) algaephagous ciliates, (B–D) bacterio–detritophagous ciliates, (O) nonselective omnivores, (P) predators, and (H) hystophagous ciliates.

detritophagous species constituted 47% of the total abundance of ciliates (Fig. 3). In the elodea, the biomass of ciliates correlated with the concentration of chlorophyll *a*, while in the sedge the ciliate biomass was related to their food resources (algae, bacteria, and flagellates) and potential consumers (rotifers and Chydoridae) (Table 2).

Forty species of Rotifera, 14 species of Cladocera, and 12 species of Copepoda were found in the zooplankton samples. In June and July, the total biomass of the zooplankton (Crustacea and Rotifera) was twofold higher in the sedge than in the elodea thickets. Later these differences were less pronounced. The abundance of Rotifera (Fig. 4) and Cladocera (Fig. 5a) was higher in the sedge phytocenosis (Table 1) throughout the study period. The distribution of Copepoda depended on the age and species structures. Copepodite and adult Cyclopidae preferred to inhabit sedge habitats, while nauplius Copepoda and copepodite and adult Calanidae (*Eudiaptomus transylvanicus* (Daday)) commonly occurred in elodea thickets (Fig. 6).

*Mesocyclops leuckarti* (Claus) was the most abundant adult cyclops in both phytocenoses. *Eucyclops macruroides* (Lilljeborg), *Diaphanosoma brachyurum* (Liévin), *Chydorus sphaericus* (OF Müller), *Graptole-*

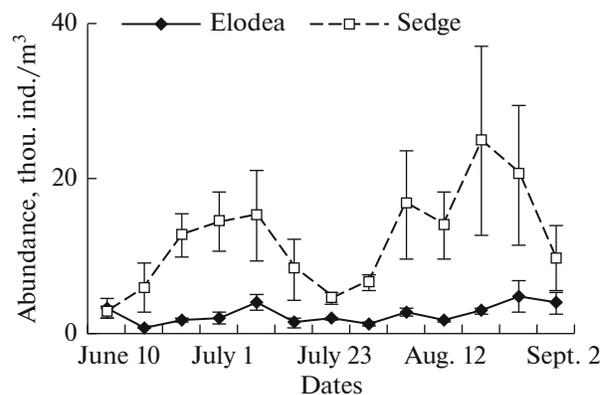


Fig. 4. Abundance of Rotifera in the two phytocenoses. Confidence intervals are given.

