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EUROPEAN LARGE LAKES IV

# Is fish able to regulate filamentous blue-green dominated phytoplankton?

**Tiina Nõges · Ain Järvalt · Juta Haberman ·**
**Priit Zingel · Peeter Nõges**

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**Abstract** Efficient zooplankton grazing is a prerequisite for establishing a cascading food web control over phytoplankton in a lake. We studied if the top-down impact of fish could reach phytoplankton in a lake where the grazing pressure of small-sized zooplankton on filamentous phytoplankton is considered weak. We analysed >30 years of data on plankton, fish catches, hydrochemistry, hydrology, and meteorology from Võrtsjärv, a large and shallow eutrophic lake in Estonia with intensive commercial fisheries. The lake's unregulated water level has been considered the strongest factor affecting the ecosystem through modifying sediment resuspension, internal loading of nutrients, and underwater light conditions and spawning conditions for fish. We found a negative relationship between phytoplankton biomass and pikeperch biomass indicating a potential top-down cascading effect in the food web. Top-down control of phytoplankton by zooplankton was reflected in a negative relationship between phyto- and zooplankton biomasses. A decrease of the individual weight of crustacean zooplankton with increasing biomass of small fish suggested top-down control of zooplankton by planktivorous fish. In contrast, we could not demonstrate a direct linkage between piscivorous fish and small fish. The top-down food web impact of piscivores, however, was manifested at zooplankton level in a positive correlation of pikeperch biomass with the biomass of dominating cladoceran species *Bosmina coregoni* and the individual weight of copepods. At high biomasses of small fish, ciliate domination over metazooplankton increased and thus enhanced the strength of the microbial food web. According to our results, fishery management measures that increase small plankti- and benthivorous fish biomass have to be avoided as they have a cascading negative effect on the ecosystem health.

**Keywords** Ecosystem-based fishery management · Large shallow lake · Food web interactions · Fish · Phytoplankton · Zooplankton · Ciliates

## Introduction

In large lakes, fish yield is one of the most important provisioning ecosystem services, whose value depends

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T. Nõges (✉) · A. Järvalt · J. Haberman ·
P. Zingel · P. Nõges
Centre for Limnology, Institute of Agricultural and Environmental Research, Estonian University of Life Sciences, Rannu, 61117 Tartu County, Estonia
e-mail: tiina.noges@emu.ee

largely on fish community composition. Not less important is the regulatory service that various fish species provide through their cascading impact on plankton composition and the occurrence of blooms, i.e. water quality that affects other ecosystem services as the recreational value. Commercial fishery, by modifying both the standing stock and community structure of fish, is an important anthropogenic stressor controlling ecosystem status and its services. The so-called 'fishing down' of predators may have cascading top-down effects and can even shift entire ecosystems between alternate stable states (Scheffer et al., 2001). Also, introduction and stocking of fish have top-down effects on the food web either directly or indirectly through affecting native fish stocks (Post, 2012).

In the present study, we addressed the question whether the cascading top-down impact of fish community changes could reach phytoplankton community also in a lake where small-sized zooplankton is assumed not to be able to exert remarkable grazing pressure on large-sized phytoplankton (Agasild et al., 2013). We analysed the possible effects of fish and fisheries using long-term data on fish biomass and catches, biomass and composition of lower trophic levels, nutrient status, and water level of Lake Võrtsjärv, a large and shallow eutrophic lake in Estonia. Võrtsjärv has intensive commercial fisheries with well-documented catches. The main commercial profit is coming from eel (*Anguilla anguilla* (L.)), which has been regularly stocked in the lake since the 1950s. Banning of the small-meshed fishing gear in the beginning of the 1970s caused a major change in the age and size structure of fishes and contributed to the establishment of predatory fish (pikeperch (*Sander lucioperca* (L.)) and pike (*Esox lucius* (L.))) control over previously dominant ruffe (*Gymnocephalus cernuus* (L.)) and roach (*Rutilus rutilus* (L.)) populations (Pihu & Mäemets, 1982). Earlier, young stages of predatory fish were caught out together with other small fish that weakened the overall predatory pressure. Võrtsjärv has suffered from increasing nutrient loads since the 1950s. The lake's water level is unregulated and the long-term amplitude of water level fluctuations exceeds the mean depth of the lake. In view of the results of our previous studies showing hydrology as the main driving force in Võrtsjärv ecosystem and phosphorus concentration as the leading factor in low-water periods (Nõges et al., 2010a, b), our working hypothesis for this study was that bottom-up factors such as water level and nutrient concentrations predominate in regulating phytoplankton abundance and that the impact of fish community is comparatively minor. If so, also the effect of different fisheries management strategies on water quality would be negligible.

## Materials and methods

### Site description

Lake Võrtsjärv, the second largest lake in the Baltic countries, is located in a shallow pre-glacial basin in southern Estonia, centred around 58°17′N and 26°03′E. At the mean water level of 33.63 m above sea level, the lake area is 270 $km^2$, volume 750 million $m^3$, mean depth 2.8 m, and maximum depth 6 m. The absolute water level range of 3.1 m exceeds the mean depth of the lake and is the most powerful factor affecting ecosystem functioning through modified spawning conditions for fish, sediment resuspension, internal loading of nutrients, and underwater light conditions. As many European lakes, Võrtsjärv has suffered from increasing nutrient loads, mainly from agriculture, since the 1950s, and eutrophication is considered the strongest stressor in the ecosystem (Nõges & Nõges, 2012).

