

The influence of macrophyte ecological groups on food web components of temperate freshwater lakes

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ABSTRACT

Aquatic macrophyte taxonomic composition, species abundance and cover determine the physical structure, complexity and heterogeneity of aquatic habitats – the structuring role of macrophytes. These traits influence richness, distribution, feeding and strength of the relationships between food web communities in lakes. The aim of this study was to determine how lakes with different dominating macrophyte ecological groups affect planktonic food web components, emphasising the influence on young of year (YOY) fish and large ($\geq 1+$) fish community. We hypothesised that different dominating macrophyte ecological groups have different structural effects on food web components and YOY fish growth, abundance and feeding. Studied lakes categorised into three different macrophyte ecological groups – lakes dominated by emergent, floating+floating-leaved or submerged vegetation. We found that all dominating ecological groups had a strong influence on plankton communities (except heterotrophic bacterioplankton and nanoflagellates), YOY fish and large fish. Floating-leaved plant dominance was positively related to planktonic food web structure and YOY fish weight, length, abundance and the consumption of zooplankton as a prey of all major species of YOY fishes. Larger fish tended to favour the presence of emergent vegetation. This conclusion has important implications for local managers and conservationists in respect to the maintenance and protection of littoral habitats and fish resources.

1. Introduction

Macrophytes as “underwater forests” are a key component in the structure of aquatic environments and have a great influence on the structure and functioning of lake ecosystems, particularly for shallow lake food webs (Jeppesen et al., 1998). Macrophytes increase physical structure, habitat complexity and heterogeneity, influence physical and chemical properties in lakes and affect various food web components (Sand-Jensen and Frost-Christensen, 1998). Amongst macrophytes, canopy-forming floating and floating-leaved plants are of greatest importance for all the other species as they modify the underwater light climate and habitat conditions becoming the key-stone species or edificatory species (Braun-Blanquet, 1964). Macrophyte beds affect underwater light climate as large stands of macrophytes hinder light penetration into deeper areas (Binzer and Sand-Jensen, 2006).

Macrophyte carpets can modify the hydrodynamics of lakes by dampening wave action, calming down water currents (Gregg and Rose, 1982; Madsen and Wrancke, 1983) and limiting sediment resuspension from the bottom and/or nutrient trapping (James and Barko, 1990; Scheffer, 1998; Vermaat et al., 2000).

Macrophytes are the principal primary producers beside lake phytoplankton (PP) competing with PP for the same limiting resources (Allende et al., 2009). Several macrophyte associated mechanisms, direct and indirect ones, support macrophyte dominance over PP. Direct mechanisms are associated with plants themselves as they create still water environment by calming down currents and waves and poor light conditions for PP because of shading by their own large growth forms. On the other hand, some macrophyte species are known to release or secrete chemical substances called allelochemicals („biochemical weapons“) into a surrounding environment, which have inhibiting or

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stimulating effect on competing plants and algae (Jasser, 1995; Hilt et al., 2006; Lürling et al., 2006; Gross et al., 2007). Indirect mechanisms are connected with the provision of refuges and habitats for grazers on PP and with the modification of nutrient regime by metabolic activity of plants. The story goes more complicated as there exist also second level determinants (e.g. fish predation on algal grazers, additional nutrient loads from catchment), which affect these direct and indirect mechanisms of macrophytes (Søndergaard and Moss, 1998). Vegetated littoral areas of lakes provide structures and refuges for zooplankton (ZP) and small fish from predatory animals in fish-prey systems (Schriver et al., 1995) and nursery areas to fish for recruitment and production (Urho, 2002). Larger ZP tend to favour the boundary zone between macrophyte beds and the pelagial as an important daytime refuge. However, their migration into the edges of macrophyte beds and back can again be modified by fish (Burks et al., 2002). Dense macrophyte beds colonising only 3% of a lake bottom is enough to increase the grazing potential of ZP in the pelagial by 100% (Lauridsen et al., 1996). Hence, via offering physical refuge for ZP and juvenile planktivorous fish, macrophytes promote the structural shift in prey-consumer communities (Burks et al., 2002) and thus indirectly alter the top-down energy flow in the system.

However, macrophytes also influence the interactions between piscivorous and prey fishes (Jeppesen et al., 1998). Several adult fish species like tench (*Tinca tinca* L.), rudd (*Scardinius erythrophthalmus* L.) and pike (*Esox lucius* L.) live in stands of emergent and floating-leaved plants. The submerged macrophytes form important feeding habitats for perch (*Perca fluviatilis* L.), roach (*Rutilus rutilus* L.), bleak (*Alburnus alburnus* L.) and eel (*Anguilla anguilla* L.), while ruff (*Gymnocephalus cernua* L.) prefer charophyte (*Chara* spp.) beds (de Nie, 1987). Macrophytes affect both competitive and predatory interactions between different species and sizes of fishes (Winfield, 1986). Thus, macrophytes influence the relations of macroinvertebrates to fish predators and reduce vulnerability of prey fish to piscivores (Eklöv and Diehl, 1994). Shoot density and physical complexity of particular macrophyte species can greatly change the habitat structure that affects the important features of the predator-prey interactions (e.g. behaviour of predator, encounter rate or visibility of prey) (Michel and Adams, 2009). Plant architecture is also known to greatly affect the spatial distribution of fish (Meerhoff et al., 2003; Teixeira-De Mello et al., 2009) and macroinvertebrates (Soszka, 1975; Miller et al., 1989; Mhlanga and Siziba, 2006; Ali et al., 2007). In temperate lakes, regardless of water turbidity or trophic state, free-floating plants have been shown to support higher fish densities compared to those associated with submerged macrophytes (Teixeira-De Mello et al., 2009). Traditionally, dense reed habitat has not been considered desirable for the exploitation of fish populations (de Nie, 1987). However, some studies have stressed the importance of the reed swamps and other emergent vegetation for fish populations in Lake Constance (de Nie, 1987). Even though macrophyte stands are crucial for YOY fish growth and survival there is still not enough corresponding information available. Habitat use by YOY fish and the effects of macrophyte type on the feeding and development of YOY fish have been largely unstudied. Moreover, despite the fact that ciliated protozoans can form an important diet source for YOY fish larvae (Zingel et al., 2012, 2019), their role is often neglected from studies that assess habitat choice or feeding of young fish (Montagnes et al., 2010).

The aim of this study was to compare the effect of dominating macrophyte ecological groups (submerged, floating+floating-leaved and emergent) on planktonic food web components (heterotrophic bacterioplankton (HBP), heterotrophic nanoflagellates (HNF), ciliates, metazooplankton (MZP), PP) in littoral and pelagial of similar lake type. The influence of dominating macrophyte ecological groups was assessed with respect to YOY fish (abundance, dominant species, individual body length and weight, and consumption of zooplankton as a prey) and large ($\geq 1+$) fish (taxonomic composition and the fish catches WPUE (weight per unit effort, grams per net within 12 h)). We hypothesised that emergent, submerged and floating+floating-leaved vegetation have different structural effects on measured food web components and

create different top-down effects.

