Influence of aquatic macrophytes on the littoral zone habitats of the Lake Ladoga, NW Russia

Vliv vodních makrofyt na stanovištní faktory v pobřežní zóně Ladožského jezera

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Dedicated to the memory of Slavomil Hejný

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Hydrobotanical and hydrobiological field work was carried out at Lake Ladoga in NW Russia, mostly at Impilahti Bay in the northern part of the lake. In a shallow medium dense stand of *Elodea canadensis* (1452 plants·m^{-2}; mean 192 g·m^{-2} of dry weight) in Impilahti Bay, between 12:00 to 18:00 hours in August 1996, the water was by 1.0–1.4 °C warmer and its pH 1.05–1.2 higher than open water. In the stand, pH increased almost to 9.0. In the same stand, water become supersaturated with O_2 to 134% at midday on a sunny August day, and to only 105% on a cloudy day. The daily pH and [O_2] fluctuations within the medium dense *E. canadensis* stand in Impilahti Bay were much less than those measured in dense stands of this species, e.g., in shallow eutrophic Czech fishponds. Communities of littoral phytophilous zooplankton, living pelagically or slightly attached on the plants, formed in the macrophyte stands. The littoral phytophilous zooplankton complex was on average 4 times more abundant and had a 38 times greater biomass per water volume (0.26–164.2 g dry weight·m^{-3}) than that in the open water near the macrophyte communities (0.05–4.91 g dry weight·m^{-3}) or was 3 times more abundant and had on average a 10 times greater biomass, respectively, than that in the open water in the middle of the bay. This does not accord with theory, which predicts that ecotones have the highest biodiversity and productivity.

Keywords: Higher aquatic plants, physical and chemical factors, littoral phytophilous zooplankton, littoral zone, open water, Lake Ladoga, NW Russia

Introduction

Higher aquatic macrophytes are an important component of the biota of the littoral zones of lakes and reservoirs. It is generally accepted that helophyte coenoses are the most productive of plant communities (Hutchinson 1975, Wetzel 1989, Westlake et al. 1998). As shown, e.g., by Gaevskaya (1966) hydrobionts utilize directly only a few percent of the macrophyte biomass. Utilization of most of the organic matter, which is produced by aquatic macrophytes, proceeds through bacterial destruction. However, the role of aquatic macrophytes is not only based on their primary production. They also change the microclimate in littoral zones, influence hydrochemical processes, and serve as a substrate for development of periphyton and phytophilous invertebrates. Therefore, through their activity, aquatic macrophytes create specific ecological conditions in littoral zones, which affect the functioning of other

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aquatic biota. Much of the research of the Institute of Botany of the former Czechoslovak Academy of Sciences at Průhonice and Třeboň, under the Director Slavomil Hejný, was on these subjects (e.g., Přibáň 1973, Přibáň et al. 1977, 1986, Westlake et al. 1998). Carpenter & Lodge (1986) reviewed thoroughly literature on the influence of submerged macrophytes on the processes occurring in aquatic ecosystems. They stressed that there was a shortage of investigations on the influence of submerged macrophytes on the aquatic environment. Out of 193 papers reviewed, only 22 were devoted to this subject. Thus we present here the result of work done in large lakes in NW Russia, mainly Lake Ladoga.

The aim of the present paper was to demonstrate the effect of communities of higher aquatic macrophytes on the diurnal course of water temperature, pH, and oxygen concentration, and compare this with what occurs in open water without macrophytes. Furthermore, we recorded the abundance and biomass of a particular fraction of zooplakton, termed "littoral phytophilous zooplankton", and compared them with that in other macrophyte communities, at the boundaries of these macrophyte communities and in open water, and in open water without macrophytes along transect in Impilahti Bay.