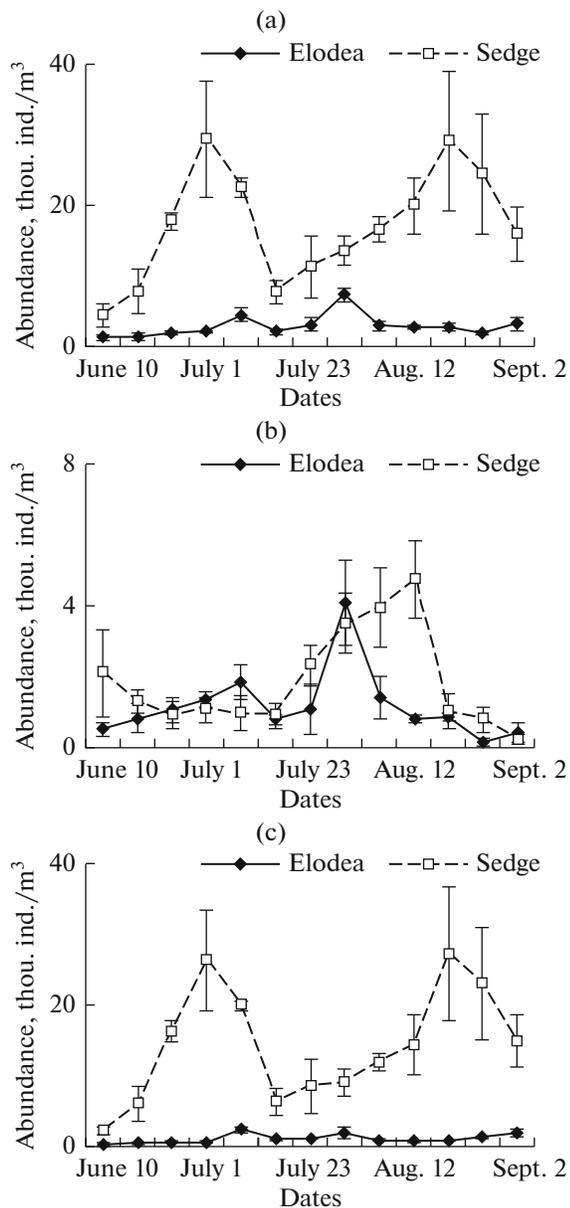


Fig. 5. Abundance of Cladocera: (a) total, (b) *Diaphanosoma brachyurum*, and (c) Chydoridae family. Confidence intervals are given.

*beris testudinaria* (Fischer), *Lecane luna* (Müller), *L. (M.) bulla* (Gosse), *Mytilina ventralis* (Ehrenberg), *Brachionus quadridentatus* Herman, *Euchlanis dilatata* Ehrenberg, and rotifers of the order Bdelloida occurred in elodea and sedge thickets. However, the abundances of the above species, except for *Diaphanosoma brachyurum*, were higher in sedge habitats. The abundance of *D. brachyurum* did not differ between the two phytocenoses, except for a short period in mid-August, when the number of individuals and their biomass were higher in the sedge (Fig. 5b).

In the sedge, we recorded rotifers *Euchlanis deflexa* Gosse and *Dicranophorus grandis* Ehrenberg, copepod

*Ectocyclops phaleratus* (Koch), cladocerans *Macrothrix* sp., *Oxyurella tenuicaudis* (Sars) and *Ceriodaphnia setosa* Matile. *C. quadrangula* (OF Müller) was found in both phytocenoses. Cladocerans of Chydoridae family, mainly *Chydorus sphaericus*, contributed, on average, 81% to the total cladoceran abundance in the sedge (Fig. 5c). In the elodea, crustaceans of Chydoridae family contributed, on average, 38% to the total cladoceran abundance.

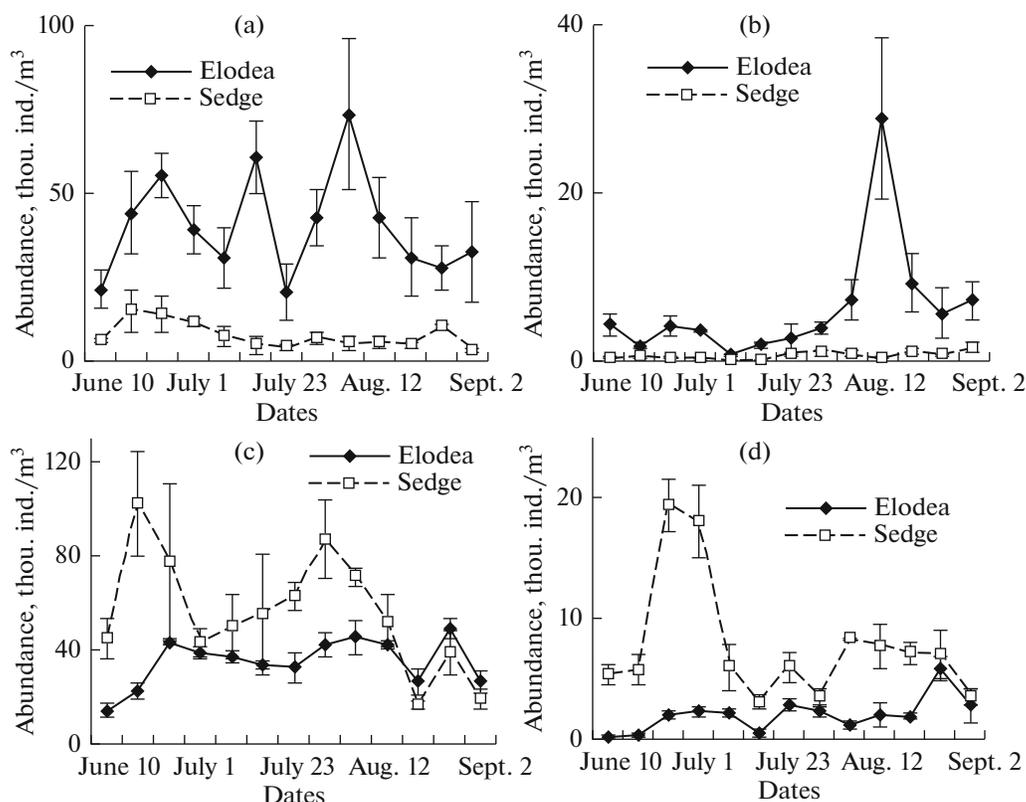
A peculiar feature of elodea phytocenosis was the mass development of calanoid copepod *Eudiaptomus transylvanicus*, the number of which averaged 7%, ranging from 1 to 23% of the total number of zooplankton individuals, and 36%, varying from 6 to 61% of the total zooplankton biomass. In the sedge, this species was absent or rare. Elodea thickets were preferred by cladoceran species *Bosmina longirostris* (O.F. Müller) and rotifera species *Keratella cochlearis* (Gosse).