2. Material and methods

2.1. Study area

Studies were carried out in eight northern temperate lakes, four located in Latvia (Lake Auciema, L. Riebinu, L. Laukezers, L. Vārzgūnes) and four in Estonia (L. Akste, L. Kaiavere, L. Prossa, L. Nohipalo Valgjärv) (Fig. 1). In general, the studied lakes were relatively small, shallow and presented different national lake types with different colour (light to dark brown) and hardness of water (soft to very hard) (Table 1). Surveys were conducted mostly three times a year (2019) from spring (May/June) to summer (July/August) and autumn (September) in littoral and pelagic habitats of the lakes to collect and analyse whole food web components from bacteria to fish and macrophytes – HBP, HNF, ciliates, MZP, PP, YOY fish, large ($\geq 1+$) fish and macrophytes (Tables 2, 3). Plankton communities were sampled thrice a year (2019) with no replications (Table 3). From each lake, two samples per planktonic group (HBP, HNF, ciliates, PP, MZP) per season were collected: one from littoral (an inshore area covered with macrophytes) and one from pelagic habitat (an open water column in deepest part of each lake without aquatic vegetation or sparse vegetation (e.g. in lakes where macrophytes covered whole lake bottom)). Only one sampling site per lake was used as earlier studies in one of the largest lake in Estonia have shown the representativeness of a single sampling site per large lake and low spatial variability in planktonic and water-chemistry data (Nöges and Tuvikene, 2012). Altogether, 48 samples per planktonic group were seasonally (spring to autumn) collected from the lakes. Macrophytes and YOY fish (YOY larvae in spring and YOY juveniles in summer and autumn) were also studied thrice a year (2019) and large fish once (summer, 2018 or 2019) a year (Table 3). Physico-chemical parameters were also measured from both littoral and pelagic habitats of the lakes during the three sampling sessions (Tables 1, 3). In 2020, only large fish community samplings and physico-chemical measurements were repeated both in Estonian and Latvian lakes.

2.2. Sampling

Plankton samples (HBP, protozooplankton (PZP), PP, MZP) were taken from depth-integrated lake water (0.5 and 1 m interval) using a Ruttner water sampler. For HBP, PZP and PP, 100–250 ml samples were used, and for MZP 10 L samples of depth-integrated lake water was filtered through a 48 μm plankton net. HBP and HNF were studied using DAPI direct count (Porter and Feig, 1980) via epifluorescence microscopy. Ciliates and PP were processed via inverted microscopy following Utermöhl (1958) and MZP in Bogorov's chambers using stereomicroscopy (Table 2). Ciliate species were divided and counted in two broad categories: picovorous (ciliate species whose main food is bacterioplankton) and nanovorous (ciliate species whose main food is nanoplankton or even larger objects) ciliates to detect any grazing effects on lower trophic levels. PP cells were divided and counted in six different size classes (SC1 2–5 μm , SC2 5–15 μm , SC3 15–30 μm , >SC3 >30 μm , colonial forms, filamentous forms, according to maximum linear length of a cell/colony/filament) to detect any grazing effects on PP community. MZP individuals were divided and counted in the following groups: rotifers, cladocerans, copepods and veligers (if present).

Small fish (YOY fish larvae and juveniles) were sampled using three different methods – a scoop-net, bongo net and beach seine (Table 2). In spring, YOY fish larvae were sampled using a bongo net in pelagic habitats and a scoop-net in littoral habitats by hauling the nets horizontally through the water column. YOY fish larvae from pelagic areas were collected by multiple horizontal hauls at 1 m depth using a conical tow net. Larval densities were calculated using respective tow volumes. In summer and autumn, a beach-seine methodology was used only in

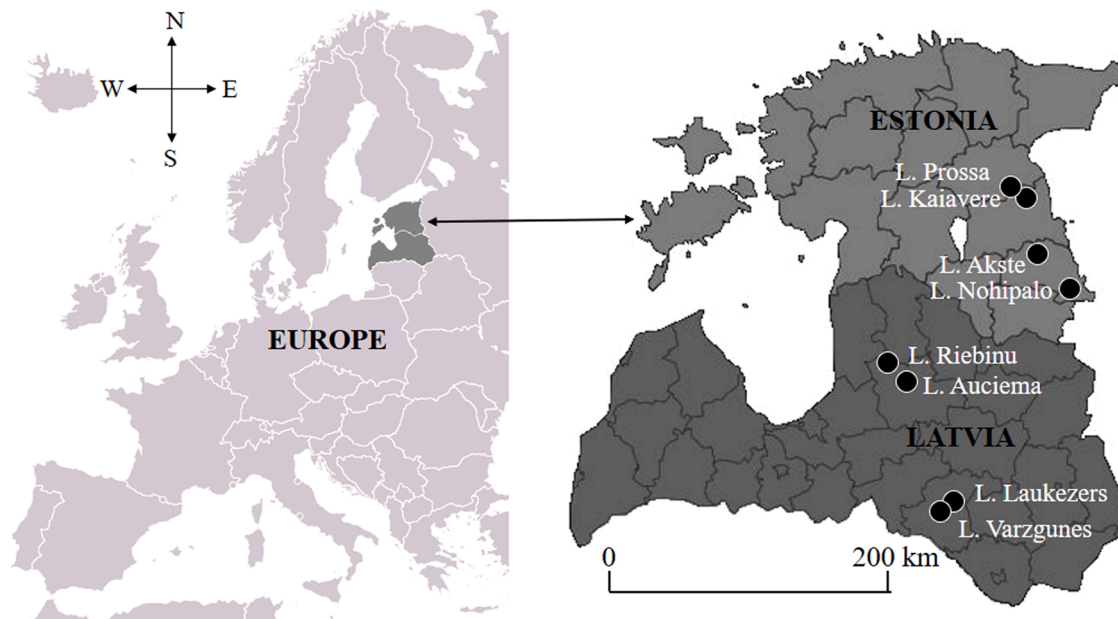


Fig. 1. Location of the study lakes throughout Latvia and Estonia (locations are marked by black dots).

Table 1

Characteristic morphometry and average physico-chemical features of 4 Estonian and 4 Latvian study lakes in 2019.

Lake	Lake type	Area (ha)	Mean depth (m)	Max depth (m)	Secchi depth (m)	Tot P (mg/L)	Tot N (mg/L)	O ₂ (mg/L)	O ₂ sat (%)	pH	Cond. (μS/cm)
Kaiavere	II (EE)	248	2.8	5	1.1	0.027	1.37	10.7	108.2	8.40	399.9
Auciema	II (LV)	75.5	2.3	4.4	1.1	0.047	1.40	10.4	104.4	8.52	370.6
Nohipalo V.	V (EE)	7	6.2	12.5	4.4	0.007	0.24	9.3	93.4	8.19	10.5
Laukezers	V (LV)	50.4	6.7	19.8	5.3	0.012	0.38	11	110.2	8.58	75.6
Prossa	II (EE)	24.2	2.2	4.2	2.4	0.009	0.99	11.4	116.9	8.08	328.4
Riebinu	V (LV)	41.1	1.9	2.7	1.9	0.021	0.94	10.2	104.4	8.50	197.2
Akste	IV (EE)	5.5	–	4.3	0.8	0.053	0.94	8.3	84.2	6.93	17.8
Värzgunes	IV (LV)	43	1	2	1.2	0.038	0.85	9.1	92.7	8.11	483.9

Abbreviations: EE – Estonia; LV – Latvia; Tot P – total phosphorus; Tot N – total nitrogen; cond – conductivity; lake types: II(EE) – shallow lakes with medium water hardness, II(LV) – very shallow brown-water lake with high water hardness, V(EE) – soft-water light coloured lakes, V(LV) – shallow clear-water lake with high water hardness, IV(EE) – soft-water brown-coloured lakes, IV(LV) – very shallow brown water lake with low water hardness.

littoral habitats of the lakes (Table 2). From each lake, several hauls were made and the abundance of fish was calculated based on the total seining area. YOY fish species were identified according to Koblitckaya (1981) and individuals were measured (total length) and weighed. YOY fish larvae were preserved in ethanol to estimate larval fish diet. Fish larvae gut content analysis was performed with epifluorescence microscopy (Fukami et al., 1999) and followed the first gut quarter methodology as suggested by Zingel et al. (2012).