Material and methods

Field work was carried out at Lake Ladoga, NW Russia. The basic data were collected from littoral zones of Lake Ladoga, but the most detailed investigations were carried out in Impilahti Bay (61°19'N, 31°10'E) in the rocky region of Lake Ladoga (Raspopov et al. 2000). Water chemistry factors (pH, [O_2], temperature,) within selected communities of aquatic macrophytes and in free water were measured at a depth of 10 cm below the water surface (Golterman & Clymo 1969, Semenov 1977). The analytical methods used for monitoring Lake Ladoga by the Institute of Limnology of the Russian Academy of Sciences were (Frumin et al. 1999): pH measured by pH meter and pH electrode, dissolved oxygen concentration estimated by Winkler titrimetric method, free-CO_2 concentration by acidobasic titration with Na_2CO_3, and water transparency by Secchi disk. Species composition, structure of macrophyte communities (dry weight·m^{-2}, herb layer, abundance, density, coverage), phenological stage, vitality, animal grazing, area of each plant community, and macrophyte primary production were estimated (Katanskaya 1981, Raspopov 1992, 1999). One measurement of these parameters was performed in each plant community. In August 1996, during the period of the most intensive measurements, a total of 28 phytosociological records were made and 16 biomass samples were collected.

Planktonic invertebrates were collected in the open water using a 70-μm mesh plankton net. In the aquatic macrophyte stands, the water was sampled with a 10-litre vessel and filtered through a net. To estimate the littoral phytophilous zooplankton associated with the plants, plant samples were collected using a wide plastic tube. The tube isolated several plants, which were then cut off. Each plant sample was thoroughly washed in filtered water in a large cuvette and cleaned using a fine brush to release fixed invertebrates. The washed-off zooplankton was concentrated using the same 70-μm net. Results are expressed per m^3 of macrophyte stand, where the number of plants·m^{-2} were estimated together with the quantity of washed-off planktonic organisms, and number of zooplankton·m^{-3} of water among the plants (Andronikova & Raspopov 2000). Dry weight of phytophilous zooplankton was estimated. Non-planktonic organisms (insect larvae, worms, etc.) were not counted and weighed. At each microsite, 3–5 parallel samples were taken. Statistical significance of the data was tested by ANOVA (Tukey HSD test). Botanical nomenclature is that of Raspopov (1992).

Results

In a medium dense stand of *Elodea canadensis* (1452 plants·m^{-2}; 192 g·m^{-2} of dry weight) in Impilahti Bay of Lake Ladoga in August 1996, the water was 1.0–1.4 °C warmer and the pH was 1.05–1.2 higher than open water from 12:00 to 18:00 hours (Fig. 1a). In the stand, pH rose almost to 9.0. During night and early morning, the situation was slightly reversed. The same medium dense *Elodea canadensis* community supersaturated the water within the stand with O_2 to 134% at midday on a sunny August day, and 105% on a cloudy day (Fig. 1B). Water transparency in all macrophyte communities was to the bottom, and to ca. 2.5 m in open water.