## DISCUSSION

In phytocenoses of both types, the spatial structures of the habitats were complex owing to the high density of plants. Euplanktonic species commonly avoid such conditions. Nevertheless, in the elodea phytocenosis, *Eudiaptomus transylvanicus* successfully developed in the plankton. Its movements and feeding were apparently not constrained by elodea thickets. *E. transylvanicus* attained the highest abundance in the second half of the summer, when elodea sprouts grew considerably in length and reached the surface, thus reducing the water layers free from plants. Diaptomids are known to have a greater selectivity in their food consumption, in particular, algae, than daphnia species (DeMott, 1989). The successful development of *E. transylvanicus* in the elodea phytocenosis means that the composition and size of the phytoplankton species met its nutritional requirements. In addition, this species could graze on ciliates, the abundance of which in the elodea was quite high. It was found that *Diaptomus* sp. consuming ciliates are able to reduce their numbers to very low levels (Adrian and Schneider-Olt, 1999).

In the sedge phytocenosis, zooplankton was mainly represented by predators, namely, adult and copepodite Cyclopidae, as well as filter-feeders associated with the substrate, i.e., cladocerans of the family Chydoridae and rotifers.

The effects of higher aquatic plants on food resources of zooplankton via their impact on the balance of nutrients and the turnover of carbon is the main driver of zooplankton distribution. Since the diet of planktonic crustaceans can include algae, protozoa, and bacteria (depending on their abundance), the distribution of ciliates along trophic groups can be an important indicator of food resources for zooplankton. Many species of ciliates are highly selective, preferring food particles of certain sizes, shapes, and



**Fig. 6.** Abundance of Copepoda: (a) nauplii, (b) adults and copepodites of *Eudiaptomus transylvanicus*, (c) copepodites of Cyclopidae, and (d) adult Cyclopidae. Confidence intervals are given.

qualities (Burkovskii, 1984). In elodea phytocenosis, algaephagous ciliates were most abundant, while in the phytocenosis of the sedge, bacterio-detrifagous ciliates prevailed (Fig. 3). Therefore, in the elodea, the basic food resource for zooplankton was algae, while in the sedge it was bacteria and detritus.

Higher aquatic plants, especially those which are largely associated with water (many submerged species), are in a competitive relationship with algae. Some hydrophytes were shown to exert an allelopathic influence. For example, Vanderstukken et al. (2014) found that elodea can control phytoplankton development via allelochemicals. However, Erhard and Gross (2006) showed that elodea affected only blue-green, mostly epiphytic, algae, and it did not have any impact on green algae, i.e., *Scenedesmus brevispina* (G.M.Sm.) Chodat. The high abundance of algaephagous ciliates in the elodea phytocenosis indicates that phytoplankton was not affected significantly by the plants; i.e., the nutrient concentrations were sufficient to support the growth of both higher plants and algae.

In aquatic biocenoses, the development of planktonic algae is closely related to the development of bacteria. On the one hand, these organisms compete for resources; on the other hand, their excretions can stimulate their growth. The balance of these processes determines the abundance ratio of algae and bacteria.