Large fish were studied using Nordic type multimesh gillnets, which followed the standards LVS EN 14757:2015 and EVS-EN 14757:2005. The samples were collected from littoral and pelagic habitats of the lakes once (summer) a year. In both littoral and pelagic habitats, floating and bottom-set gillnets were used. In 2019, only fish communities in four Estonian lakes were studied: 2 gillnets (floating+bottom-set) were put into littoral habitats and 2 gillnets (floating+bottom-set) into pelagic habitats per lake (altogether 4 gillnets per lake). Fish communities of four Latvian lakes were sampled in the summer of 2018 (Institute for Environmental Solutions, 2017, 2018a,b,c). Large fish community samplings were repeated also in 2020 both in Estonian and Latvian lakes. Due to the absence of large fish data from Latvian lakes in 2019 we calculated average values on the basis of 2018 and 2020 fish data and used average values in further analyses. According to the standards LVS EN 14757:2015 and EVS-EN 14757:2015, year-to-year variation in fish biomasses and abundances within a lake between successive years has

been usually low, therefore calculated average values for Latvian lakes are correct. In Latvia the number of gillnets set into the different habitats of the lakes varied by lake (finally average was used from gillnets used per habitat). Upon capture fish species were identified, measured (individual body weight and total length) and weight per unit effort (WPUE, grams per net within 12 h) was calculated.

To analyse the influence of macrovegetation on lake food webs, macrophyte data were collected thrice a year from a boat by using a transect method in combination with sampling quadrats (1×1m for emergent plants in every 5 m, 2×2m for floating-leaved and submerged plants in every 10 m) (Feldmann and Nöges, 2007). Sampling was performed by a scaled rope with a grapnel end and carried out irrespective of the presence or absence of macrophytes. The number of macrophyte transects per lake was determined using Jensen's formula following the Chilinska modification and calculated separately for smaller (<0.2 km²) and larger (>0.2 km²) lakes (Jensen, 1977; Chilinska, 2015). The use of different size of sampling quadrates for emergent, floating-leaved and submerged plants can be explained by the circumstance that different macrophyte groups are intrinsically scale-dependent units, basically ruled by species size, growth patterns and interactions among plant individuals, as well as by the physical and ecological heterogeneity (Gigante et al., 2016). As emergent plants are usually structurally less complex and form homogenous and dense vegetation stands, a smaller sampling quadrat with dimensions of 1×1 m was used.

Table 2
Sampling methodology for planktonic food web components.

Group	Indicators	Study time	Methods	Details & comments	Ref.
Heterotrophic bacteria	Total abundance, total biomass	Spring, summer, autumn, 2019	DAPI direct count/ EFM (1000x magnification, violet light)	Subsamples 3 ml, glutaraldehyde (1% final conc.), DAPI (final conc. of 10 µg ml ⁻¹), black polycarbonate filters (0.22 µm), stored at – 20 °C until counting, at least 200 cells counted	Porter and Feig (1980)
Heterotrophic nanoflagellates	Total abundance, total biomass	Spring, summer, autumn, 2019	DAPI direct count/ EFM (400x magnification, violet light)	Subsamples 3 ml, glutaraldehyde (1% final concentration), DAPI (final conc. of 10 µg ml ⁻¹) black polycarbonate filters (0.8 µm), stored at – 20 °C until counting, at least 200 cells counted	Porter and Feig (1980)
Ciliates	Taxonomic composition, total abundance, total biomass	Spring, summer, autumn, 2019	Utermöhl technique/ IM (400–1000x magnification)	Subsamples 50 ml, acidified Lugol's solution (0.5% of final conc.), for biomass calculations, the first 20 measurable individuals from each taxon measured, specific gravity was assumed to be 1.0 g/ml, biomass expressed in wet weights	Utermöhl (1958); Finlay (1982)
Phytoplankton	Taxonomic composition, total abundance, total biomass	Spring, summer, autumn, 2019	Utermöhl technique/ IM (400x magnification)	Subsamples 50 ml, acidified Lugol's solution (0.5% of final conc.), at least 400 measurable units (filaments, cells, colonies) counted, algal biomass in carbon units was assessed using a biovolume conversion factor of 100 fg C µm ⁻³	Utermöhl (1958); Nixdorf and Arndt (1993)
Metazooplankton	Taxonomic composition, total abundance, total biomass	Spring, summer, autumn, 2019	Bogorov's chambers/ SM (80x magnification)	Subsamples 50 ml, acidified Lugol's solution (0.5% of final conc.), for MZP biomass calculations, at least the first 20 individuals from each taxon measured; the individual weights of rotifers were estimated from average lengths according to Ruttner-Kolisko (1977); The lengths of crustaceans were converted to wet weights according to Studenikina and Cherepakina (1969) for nauplii, and to Balushkina and Winberg (1979) for other groups.	Ruttner-Kolisko (1977); Studenikina and Cherepakina (1969); Balushkina and Winberg (1979)
Large fish (≥1 + fish)	Taxonomic composition, WPUEs	Summer 2018 or 2019/ Summer, 2020	Nordic gillnetting	Fish were sampled by Nordic type multimesh gillnets (height 1.5 m; length 30 m; total of 12 sections; length of each section 2.5 m; mesh sizes of sections in mm: 43; 19.5; 6.25; 10; 55; 8; 12.5; 24; 15; 5; 5; 35; 29), which followed in general terms the standards LVS EN 14757:2015 and EVS-EN 14757:2005.	
0 + fish larvae and juveniles (YOY fish)	Taxonomic composition, total length, weight	Spring, summer, autumn, 2019	Scoop-net, bongo net, beach-seine	Pelagic sampling of YOY larvae by hauling the conical bongo net (mouth diameter 50 cm, mesh size 0.5 mm) horizontally through the water column using a boat (approximately at 1-m depth, 10 min, ~ 2 m s ⁻¹); Littoral sampling of YOY larvae by several random drawings through the water column using a scoop net (mouth diameter 40 cm, mesh size 0.5 mm, equipped with 2 m handle) Littoral sampling of YOY juveniles by beach-seine (length of seine 10 m, length of ropes at the ends of the seine – 20 m, seine height from the centre 2 m, seine height at the ends 1 m, height decreases smoothly from two metres to one metre, mesh size 2 mm)	

Abbreviations: EFM – epifluorescence microscopy, IM – inverted microscopy, SM – stereo-microscopy; YOY fish – young of year fish or 0 + fish.