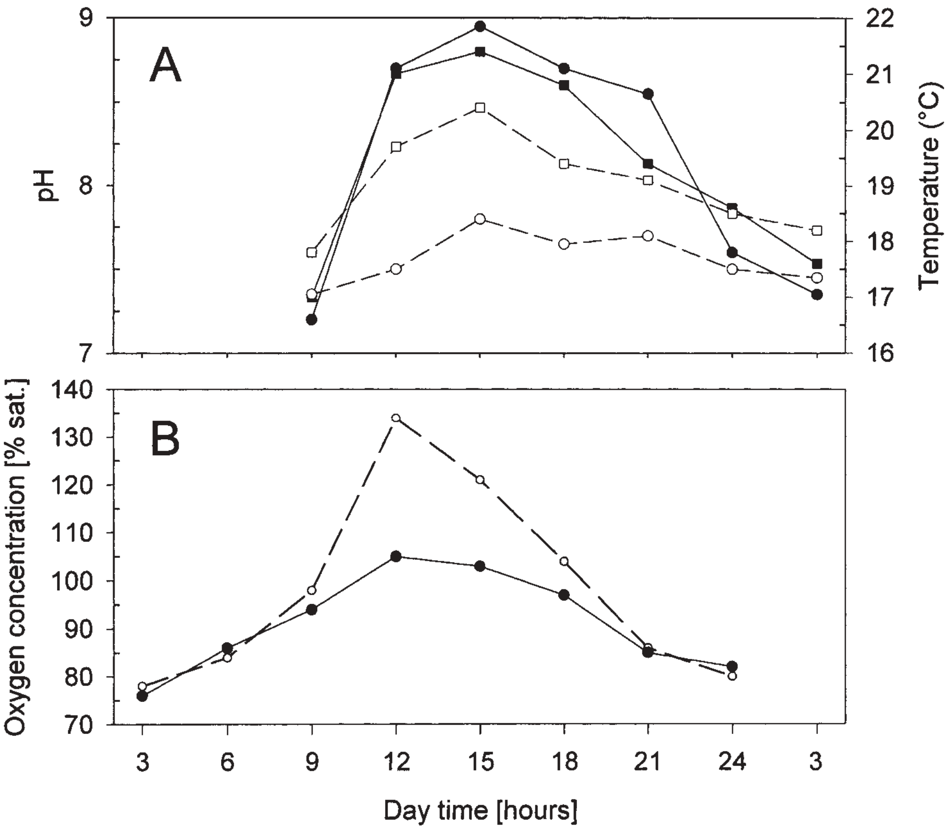

Fig. 1. – Physical and chemical factors 10 cm below the water surface in a medium dense *Elodea canadensis* community (plant coverage 100%, density 1452 plants·m^{-2}, dry biomass 192 g·m^{-2} – one sampling, water depth 65–80 cm) and in open water at Impilahti Bay, Lake Ladoga, in August 1996. The open water measurements were taken about 80 m away from the *E. canadensis* community; water depth 2.4 m. (A) diurnal time-course of water temperature (squares) and pH (circles) within *Elodea* community (solid symbols and full lines) and in open water (empty symbols and dashed lines), 9–10 August 1996. (B) diurnal time-course of dissolved oxygen concentration within the *Elodea* community on a sunny (empty symbols) and a cloudy day (full symbols).

Table 1. – Abundance (10^3 individuals·m^{-3} of water within plant community) and biomass (g dry weight·m^{-3}) of littoral phytophilous zooplankton within aquatic macrophyte communities, in the open water at the boundary of macrophyte communities, and in the middle of Impilahti Bay, Lake Ladoga, in August 1996. Aquatic macrophyte communities were dominated by *Phragmites australis, Sparganium emersum, Potamogeton perfoliatus, P. natans, Nuphar lutea, Sagittaria sagittifolia, Myriophyllum spicatum,* and *Elodea canadensis.* Mean data ±1 SE are shown. At each microsite, 3–5 parallel samples were collected. Means bearing different letters column-wise are significantly different at P < 0.05.

Sampling sites	No. of sites	Abundance	Biomass
Within macrophyte communities	9	860±487a	54.5±17.3a
Open water at the boundary of macrophyte communities	8	208±77.0a	1.42±0.52b
Open water in the middle of bay	7	277±66.5a	5.44±1.94b

Table 2. – Abundance (per m^3 of water within plant community) and total biomass (g dry weight·m^{-3} of macrophyte community or open water) of littoral phytophilous zooplankton within aquatic macrophyte communities, and the biomass of washed-off littoral phytophilous zooplankton (also in % of the total zooplankton biomass) within aquatic macrophyte communities, in open water at the boundary of macrophyte communities, and in open water in the middle of the transect at Impilahti Bay, Lake Ladoga, in August 1996. Typical data are shown.

Plant community dominated by	Total phytophil. zooplankton no. (in 10^3 ind·m^{-3})	Total littoral zooplankton biomass (g·m^{-3})	Washed-off zooplankton biomass (g·m^{-3})	% of washed-off zooplankton biomass
Mixed community[1]	4543	128	119	93
Elodea canadensis	874	57.1	48.9	86
Myriophyllum spicatum	2072	39.7	33.7	80
Potamogeton perfoliatus	859	33.0	25.4	77
Nuphar lutea	356	15.4	7.9	51
Sparganium emersum	604	15.5	2.6	17
Phragmites australis	131	2.3	0.06	3
On the boundary of *E. canadensis* community	85.0	1.6	–	–
On the boundary of *S. emersum* community	35.3	0.6	–	–
Open water, middle of the transect	165	13.0	–	–

[1] Dominated mainly by *Potamogeton natans, Nuphar lutea*, and *Utricularia vulgaris*.