In elodea phytocenosis, phytoplankton prevailed over bacteria. A negative correlation was established between the concentration of chlorophyll *a* and the number of bacteria (Table 2). Lower bacterial activity in the elodea phytocenosis compared to that in areas without plants was also observed by other researchers (Pokorný et al., 1984).

Concentrations of algae pigments in the elodea habitats decreased in the second half of the summer owing to the grazing pressure of algae consumers and a reduction in phosphorus availability for phytoplankton due to its deposition with  $\text{CaCO}_3$  (Granéli and Solander, 1988). Insoluble salts of  $\text{CaCO}_3$  were released as a result of a shift in the carbonate equilibrium caused by a pH increase during day hours owing to active photosynthesis by elodea (Pokorný et al., 1984), the phytomass of which had increased significantly by this time. On the contrary, in the sedge phytocenosis, there may be high concentrations of phosphorus in the water, because *Carex riparia* is a species indicator of enhanced trophic level. The development of this species is commonly recorded in areas with high concentrations of the total P (Sager and Lachavanne, 2009).

In the phytocenosis of elodea, zooplankton was involved in the classical grazing food web, while in the sedges it was more closely associated to the compo-

nents of the “microbial loop” and participated in the transfer of carbon through detrital chains. Long-term accumulations of plant residues in the sedge area promote the development of destructor organisms, including heterotrophic bacteria. In the conditions of low water levels and a considerable thickness of sediments, the exchange of substances between soil and water occurs more intensively, mainly due to the vital activity of benthic organisms (Mermillod-Blondin et al., 2008; Mieczan et al., 2015). Adults and copepodites of cyclops accumulated in the sedge because these habitats were rich in food resources, namely, ciliates (mainly bacterio–detritophagous species) and flagellates. It was shown (Zingel et al., 2016) that an increase in Copepoda biomass caused a shift in the structure of the ciliate community; i.e., the abundance of large forms was markedly reduced, while that of small bacteriophagous ciliates increased. *Chydorus sphaericus*, which dominated in the cladoceran community in the sedge, was also able to affect the number of ciliates (Ventelä et al., 2002). We found a correlational relationship between the abundance of Chydoridae and biomass of bacterio–detritophagous ciliates (Table 2). The relationship between crustacean plankton and ciliates is recognized as an important mechanism regulating the energy flow between meta- and protozooplankton (Zingel et al., 2016). The direct correlation of the abundance and biomass of Chydoridae in the sedge with the number of bacteria (Table 2) obviously manifested the connection of links along the food chains: bacteria – ciliates – *Chydorus sphaericus* and detritus + bacteria – Chydoridae.

Nauplii, the first stage of the Cyclopidae, preferably dwell in the elodea, where there is enough food and low predation pressure from adult cyclops.

The microfilter feeder *Diaphanosoma brachyurum*, grazing on both small algae and bacteria, did not demonstrate any preference for either studied phytocenoses. It is known that this species is not sensitive to environmental factors such as pH, humification, and trophic levels, and its mass development was observed in the pelagic zone as well as in the littoral with and without vegetation cover (Korovchinskii, 2004). The abundance of *D. brachyurum* increased in the sedge, while chlorophyll concentration decreased in elodea phytocenosis. Migrating to areas with more favorable food conditions, this species can be more frequently attacked by cyclops, which were more abundant in the sedge. It is known (Korovchinskii, 2004) that juveniles of *D. brachyurum* often become a prey of late copepodite and adult *Mesocyclops*. From mid-August, the number of *D. brachyurum* fell in both phytocenoses.

## CONCLUSIONS

Phytocenoses of elodea and sedge differed by trophic conditions for zooplankton, resulting in its different distribution and abundance. In the elodea, the basic food resources for zooplankton were algae, while

in the sedge they were bacteria and protozoa. In the sedge phytocenosis, the biomass of zooplankton and its diversity calculated in biomass units were greater than in the elodea. In these two types of thickets, plankton crustacean communities were distinguished by the species composition and age structures of Cyclopidae; ciliate communities differed in abundance of trophic groups.

## ACKNOWLEDGMENTS

We are grateful to our colleagues at the Papanin Institute for Biology of Inland Waters, namely, E.V. Garin for assistance in identifying the sedge and N.A. Lapteva and I.V. Rybakova for help in collecting samples and counting bacteria.