Floating-leaved and submerged plants are larger and structurally more complex, and grow usually in sparser stands, hence the larger sampling quadrat of 2 × 2 m seemed to be justified and is also in accordance with recently proposed standards (Chytrý and Otýpková, 2003; Dengler et al., 2008; Gigante et al., 2016). Altogether, data were collected from 150 transects and 1082 sampling quadrats (Table 4). In each transect (perpendicular to the coastline), which extended from the water line to the point of maximum macrophyte depth, macrophytes were identified taxonomically and depth limits were recorded. Classification of aquatic plants into different ecological plant zones (emergent, floating-leaved, submerged plants) followed Arber (1920) and Sculthorpe (1967). In sampling quadrats, shoot density (shoots/m²), coverage (% cover from lake bottom) and plant height (m) were measured. In case of whole lake macrophyte coverage, the transects started from a water edge of one shore and extended to the opposite shore. For each lake, the following species parameters were calculated: frequency (%), abundance (%), percentage volume infested (hereafter PVI) (Canfield et al., 1984),

Shannon-Wiener or Shannon (Shannon, 1948) index (hereafter H' index) and effective number of species (hereafter ENS) (Hill, 1973) as follows:

$$\text{Frequency of species } F(\%) = \frac{N_a}{N} \times 100 \quad (1)$$

where N_a is the number of transects in which species a was present; N is the total number of transects.

$$\text{Abundance of species } A (\%) = \frac{n_s}{n} \times 100 \quad (2)$$

where n_s is the total shoot density of species s in all quadrats of one transect; n is the total shoot density of all species in all quadrats of the transect.

$$\text{Percentage volume infested } PVI(\%) = \frac{\text{coverage} \times \text{plant height}}{\text{water depth}} \quad (3)$$

Table 3

Sample design and collection of different food web components both from littoral and pelagial sites of all the study lakes in 2019 and 2020. (In every season the samples were collected from both lake sites - littoral and pelagial habitats, per habitat only one sample per biotic group was collected (no replications). Abbreviations: * - In case of Latvian lakes we used average values of fish indices which were calculated on the basis of fish data collected in 2018 and 2020.

Community/ sampling time	2019			2020
	Spring	Summer	Autumn	Summer
Heterotrophic bacterioplankton	x	x	x	
Heterotrophic nanoflagellates	x	x	x	
Ciliates	x	x	x	
Phytoplankton	x	x	x	
Metazooplankton	x	x	x	
Macrophytes	x	x	x	
Fish (≥ 1 + fish)		x*		x
YOY fish larvae	x			
YOY fish juveniles		x	x	
Water chemistry	x	x	x	x

$$\text{Shannon-Wiener index } H' = -\sum(N_i \times \ln N_i) \quad (4)$$

where N_i is relative abundance of species i .

$$\text{Effective number of species } ENS = \exp(H') \quad (5)$$

where H' is Shannon index; EXP is exponential.

2.3. Statistical analysis

Data were analysed using multivariate factor analysis and non-parametric Spearman's rank order correlation analysis offered by STATISTICA 8.0 (StatSoft Inc, 2007). Firstly, multivariate factor analysis was used to group the studied lakes according to macrophyte data and to obtain the factor scores for further correlation analyses. In factor analysis, macrophyte species abundance of ecological zones, PVI, total number of species, species number of ecological zones, H' index and ENS were used as input data to distinguish the factors (in this case lakes dominated by different macrophyte ecological groups) among lakes. Secondly, Spearman correlation analysis was performed between saved factor scores and all the other food web components (e.g. total abundance and biomass of HBP, HNF, ciliates [as well as total abundance and biomass of pico- and nanovorous ciliates], MZP [rotifers, copepods, cladocerans], PP [as well the abundance and biomass of different size classes of phytoplankters], YOY fish [length, weight, abundance, food consumption], large fish [number of taxa, WPUEs]). All correlation

Table 4

Overview of macrophyte methodology and main macrophyte community indices for the study lakes in 2019.

Lake	Number of transects per season/ per year	Number of sampling quadrats per year	Dominant taxon in emergent plants	Dominant taxon in floating & floating-leaved plants	Dominant taxon in submerged plants
Kaiavere	13/39	343	<i>Phr. australis</i>	<i>Nu. lutea</i> = <i>Nymphaea</i> spp	<i>F. antipyretica</i> = <i>Pot. lucens</i>
Auciema	6/18	86	<i>Phr. australis</i>	<i>Nu. lutea</i>	-
Nohipalo	3/9	56	<i>Carex</i> spp	<i>Nu. lutea</i> = <i>Spar. gramineum</i>	<i>F. antipyretica</i> = <i>Isoetes lacustris</i>
Laukezers	6/18	81	<i>Phr. australis</i>	<i>Pot. natans</i>	<i>Pot. perfoliatum</i> = <i>Elo. canadensis</i>
Prossa	5/15	145	<i>Phr. australis</i>	<i>Nu. lutea</i>	<i>Chara</i> spp.
Riebinu	9/27	156	<i>Phr. australis</i>	<i>Nu. lutea</i>	<i>Str. aloides</i> = <i>Elo. canadensis</i>
Akste	4/12	73	<i>Carex</i> spp	<i>Nym. alba</i>	-
Värzģunes	4/12	142	<i>Phr. australis</i>	<i>Nu. lutea</i>	<i>Cer. demersum</i> = <i>Myriophyllum</i> spp = filamentous algae

Abbreviations: *Phr. australis* – *Phragmites australis*, *Nu. lutea* – *Nuphar lutea*, *Spar. gramineum* – *Sparganium gramineum*, *Pot. natans* – *Potamogeton natans*, *Nym. alba* – *Nymphaea alba*, *F. antipyretica* – *Fontinalis antipyretica*, *Pot. lucens* – *Potamogeton lucens*, *Iso. lacustris* – *Isoetes lacustris*, *Pot. perfoliatum* – *Potamogeton perfoliatum*, *Cer. demersum* – *Ceratophyllum demersum*, *Str. aloides* – *Stratiotes aloides*, *Elo. canadensis* – *Elodea canadensis*.

analyses were performed separately for littoral and pelagic habitats within the same lake type. For both analyses all the seasonal (spring, summer, autumn) data were pooled together because of low data variability between sampling events in different times of the study year (2019).

3. Results

3.1. Macrophyte community characterisation

Total number of macrophyte species ranged from 3 to 19 with L. Akste having the lowest count and L. Prossa the highest (Fig. 2). Emergent plants were dominated mostly by *Carex* spp. or *Phragmites australis* (Cav.) Trin. ex Steud., floating-leaved plants by *Nuphar lutea* (L.) Smith, *Nymphaea* spp. or *Potamogeton natans* L., and submerged plants by macroalgae, mosses or vascular plants (Table 4). PVI was lowest (2.5%) in L. Nohipalo and highest (48.9%) in L. Prossa (Fig. 2). Species diversity (quantified as the Shannon index H') ranged from 0.74 to 2.21 with the lowest values found in L. Akste and Nohipalo and the highest in L. Riebinu and Auciema. ENS was also highest in L. Riebinu (9.11) and Auciema (6.76) and lowest in L. Akste (2.10) and Nohipalo (4.15).

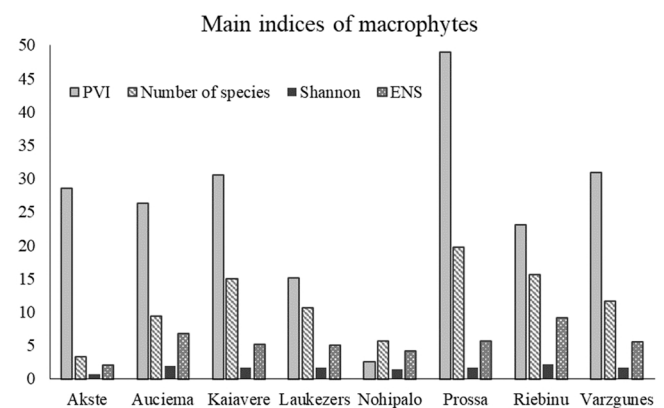


Fig. 2. Main indices of macrophytes (percentage volume infested (PVI), total number of macrophyte species, Shannon index of macrophytes, and effective number of macrophyte species (ENS)) in studied lakes in 2019.