Littoral phytophilous zooplankton communities formed in macrophyte communities and the littoral phytophilous zooplankton complex was on average 4 times more abundant and had a 38 times greater biomass per water volume than that in the open water near the macrophyte communities, and was 3 times more abundant and had on average 10 times greater biomass, respectively, than that in the open water in the middle of the bay (Table 1). The range of littoral phytophilous zooplankton biomass values was 0.26–164.2 g dry weight·m^{-3} in the plant communities, but only 0.05–4.91 g dry weight·m^{-3} in the boundaries between these communities and the open water. The same distribution of littoral phytophilous zooplankton occurred along the transect in the Impilahti Bay, i.e., the maximum abundance and biomass was in the submerged macrophyte communities and the lowest in the open water and near macrophyte communities (Table 2). The greatest littoral phytophilous zooplankton abundance and biomass were found in mixed macrophyte communities (dominated by *Potamogeton natans, Nuphar lutea, Utricularia vulgaris*), while the least were in an emergent *Phragmites australis* community. The washed-off littoral zooplankton biomass as a proportion of the total littoral phytophilous zooplankton biomass was highly variable in aquatic and wetland plant communities in Impilahti Bay in August 1996 (Table 2). In plant communities dominated mainly by submerged or floating-leaved species, the proportion of the total biomass consisting of washed-off zooplankton was 77–93%, in a *Nuphar lutea* community it was 51%, while in an emergent *Phragmites australis* community it was only ca. 3%.

Discussion

The significance of submerged macrophyte communities for short-term changes in aquatic environments is high. The physiology and morphology of higher aquatic macrophytes result in specific temperature regime in stands of these plants (Pokorný & Ondok 1991). The floating foliage of pleustophytes (*Nuphar lutea, Nymphaea candida, Potamogeton natans,* etc.) absorb solar radiation at the water surface. The factor that determines the local water temperature in pleustophyte stands is the density of floating foliage, LAI (leaf area index). The higher the LAI the more incident solar energy is prevented from penetrating the water. At the surface the daily water temperature is higher than outside the plant community. This temperature difference may reach 2–3 ºC. At night, floating foliage radiates more heat than open water and the temperature in the upper water layers in such stands declines faster. Thus, the diurnal water temperature fluctuations in pleustophyte stands are greater than those in open water. The afternoon surface water temperature measured in open water in Impilahti Bay was up to 18.4 ºC (Fig. 1a). Similar temperatures between 16–18 ºC are reported as a long-term average for open water in the rocky regions of the northern part of Lake Ladoga in August; average air temperatures are usually 0.2–0.3 ºC higher (Rumyantsev & Drabkova 2002).

Similar situations occur in submerged macrophyte stands. Temperature patterns the reverse of those in submerged macrophyte stands occur in dense emergent helophyte stands due to the absorption of solar energy by emergent foliage during the day-time and decreased heat emission from water at night (Přibáň 1973, Přibáň et al. 1986). Generally, the temperature regime in water in dense helophyte stands is similar to that in open water.

During the day, marked fluctuations in O_2 and CO_2 concentrations occur in standing water in submerged macrophyte and, to a lesser extent, pleustophyte communities (for review see Pokorný & Ondok 1991). One of the key factors determining the O_2 concentration within aquatic macrophyte stands is sunlight. However, direct measurements of photosynthetically active radiation were not made at Impilahti Bay during the diurnal pH and [O_2] measurements. The records of the nearest meteorological station at Sortavala (ca. 40 km) indicate that the mean global sun radiation (direct + diffusive) is 389 (range 310–469) $MJ \cdot m^{-2} \cdot month^{-1}$ in August. This corresponds to an average of 5.1–7.2 $MJ \cdot m^{-2} \cdot day^{-1}$ on a cloudy and to 18.9–19.4 $MJ \cdot m^{-2} \cdot day^{-1}$ on a sunny August day. Assuming the irradiance is sufficient for 12-h of photosynthesis per day, the mean daily irradiance ranges between 118–167 $W \cdot m^{-2}$ for a cloudy, and 438–449 $W \cdot m^{-2}$ for a sunny August day. Comparable values were recorded by Pokorný & Ondok (1991) for the Czech Republic.