## REFERENCES

- Adrian, R. and Schneider-Olt, B., Top-down effects of crustacean zooplankton on pelagic microorganisms in a mesotrophic lake, *J. Plankton Res.*, 1999, vol. 21, no. 11, pp. 2175–2190.
- Belova, M.A., The bacterial destruction of macrophytes in different-types lakes, *Extended Abstract of Cand. Sci. (Biol.) Dissertation*, Kiev, 1982.
- Bernard, J.M., Solander, D., and Květ, J., Production and nutrient dynamics in *Carex* wetlands, *Aquat. Bot.*, 1988, vol. 30, nos. 1–2, pp. 125–147.
- Burkovskii, I.V., *Ekologiya svobodnozhivushchikh infuzorii* (Ecology of Free-Living Infusorians), Moscow: Mosk. Gos. Univ., 1984.
- Carey, P., *Marine Interstitial Ciliates: An Illustrated Key*, New York: Chapman and Hall, 1991.
- Chorik, F.P., *Svobodnozhivushchie infuzorii vodoemov Moldavii* (Free-Living Infusorians from Reservoirs of Moldavia), Chisinau: Akad. Nauk Mold. SSR, 1968.
- DeMott, W.R., Optimal foraging theory as a predictor of chemically mediated food selection by suspension-feeding copepods, *Limnol. Oceanogr.*, 1989, vol. 34, no. 1, pp. 140–154.
- Dykyjová, D., Selective uptake of mineral ions and their concentration factors in aquatic higher plants, *Folia Geobot. Phytotax.*, 1979, vol. 14, no. 3, pp. 267–325.
- Erhard, D. and Gross, E.M., Allelopathic activity of *Elodea canadensis* and *Elodea nuttallii* against epiphytes and phytoplankton, *Aquat. Bot.*, 2006, vol. 85, no. 3, pp. 203–211.
- Foissner, W. and Berker, H., A user-friendly guide to the ciliates (Protozoa, Ciliophora) commonly used by hydrobiologists as bioindicators in rivers, lakes, and waste waters, with notes on their ecology, *Freshwater Biol.*, 1996, vol. 35, no. 2, pp. 375–482.
- Granéli, W. and Solander, D., Influence of aquatic macrophytes on phosphorus cycling in lakes, *Hydrobiologia*, 1988, vol. 170, no. 1, pp. 245–266.
- Hammer, Ø., Harper, D.A.T., and Ryan, P.D., PAST: paleontological statistics software package for education and data analysis, *Palaeontol. Electron.*, 2001, vol. 4, no. 1, pp. 9–15.