3.2. Outcome of analysis of macrophyte indices

Factor analysis of macrophyte indices divided lakes into three factors, which explained 75% of the total variability (Table 5). **Factor 1** (hereafter emergent plant lakes (F1)) can be considered as lakes dominated by emergent vegetation where higher factor loadings were ENS of emergent plants, H' index of emergent plants, total H' index and total ENS. **Factor 2** (hereafter submerged plant lakes (F2)) associated with lakes dominated by submerged vegetation included factor loadings e.g. total number of submerged plant species, H' index of submerged plants, ENS of submerged species, and abundance of submerged plants. **Factor 3** (hereafter floating+floating-leaved plant lakes (F3)) is associated with lakes dominated by floating+floating-leaved plant vegetation where higher factor loadings included PVI, H' index of floating+floating-leaved plants and ENS of floating+floating-leaved species (Table 5).

3.3. Dominant vegetation type and food web component interactions

In both habitat types (littoral and pelagial), the highest number of statistically important interactions between vegetation type scores and food web components were found in floating+floating-leaved lakes (F3 lakes; Table 6) and emergent plant lakes (F1 lakes; Table 6) and these interactions were rarest in submerged plant lakes (F2 lakes; Table 6). In littoral habitats, statistically important correlations between macrophyte type and other food web members were found in floating+floating-leaved plant lakes and in pelagic habitats highest number of statistically important correlations between macrophyte type and other biotic communities were found in emergent plant lakes. Submerged plant lakes showed minor influence on overall food web components in both habitats (Tables 6–8). Overall, our study revealed that in both habitats, ciliates, MZP and PP were affected mostly by floating+floating-leaved and emergent plant vegetation, YOY fish larvae by floating & floating-leaved plants and large fish by emergent plants. HBP and HNF were not at all influenced by lake type (F1-F3) both in littoral and pelagic habitats (Table 7).

3.3.1. The influence of emergent plants

In littoral habitats of F1 lakes, the type of dominant vegetation had the greatest impact on PP (Table 7) and large fish indices (Table 8). The type of dominant vegetation in littoral habitats of F1 lakes negatively affected the abundance of SC3 phytoplankton; and positively the abundance and biomass of PP colonial forms, and the biomass of SC1 and SC2 phytoplankters (Table 7). Littoral habitats of F1 lakes had a positive influence on the total number of fish taxa in the lake and on average WPUEs per lake and habitat (Table 8). Moreover, total length of YOY roach was also positively correlated with the dominant vegetation type in littoral habitats of F1 lakes (Table 8).

Table 5
'Varimax-normalised' rotated factor loadings of macrophyte community variables (abs > 0.7) and the direction of their influence (+ or -) in the investigated lakes.

Variable	F1	F2	F3
Percentage volume infested			+ 0.76
Total number of submerged species		+ 0.83	
Total Shannon index	+ 0.93		
Total ENS	+ 0.89		
Shannon index of emergent plants	+ 0.75		
ENS of emergent plants	+ 0.72		
Shannon index of floating & floating-leaved plants			+ 0.86
ENS of floating & floating-leaved plants			+ 0.86
Shannon index of submerged plants		+ 0.90	
ENS of submerged plants		+ 0.95	
Abundance of submerged plants		+ 0.78	
Total percentage of variability	25.7	22.6	26.7

Abbreviations: ENS – effective number of species; F1 – emergent plants lakes; F2 – submerged plants lakes; F3 – floating & floating-leaved plants lakes.

Table 6
Yearly average indices of food web components in littoral and pelagic habitats of the study lakes in 2019.

Lake	Aucema		Laukezers		Riebinu		Värzguines		Akate		Nohipalo V		Prossa		Kaiavere	
	Lit	Pel	Lit	Pel	Lit	Pel	Lit	Pel	Lit	Pel	Lit	Pel	Lit	Pel	Lit	Pel
Habitat/indices	8.22	10.42	4.15	3.74	4.31	7.07	4.67	6.32	5.83	6.32	3.21	2.79	6.07	5.75	8.07	8.28
HBP A (10 ⁶ cells ml ⁻¹)	1.15	1.34	0.60	0.59	0.51	0.71	0.60	0.80	0.68	0.80	0.45	0.43	1.65	0.78	0.67	0.81
HBP B (µg C ml ⁻¹)	4564	4977	4809	3011	4825	1200	4406	13,136	48,164	13,136	3565	6038	2153	1864	8418	5865
HNF A (ind ml ⁻¹)	0.09	0.09	0.15	0.09	0.09	0.02	0.06	0.16	0.91	0.16	0.05	0.11	0.04	0.05	0.20	0.13
HNF B (µg C ml ⁻¹)	9128	7598	5937	31,375	35,559	20,913	46,728	10,171	33,828	10,171	7798	38,592	26,059	67,182	25,464	46,093
Ciliate A (ind L ⁻¹)	0.17	0.17	0.04	0.18	0.25	0.24	0.32	0.25	0.29	0.25	0.07	0.25	0.25	0.55	0.20	0.42
Ciliate B (mg L ⁻¹)	1154	1605	38	102	832	1577	1773	3366	1241	3366	127	622	968	1448	1612	1225
MZP A (ind L ⁻¹)	0.89	1.42	0.08	0.34	0.74	2.25	3.35	2.39	1.33	2.39	4.49	0.68	0.31	0.73	0.77	0.90
MZP B (g m ⁻³)	71,217	66,133	26,883	29,917	42,417	43,880	90,583	77,883	66,333	77,883	24,033	25,250	33,050	34,467	51,233	60,400
PP A (ind L ⁻¹)	2.52	2.32	0.36	0.37	0.75	0.77	0.65	0.65	0.70	0.65	0.60	0.51	0.89	0.69	1.11	1.22
PP B (mg L ⁻¹)	228.33	250.75	117.26	0	430.89	0	105.13	260.74	26.59	260.74	19.78	0	458.70	339.12	386.66	340.95
Tot ZP cons. by YOY fish pl m ⁻³	2.75	0.08	0.50	0	2.29	0	1.80	0.09	0.03	0.09	0.22	0	2.14	0.72	2.25	1.29
Tot ZP cons. by YOY fish mg m ⁻³	5664	5999	1853	765.1	3458	3797	1303	204.3	159.5	204.3	4.892	85.65	861.7	1201	2561	2726
Average WPUE (g) per habitat	5831	5831	1128	1128	3627	3627	1641	181.9	181.9	181.9	45.27	45.27	1031	1031	2643	2643

Abbreviations: Lit – littoral; Pel – pelagic; HBP – heterotrophic bacterioplankton; HNF – heterotrophic nanoflagellates; PP – phytoplankton; A – total abundance; B – total biomass; Tot ZP cons. by YOY fish pl m⁻³ – total zooplankton consumption by all 0 + fish species plankton/m³; Tot ZP cons. by YOY fish mg m⁻³ – total zooplankton consumption by all 0 + fish species mg/m³; WPUE – weight per unit effort (g/net within 12 h).

Table 7

Spearman correlation coefficients between factors (F1-F3) and planktonic food web members (heterotrophic bacterio-, protozoa- (ciliates, heterotrophic nanoflagellates), metazoan- and phytoplankton) in littoral and pelagic habitats of the lakes. Marked correlations are significant at $p < 0.05$; not significant correlations are marked with “-”.