The daily pH and [O_2] fluctuations within the medium dense *E. canadensis* community at Impilahti Bay (Fig. 1A, B) are much lower than those measured in dense stands of the same species in shallow eutrophic fishponds in the Czech Republic (cf. Pokorný & Ondok 1991). This indicates that Impilahti Bay is much more oligotrophic biotope (Raspopov et al. 2000) than the very eutrophic Czech fishponds (*E. canadensis* biomass up to 300–450 g dry weight·m^{-2}; Pokorný et al. 1984) and the relatively looser *E. canadensis* communities at the former site influence the chemistry of open water without macrophytes much less.

The investigation of the zooplankton density inside and outside submerged macrophyte communities at Impilahti Bay was aimed at determining whether lake littoral zooplankton communities prefer or avoid macrophytes. Littoral phytophilous zooplankton use higher aquatic macrophytes as a substrate for their development. This zooplankton is made up of species that are not only suspended in the water within a plant stand as are typical zooplankton but of those that live on plant surfaces and graze on fine detritus. Taxonomically, these organisms in Impilahti Bay belonged mainly to the *Chydoridae* family (*Cladocera*) and *Copepoda*.

Generally, communities of higher aquatic macrophytes in shallow standing waters provide a specific environment for littoral phytophilous zooplankton, which is very different from that in the pelagic zones. Evidently, it is important for these zooplanktonic organisms that they are able to tolerate great diurnal fluctuations in O_2 concentration and pH as shown in Fig. 1. In general, the species in littoral phytophilous zooplankton differ from those in open lake water. Their abundance and biomass depends on dominant plant species in aquatic macrophyte communities. Of the microhabitats investigated at Impilahti Bay, Lake Ladoga, the lowest zooplankton abundance and biomass occurred at the boundary of aquatic macrophyte communities and open water. This finding is not in accord with the theory of ecotones as microhabitats with the highest biodiversity and productivity. Species of the littoral phytophilous zooplankton complex might be attracted to aquatic macrophyte stands by organic substances released by macrophytes (e.g., Søndergaard 1981) or by the presence of heterotrophs utilizing these substances as a carbon source.

These results are also of great methodological importance. For an accurate estimate of the total biomass of littoral phytophilous zooplankton within an aquatic plant community, one needs to wash the zooplankton of freshly harvested plant biomass in addition to taking the usual water samples from plant stands. Otherwise, the number and biomass of littoral zooplankton may be greatly underestimated.

Souhrn

Hydrobotanický a hydrobiologický výzkum byl prováděn v Ladožském jezeře v SZ Rusku, především v severní části jezera v zálivu Impilahti. Ve středně hustém porostu *Elodea canadensis* (1452 rostlin·m^{-2}, 192 g sušiny·m^{-2}, hloubka vody 65–80 cm) byla v srpnu 1996 mezi 12 až 18 h teplota vody v hloubce 10 cm pod hladinou o 1.0–1.4 °C vyšší a pH o 1.05–1.2 vyšší než ve volné vodě bez rostlin a pH v porostu dosáhlo téměř hodnoty 9,0. Stejný porost byl schopen přesytit vodu kyslíkem na 134% nasycení během slunečného srpnového dne, avšak jen na 105% během zamračeného dne. Přesto jsou diurnální oscilace koncentrace O_2 a pH v porostu *E. canadensis* v zálivu Impilahti mnohem nižší než v hustých porostech stejného druhu např. v eutrofních českých rybnících. Společenstva litorálního fytofilního zooplanktonu, který může žít volně ve vodě nebo je mírně přichycen k rostlinám, byla vytvořena ve společenstvech makrofyt. Komplex litorálního fytofilního zooplanktonu měl průměrně 4krát vyšší abundanci a asi 38 krát vyšší sušinu na objem vody (0.26–164.2 g·m^{-3}) než v ekotonech na hranici porostů makrofyt a volné vody (0.05–4.91 g·m^{-3}) a zároveň měl 3× vyšší abundanci a 10× vyšší sušinu než ve volné vodě uprostřed zálivu. Toto zjištění je v rozporu s obecnou teorií ekotonů, podle níž je v ekotonech nejvyšší biodiverzita i produktivita.

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