- ISO 5813-83: *Opređenje rastvorenog kisloroda. Iodometričeskij metod* (ISO 5813-83: Determination of Dissolved Oxygen. Iodometric Method), Moscow, 2010.
- Kahl, A., *Urtiere oder Protozoa. Wimpertiere oder Ciliata (Infusoria)*, Jena: Die Tierwelt Deutschlands, 1930–1935.
- Korovchinskii, N.M., *Vetvistousye rakoobraznye otrjada Ctenopoda mirovoi fauny (morfologiya, sistematika, ekologiya, zoogeografiya)* (Ctenopoda Crustaceans in the World Fauna: Morphology, Systematics, Ecology, and Zoogeography), Moscow: KMK, 2004.
- Longhi, D., Bartoli, M., and Viaroli, P., Decomposition of four macrophytes in wetland sediments: organic matter and nutrient decay and associated benthic processes, *Aquat. Bot.*, 2008, vol. 89, no. 3, pp. 303–310.
- Lukina, G.A., Exudation of amino acids by macrophytes, in *Flora i produktivnost' pelagicheskikh i litoral'nykh fitocenozov vodoemov basseina Volgi* (Flora and Productivity of Pelagic and Littoral Phytocenoses of Reservoirs of Volga River Basin), Tr. Inst. Biol. Vnutr. Vod, Ross. Akad. Nauk, Leningrad: Nauka, 1990, no. 59 (62), pp. 147–152.
- Mamaeva, N.V., *Infuzorii basseina Volgi* (Infusorians of the Volga River Basin), Leningrad: Nauka, 1979.
- Massachiro, O. and Takuo, N., Decomposition of aquatic plant *Elodea nuttallii* from Lake Biwa, *Verh. Int. Verein. Limnol.*, 1994, vol. 25, pp. 2276–2278.
- Mermillod-Blondin, F., Lemoine, D., Boisson, J.-C., Malet, E., and Montuelle, B., Relative influences of submersed macrophytes and bioturbating fauna on biogeochemical processes and microbial activities in freshwater sediments, *Freshwater Biol.*, 2008, vol. 53, no. 10, pp. 1969–1982.
- Mieczan, T., Niedźwiecki, M., and Tarkowska-Kukuryk, M., Effects of rotifers, copepods and chironomid larvae on microbial communities in peatlands, *Eur. J. Protistol.*, 2015, vol. 51, pp. 386–400.
- Morris, J.T. and Lajtha, K., Decomposition and nutrient dynamics of litter from four species of freshwater emergent macrophytes, *Hydrobiologia*, 1986, vol. 131, no. 3, pp. 215–223.
- Pokorný, J., Květ, J., Ondok, J.P., Toul, Z., and Ostrý, I., Production-ecological analysis of a plant community dominated by *Elodea canadensis* Michx, *Aquat. Bot.*, 1984, vol. 19, nos. 3–4, pp. 263–292.
- Porter, K.G. and Feig, Y.S., The use of DAPI for identifying and counting of aquatic microflora, *Limnol. Oceanogr.*, 1980, vol. 25, no. 5, pp. 943–948.
- Ratushnyak, A.A., The role of intravital exudation by higher aquatic plants in the processes of water self-purification, *Extended Abstract of Cand. Sci. (Biol.) Dissertation*, Kazan, 1993.
- Sager, L. and Lachavanne, J.-B., The M-NIP: a macrophyte-based nutrient index for ponds, *Hydrobiologia*, 2009, vol. 634, no. 1, pp. 43–63.
- Schulz, K., Timmermann, T., Steffenhagen, P., Zerbe, S., and Succow, M., The effect of flooding on carbon and nutrient standing stocks of helophyte biomass in rewetted fens, *Hydrobiologia*, 2011, vol. 674, no. 1, pp. 25–40.
- Sirenko, L.A. and Kureishevich, A.V., *Opređenje soderzhaniya khlorofilla v planktone presnykh vodoemov* (Analysis of Chlorophyll Content in Plankton of Freshwater Reservoirs), Kiev: Naukova Dumka, 1982.
- Vanderstukken, M., Declerck, S.A.J., Decaestecker, E., and Muylaert, K., Long-term allelopathic control of phytoplankton by the submerged macrophyte *Elodea nuttallii*, *Freshwater Biol.*, 2014, vol. 59, no. 5, pp. 930–941.
- Ventelä, A.-M., Wiackowski, K., Moilanen, M., Saarikari, V., Vuorio, K., and Sarvala, J., The effect of small zooplankton on the microbial loop and edible algae during a cyanobacterial bloom, *Freshwater Biol.*, 2002, vol. 47, no. 10, pp. 1807–1819.
- Verhoeven, J.T.A. and Arts, H.H.M., *Carex* litter decomposition and nutrient release in mires with different water chemistry, *Aquat. Bot.*, 1992, vol. 43, no. 4, pp. 365–377.
- Zharikov, V.V., *Kadastr svobodnozhivushchikh infuzorii vodokhranilishch Volgi (sostav, rasprostranenie po vodokhranilishcham, obzor metodov issledovaniya)* (Cadastre of Free-Living Infusorians from the Volga River Reservoirs: Composition, Distribution, and Analysis Methods), Tolyatti: Inst. Ekol. Volzhsk. Basseina, Ross. Akad. Nauk, 1996.
- Zingel, P., Agasild, H., Karus, K., Kangro, K., Tammert, H., Tönno, I., Feldmann, T., and Nöges, T., The influence of zooplankton enrichment on the microbial loop in a shallow, eutrophic lake, *Eur. J. Protistol.*, 2016, vol. 52, pp. 22–35.

Translated by I. Feniova