Lake habitat	Littoral	Pelagic	Littoral	Pelagic	Littoral	Pelagic
Factors/ indices	F1	F1	F2	F2	F3	F3
Heterotrophic bacterioplankton						
Bacterioplankton A	-	-	-	-	-	-
Bacterioplankton B	-	-	-	-	-	-
Heterotrophic nanoflagellates						
H. nanoflagellate A	-	-	-	-	-	-
H. nanoflagellate B	-	-	-	-	-	-
Protozooplankton						
Ciliate A (ind/L)	-	-	-	0.425217	0.496522	-
Ciliate B (mg/L)	-	-	-	-	0.549565	-
Picovorous ciliate A (ind/L)	-	-	-	0.442609	0.457391	-
Picovorous ciliate B (mg/L)	-	-	-	0.447826	0.480870	-
Nanovorous ciliate A (ind/L)	-	-	-	-	0.572174	-
Nanovorous ciliate B (mg/L)	-	-	-	-	-	0.478261
Metazooplankton						
Metazooplankton A (ind/L)	-	-	-	-0.417391	0.503478	0.483478
Metazooplankton B (g/m ³)	-	-	-	-	-	-
Copepods A (ind/L)	-	0.551424	-	-	0.437582	0.652316
Copepods B (g/m ³)	-	-	-	-	-	-
Rotifers A (ind/L)	-	-	-	-0.422609	0.481739	0.413913
Rotifers B (g/m ³)	-	-	-	-	-	-
Cladocerans A (ind/L)	-	0.424348	-	-	-	-
Cladocerans B (g/m ³)	-	0.439130	-	-	-	-
Phytoplankton						
Phytoplankton A (ind/L)	-	-	-0.513043	-0.441739	0.411304	-
Phytoplankton B (mg/L)	-	-	-	-	-	0.425217
Phytoplankton SC1 A (%)	-	-	-	-	-	-0.433192
Phytoplankton SC1 B (mg/L)	0.618302	0.457646	-	-	-	-
Phytoplankton SC2 A (%)	-	-	-	-	0.406957	-
Phytoplankton SC2 B (mg/L)	0.446957	-	-	-	0.542609	0.628696
Phytoplankton SC3 A (%)	-0.414851	-0.411330	-	-	-	-
Phytoplankton SC3 B (mg/L)	-	-	-	-	-	-
Phytoplankton >SC3 A (%)	-	-	-	0.404700	-	-
Phytoplankton >SC3 B (mg/L)	-	-	-	-	-	-
Phytoplankton colonial forms A (%)	0.580786	0.432044	-	-	-	-
Phytoplankton colonial forms B (mg/L)	0.496965	-	-	-	-	-
Phytoplankton filamentous forms A (%)	-	-	-	-	-	-
Phytoplankton filamentous forms B (mg/L)	-	-	-	-	-	-

Abbreviations: A – total abundance; B – total biomass; H – heterotrophic; SC1 – phytoplankton individuals with maximum linear length of 2–5 µm, SC2 – phytoplankton individuals with maximum linear length of 5–15 µm, SC3 phytoplankton individuals with maximum linear length of 15–30 µm; >SC3 – phytoplankton cells with maximum linear length of > 30 µm; F1 – emergent plants lakes; F2 – submerged plants lakes; F3 – floating & floating-leaved plants lakes; “-” – not significant.

In pelagic habitats of F1 lakes the type of dominant vegetation affected MZP, PP and large fish community indices (Table 7 and 8). The vegetation type in pelagic habitats of F1 lakes had a similar impact on the same PP community indices as in littoral habitat of F1 lakes (except the biomass of SC2 phytoplankton and the biomass of PP colonial forms) (Table 7). In littoral habitats of F1 lakes the dominating vegetation type had positive influence on the total number of fish taxa in the lake and on average WPUEs per lake and habitat (Table 8).

3.3.2. The influence of submerged plants

In littoral habitats of F2 lakes the dominant vegetation type affected only the PP community. We found only one negative interaction between the total abundance of PP and the dominant vegetation type in littoral habitats of F2 lakes (Table 7).

In pelagic habitats of F2 lakes the dominant vegetation type influenced ciliate community the most. In contrast to littoral habitats of F2, where there were no statistically significant interactions between F2 lakes and ciliate community indices, we found that in pelagic habitats of F2 lakes the vegetation type positively and almost exclusively influenced the ciliate community (total abundance of ciliates, total abundance and biomass of picovorous ciliates). There also appeared to be negative relationships between the dominant vegetation type of pelagic habitats of F2 lakes and metazoan indices (total abundance of MZP and rotifers). Similarly, with the PP community in littoral habitat of F2 lakes, we found that the total abundance of PP was similarly negatively correlated

with F2 lakes in pelagic habitat (Table 7).

3.3.3. The influence of floating and floating-leaved plants

The dominant vegetation type in littoral habitats of F3 lakes had major and solely positive impact mostly on YOY fish, ciliate and MZP community indices (Tables 7 and 8). The YOY fish species total length and weight (roach, perch, rudd, bleak, ide), abundance (roach, ide, rudd, bleak), and total ZP consumption by YOY fish species (roach, ide, rudd, bleak) were all in significant positive correlations with the dominant vegetation type in littoral habitats of F3 lakes (Table 8). Littoral habitats of F3 lakes had a positive influence on the abundance (total, picovorous, nanovorous) and biomass (total, picovorous) of ciliates, and abundance of MZP (total, rotifers, copepods) (Table 7). The dominant vegetation type in littoral habitats of F3 lakes had minor positive impacts on PP community indices (Table 7).

The type of dominant vegetation in pelagic habitats of F3 lakes mostly affected PP and MZP communities and had very little effect on ciliated protozoan and fish community indices (Tables 7 and 8). Total biomass of PP and SC2 phytoplankton, were both positively correlated with the vegetation type in pelagic habitats of F3 lakes, while the total abundance of SC1 phytoplankton had negative relationships with F3 lakes. The dominant vegetation type in pelagic habitats of F3 lakes positively influenced the exact same MZP indices (total abundance of MZP, copepods and rotifers) as in littoral habitats of F3. For ciliates and the large fish community indices, only single indices (the biomass of

Table 8

Spearman correlation coefficients between factors (F1-F3) and 0 + fish and larger fish community indices in littoral and pelagic habitats of the lakes. Marked correlations are significant at $p < 0.05$; not significant correlations are marked with “-”.

Lake habitat	Littoral		Pelagic		Littoral		Pelagic	
	F1	F1	F2	F2	F3	F3	F3	F3
Factors/ indices								
YOY fish larvae								
YOY roach average weight (g)	-	-	-	-	0.449917	-	-	-
YOY roach average length (cm)	0.414221	-	-	-	0.651050	-	-	-
YOY perch average weight (g)	-	-	-	-	0.677126	-	-	-
YOY perch average length (cm)	-	-	-	-	0.652725	-	-	-
YOY rudd average weight (g)	-	-	-	-	0.522879	-	-	-
YOY rudd average length (cm)	-	-	-	-	0.522879	-	-	-
YOY bleak average weight (g)	-	-	-	-	0.458607	-	-	-
YOY bleak average length (cm)	-	-	-	-	0.458607	-	-	-
YOY ide average weight (g)	-	-	-	-	0.409776	-	-	-
YOY ide average length (cm)	-	-	-	-	0.409776	-	-	-
YOY roach abundance (ind/m ³)	-	-	-	-	0.658746	-	-	-
YOY rudd abundance (ind/m ³)	-	-	-	-	0.436708	-	-	-
YOY bleak abundance (ind/m ³)	-	-	-	-	0.457268	-	-	-
YOY ide abundance (ind/m ³)	-	-	-	-	0.409776	-	-	-
Diet of YOY fish larvae								
Total ZP cons. by roach (pl/m ²)	-	-	-	-	0.666513	-	-	-
Total ZP cons. by roach (mg/m ³)	-	-	-	-	0.664571	-	-	-
Total ZP cons. by rudd (pl/m ²)	-	-	-	-	0.434151	-	-	-
Total ZP cons. by rudd (mg/m ³)	-	-	-	-	0.422050	-	-	-
Total ZP cons. by bleak (pl/m ²)	-	-	-	-	0.457268	-	-	-
Total ZP cons. by bleak (mg/m ³)	-	-	-	-	0.457268	-	-	-
Total ZP cons. by ide (pl/m ²)	-	-	-	-	0.409776	-	-	-
Total ZP cons. by ide (mg/m ³)	-	-	-	-	0.409776	-	-	-
Total ZP cons. by all fish sp. (pl/m ³)	-	-	-	-	0.498393	-	-	-
Total ZP cons. by all fish sp. (mg/m ³)	-	-	-	-	0.506432	-	-	-
Large fish (≥ 1 + fish)								
Number of fish taxons per lake	0.572323	0.572323	-	-	-	-	-	-
Average WPUE per lake	0.753959	0.753959	-	-	0.467612	0.467612	0.467612	0.467612
Average WPUE per habitat	0.617353	0.753959	-	-	-	-	-	0.467612

Abbreviations: YOY fish - young of year fish or 0 + fish; Total ZP cons – total zooplankton consumption; pl – plankton; sp – species; F1 – emergent plants lakes; F2 – submerged plants lakes; F3 – floating & floating-leaved plants lakes; ns – not significant; average WPUE per lake – average from all littoral and pelagic nets; average WPUE per habitat – average from floating and bottom-set nets per habitat; “-” – not significant.

nanovorous ciliates, average WPUEs per habitat) were positively correlated to pelagic habitats of F3 lakes (Tables 7 and 8).

4. Discussion

The results of our study reveal that dominant macrophyte ecological groups can explain differences in plankton, YOY fish and large fish communities and emphasises the importance of floating-leaved plants on these indices.

4.1. The influence of emergent plants

Our study indicated that the development of large fish (≥ 1 +fish) community is mostly dependent on the existence of emergent plant habitats. Large fish community indices (total number of species, WPUEs) were positively affected by lakes dominated by emergent plants, both in littoral and pelagic habitats. Our results revealed that when the smaller fish (YOY fish) tend to prefer habitats dominated by floating-leaved plants, then the larger fish (≥ 1 +fish) choose to move in to and live-in emergent plant vegetation. For instance, Radomski and Goeman (2001) also found that the relative biomass (kg/net) of fish species (e.g. northern pike *E. lucius*) had positive correlations with the occurrence of four plant species (*Sagittaria* spp., *Typha latifolia* L., *Nuphar* spp. and *Nymphaea* spp.) out of 5 species (*Scirpus acutus* Muehl. ex Bigelow., *Sagittaria* spp., *T. latifolia*, *Nuphar* spp. and *Nymphaea* spp). Their study also suggested that declines in emergent and floating-leaved vegetation (on an average a 66% reduction in vegetation coverage due to human damaging activities) in multiple Minnesota lakes resulted in lower fish production, probably due to the importance of this nearshore habitat for the growth and survival of juveniles and adults of many fish species.

In littoral habitats of F1 lakes the dominating vegetation type had a

positive effect also on PP colonial forms (total abundance and biomass of PP colonial forms). We presume that one possible explanation for abundant PP colonial forms in littoral habitats of F1 lakes can be related to the reason that they are washed out from less complex habitats due to the more wind-exposed conditions. However, the presence of mucilage of PP colonial forms together with lipids and aerotopes makes them buoyant in calm emergent habitats (Walsby and Reynolds, 1980). de Azevedo et al. (2020) also found that in conditions of high coverage of emergent plants, large colonial forms (group VII according to Kruk and Segura, 2012) were most representative but they concluded that this was mostly because in dense emergent plants nutrients were not limiting because of nutrient influxes from catchment area. Our study showed that the type of dominant vegetation in littoral habitats of F1 lakes had positive influence on the biomass of SC1 and SC2 phytoplankters, and negative influence on the abundance of SC3 phytoplankters. This can be explained by the stability of the water column in emergent plant beds, which allows the sinking of larger PP cells and favours the dominance of smaller cells. Therefore, different macrophyte growth forms have different effects on the phytoplankton community. de Azevedo et al. (2020) also showed that in scenarios of high and medium coverage of macrophytes, the most representative phytoplankters are either large sized mucilaginous algal colonies, unicellular or colonial flagellates of medium to large size algae, other large sized individuals equipped with some specialised traits (large sized filaments with aerotopes) or small cells with low sinking losses. In case of low coverage of macrophytes, phytoplankters that dominate are medium to large sized but equipped with flagella, medium size lacking specialised traits or small cells with or without flagella.

In pelagic habitats of F1 lakes the dominating vegetation type had a positive effect (besides large fish) on the MZP community (total abundance of copepods, total abundance and biomass of cladocerans).

Špoljar et al. (2012) found that vegetated shoreline areas of two Croatian reservoirs, which were dominated by emergent stands of *Hippuris vulgaris* L., favoured the development of ZP – highest ZP abundance, biomass and biodiversity in these reservoirs occurred in the stands of *H. vulgaris*. They indicated that the structural complexity of the habitat (in this case architecture of *H. vulgaris*) is a main driver of biodiversity, as also observed for benthic macroinvertebrates (e.g., Miller et al., 1989; Chilton, 1990). More complex habitats generally contain more species (Van de Meutter et al., 2008). However, in our study, MZP community was mostly favoured by F3 lakes and only then by F1 lakes; F2 lakes had negative influence of MZP community indices (Table 7).

4.2. The influence of submerged plants

Our study showed that PP community was negatively influenced by rich and abundant submerged vegetation both in littoral and pelagic habitats of F2 lakes. We found a negative relationship between total abundance of PP and the dominant vegetation type in littoral and open-water habitats of F2 lakes. As macrophytes themselves are part of the food web, they compete with PP for nutrients and other resources (Van Donk et al., 1993). Moreover, biochemical interactions between macrophytes and PP may influence the interactions between the main competitors. Several authors have revealed that relative to other macrophyte growth forms, the likelihood of allelopathic interactions increases in dense stands of submerged macrophytes (Jasser, 1995; Burks et al., 2006; Hilt et al., 2006; Lüring et al., 2006; Gross et al., 2007; Lombardo et al., 2013). They also provided a list of macrophyte species that best represent allelopathic species in Europe (*Myriophyllum spicatum* L., *Myriophyllum verticillatum* L., *Chara* spp., *Ceratophyllum demersum* L., *Stratiotes aloides* L., *Elodea canadensis* Michx., *Potamogeton* spp.) All these allelochemical-producing species were present also in our study lakes. Therefore, allelopathy might have contributed to regulate the biological communities in our study lakes.

4.3. The influence of floating and floating-leaved plants

This macrophyte type had the highest number of statistically important correlations with other food web components. Rich floating and floating-leaved plant communities with high plant volume infested (PVI) favoured the development of YOY fish species. We found that total length (roach, perch, rudd, bleak, ide), weight (roach, perch, rudd, bleak, ide) and abundance (roach, rudd, bleak, ide) of several YOY fish species and consumption of ZP by all fish species was positively correlated with the type of dominant vegetation in littoral habitats of F3 lakes. We can therefore assume that YOY fish development is mostly dependent on the existence of floating-leaved plant habitats because no other relationships (with one exception, Table 7) between YOY fish indices and the type of dominant vegetation in littoral and pelagic habitats of F2 and F1 lakes were found.

Higher food consumption by YOY fish could be directly linked to higher ZP abundances (as food sources for YOY fish). However, aspects other than higher ZP abundances in macrophyte thickets can favour the nutrition and growth of YOY fish. For example, in floating-leaved plant habitats the water transparency may be better due to increased ZP grazing pressure on PP (Cazzanelli et al., 2008). Therefore, enhanced water clarity can positively influence the YOY fish feeding conditions as YOY fish rely mainly on their vision when capturing ZP prey. This can be an important energetic aspect when considering YOY growth and development and demonstrates the importance of floating-leaved macrophytes securing YOY fish survival. Clearly, the significant positive relationship with the abundances of all major species of YOY fish suggests that floating-leaved plants create better refuges for juvenile planktivorous fish than the emergent and submerged plant beds. Thus, the floating-leaved plant beds via offering better refuge, better visibility of prey, abundant and high-quality food might create a synergistic effect to growth success of YOY.

Rich floating-leaved plant community also favoured the development of different ZP communities. Our study revealed that both PZP and MZP indices were positively correlated with rich floating-leaved plant communities. Kornijów et al. (2015) showed that increasing leaf canopy increases the populations of several plant-associated taxa of plankton communities. They showed that submerged leaves supported more invertebrates per unit area than submerged petioles or the undersides of floating leaves. Many previous studies (Jeppesen et al., 1998; Cazzanelli et al., 2008; Špoljar et al., 2012) have stated that structural complexity is a main driver of biodiversity - more complex habitats (macrophyte stands) generally support higher diversity of species. Špoljar et al. (2012) showed that higher diversity, abundance and biomass of ZP in vegetated than in non-vegetated habitats of two Croatian reservoirs is due to macrophyte coverage that provides more favourable habitat for ZP than the pelagic because of the following: diverse habitats, richness of food, refuge from pelagic predators and competitors.

Looking more closely at the correlation between ZP groups reveals the importance of ciliates. They are often very numerous in lakes, making up more than 50% of the total ZP biomass (e.g. Zingel et al., 2012), they move more slowly than most of the MZPs, are caught with ease and quickly digested by fish larvae. Our previous studies (Zingel et al., 2012) have shown that ciliates are essential food for fish larvae and that without consuming ciliates the daily food requirement for larval fish would not be met. Our results on YOY fish larvae feeding in shallow Väinameri (Zingel et al., 2019) suggested that fish growth was higher in vegetated areas. YOY larval fish feeding in macrophyte stands had higher condition factors and consumed twice the amount of ciliates as fish in pelagic habitats. We can therefore assume that the positive relationship between abundances of ciliates and dominant vegetation type in littoral habitats of F3 lakes will also help secure essential food resources for first feeding fish larvae. Larval fish usually prefer bigger nanovorous ciliate species as prey items (Zingel et al., 2012). The formerly mentioned positive relationship was found only for nanovorous ciliate abundance but not for biomass. This could indicate that selective feeding by YOY fish larvae has induced a shift towards smaller cell size in the current ciliate assemblage in littoral habitats of F3 lakes.

Ciliate abundance is often correlated to high diversity of floating-leaved macrophytes, which most likely support ciliates by providing important shelter and substrates (Karus et al., 2014). Moreover, spatial heterogeneity and food availability are strongly influenced by these macrophyte species. Higher diversity of microhabitats can provide numerous microniches but also a variety of potential shelters from predators (e.g. Karus et al., 2014). Still, there is currently very limited information available demonstrating how different macrophyte species structure and regulate planktonic ciliate communities (Schweizer, 1997). Therefore, we cannot clarify why the floating-leaved plants were favoured over submerged or emergent species. However, we also found that in pelagic habitats of F2 lakes the type of dominant vegetation had the strongest effect on ciliate community indices – the richest and most abundant submerged macrophytes supported the most abundant ciliate populations. We can only presume that floating-leaved macrophytes create habitats where the most optimal balance between various environmental factors, food availability and predation pressure was reached.

In other ZP groups, we found that the total abundance of MZP, rotifers and copepods had significant positive relationships with the dominant vegetation type of F3 lakes, while this was not evident for cladocerans and biomasses of other metazooplankters. Based on our feeding results, cladocerans were preferred as primary food source for YOY fish and were thereby strongly top-down suppressed (Karus et al., 2022). The same applied to the larger stages of copepods. Moss et al. (1998) elucidated that in less dense *N. lutea* stands the predation of juvenile perch on large *Daphnia* increases while numbers of small crustaceans and rotifers remain mostly unaffected by fish predation. Kuczyńska-Kippen and Basińska (2008) also revealed that the density of cladocerans was lower in two observed macrophyte habitats compared to pelagic zone of L. Wąsowski and related this lower cladoceran

density to higher fish predation pressure in macrophyte stands. Meerhoff et al. (2003) tested the effects of submerged (*Potamogeton pectinatus* L.) and free-floating plants (water hyacinth *Eichhornia crassipes* Mart.) and found that the planktivorous fish density, particularly the YOY fish size class, was the only factor that significantly explained microcrustacean variation in these habitats. Cazzanelli et al. (2008) showed that floating-leaved macrophytes can harbour significantly higher densities of ZP, compared to the pelagial, even during periods of high predation pressure from YOY fish. It seems logical to assume that the highest grazing pressure in floating-leaved plant stands is centred on large sized cladocerans, whilst the numbers of smaller species can remain high.

Despite the fact that our study has clearly indicated the presence of different structural communities of aquatic macrophytes and their different structuring abilities to different food web components in lakes, we still found no cascading influence on the bottom of the food web – to the level of HBP and HNF, their abundances and biomasses. Changes in bacterivore communities do not cascade down to the level of bacteria (Zöllner et al., 2003). The reason behind this may lie in rapid turnover times (0.2–2 d) of planktonic bacteria (Kirchman et al., 1982; Ducklow and Hill, 1985; Scavia and Laird, 1987). Several earlier studies have shown that bacterial growth and losses due to zooplankton grazing are in close balance (Mcmanus and Fuhrman, 1986; Bloem et al., 1989; Sanders et al., 1989) or bacterial growth estimates exceed its grazing losses (Sherr et al., 1989). Instead of changes in bacterial abundance and biomass, there are often shifts and adaptations in bacterial assemblages, which include changes in taxonomic composition, morphology and physiological activities in response to altered trophic interactions (Zöllner et al., 2003).

In conclusion, the results of our research clearly point to several structural abilities of aquatic macrophytes on food web components. These novel results also corroborate other studies aimed at the understanding of the important connectivity between macrovegetation and food web interactions in enhancing fish year-class strength (the number of fish hatched that survive and join with present fish stocks). The significant positive relationship with the abundances of all major species of YOY fish with floating and floating-leaved plants suggests that this habitat offers better refuge, abundant and high-quality food and better visibility of prey, creating a synergistic effect for juvenile fish growth success.

CRedit authorship contribution statement

Katrit Karus: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Writing – original draft, Writing – review & editing, Project administration. **Matiss Zagars:** Methodology, Investigation, Supervision, Writing – review & editing. **Helen Agasild:** Methodology, Investigation, Formal analysis, Writing – review & editing. **Arvo Tuvikene:** Methodology, Investigation, Formal analysis, Writing – review & editing. **Priit Zingel:** Methodology, Investigation, Formal analysis, Writing – review & editing, Supervision. **Linda Puncule:** Methodology, Investigation. **Madara Medne-Peipere:** Investigation, Formal analysis. **Tõnu Feldmann:** Conceptualization, Methodology, Formal analysis, Investigation, Supervision, Visualization, Writing – original draft, Writing – review & editing. **European Regional Development Fund:** Funding acquisition. **The State budget of the Republic of Latvia:** Funding acquisition. **Institute for Environmental Solutions:** Funding acquisition, Resources, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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