Among fishes, pike, eel, bream (*Abramis brama* (L.)), and pikeperch are presently the main commercial fish species in Võrtsjärv. Roach, burbot (*Lota lota* (L.)), and perch (*Perca fluviatilis* L.) are also abundant and commercially exploited. Ruffe, bleak (*Alburnus alburnus* (L.)), and lake smelt (*Osmerus eperlanus* m. *spirinchus* Pallas) have lost their commercial importance as the use of fine-meshed trawls is prohibited in the lake since the 1970s (Järvalt et al., 2004).

The phytoplankton of Võrtsjärv is dominated by two shade-tolerant filamentous cyanobacteria species, *Limnothrix planctonica* (Wołosz.) Meffert and *L. redekei* (van Goor) Meffert, occurring in plankton all year round. These species are accompanied by two other filamentous cyanobacteria, *Planktolyngbya limnetica* (Lemm.) Kom.-Legn. and *Aphanizomenon skujae* Kom.-Legn. & Cronb. The diatoms are dominated by long cylindrical *Aulacoseira* species and needle-shaped species of *Synedra*. Because of strong wave action, benthic and periphytic diatoms from genera *Surirella, Gyrosigma, Nitzschia*, and others become detached from the substrate and occur frequently in the water column (Nõges et al., 2004a).

Small-sized zooplankton of Võrtsjärv is dominated by ciliates. According to Nõges & Nõges (2012), the average year-round biomass of ciliates during 1994–2009 (1.8 g $m^{-3}$) was more than twice higher than the average biomass of metazooplankton (cladocerans, copepods, and rotifers) in the same period (0.8 g $m^{-3}$). Among ciliates, oligotrichs (the most common genera *Rimostrombidium*, *Limnostrombidium*, *Pelagostrombidium*, *Halteria,* and species *Codonella cratera* and *Tintinnidium fluviatile*) were the most numerous group (27–78%) being followed by prostomatids (11–25%), haptorids (4–34%), scuticociliates (0.3–22%), and peritrichs (Zingel & Nõges, 2010). Most numerous among metazooplankton were the rotifers *Anuraeopsis fissa* (Gosse), *Keratella cochlearis* (Gosse), *K. quadrata frenzeli* (Eckst.), *K. tecta* (Gosse), *Trichocerca rousseleti* (Voigt), *Polyarthra luminosa* Kut, in winter *Polyarthra dolichoptera* Idels., and *Synchaeta verrucosa* Nipk. The dominant crustaceans, in biomass, were the cladocerans *Bosmina longirostris* (O. F. Müller), *Chydorus sphaericus* (Müller), and the juvenile forms of copepod genus *Mesocyclops* and *Thermocyclops*. *Daphnia cucullata* was earlier quite numerous in zooplankton (Haberman, 1998), while since the 2000s only single individuals have remained (Haberman & Haldna, 2014).

## Data and analyses

In this paper, we analysed the data from years 1979–2013. For fish and fishery, we used yearly statistics on commercial fish catches and experimental trawling data. Passive fishing gears (fish traps and gill nets) were used in commercial fishery, and the intensity of fishing remained at a more or less constant level during the whole period. In experimental trawling for fish stock monitoring, fishes were caught with the bottom otter trawl (mesh size 12 mm in the codend) in the open part of lake during the ice-free period (April–November), 15–20 hauls per year. Trawlings lasting between 15 and 30 min at a trawling speed of 4.5 km $h^{-1}$ were carried out in daytime. The width of the trawl mouth was 8 m and height 2.5 m. Weight per unit effort (WPUE) of trawl was calculated in kilograms per trawl-hour. In our analysis, we used the WPUE data on main fish species and also the species-based aggregated 'small fish' WPUE that included ruffe, bleak, roach, and smelt.

During the whole period, water chemistry and phyto- and zooplankton were studied at the deepest (6 m) point of the lake 1–4 times per month. The deep sampling site located close (ca 300 m) to the eastern shore was found representative of more than 90% of the lake area (Nõges & Tuvikene, 2012). Water was taken with 1.5-L Ruttner sampler at 1-m intervals from surface to bottom and mixed in a tank. For phytoplankton, a subsample of 250 ml was preserved with acid Lugol's solution and the biomass was calculated as wet weight based on microscopic counts as described by Nõges et al. (2010a). Total phosphorus (TP) was analysed at the accredited laboratory of Tartu Environmental Research Centre Ltd. according to the methods described by Grasshoff & Kremling (1983).

Until year 2000, zooplankton samples were taken with a quantitative Juday net (85 µm mesh size) from bottom to surface. Since year 2001, 20 L of depth-integrated water was filtered through a net of 48 µm mesh size. Zooplankton samples were fixed with acid Lugol's solution and counted under stereomicroscope (Nikon SMZ1500) in the Bogorov chamber at up to × 120 magnification. For biomass calculations, the average body length of 10 individuals from each taxon was measured. Individual rotifer weights were estimated from the average length according to Ruttner-Kolisko (1977). The length of crustaceans was converted to weight according to Studenikina & Cherepahina (1969) for nauplii, and Baluskina and Vinberg (1979) for other groups. As plankton nets do not retain efficiently the smallest rotifers, the rotifer abundances before year 2000 were corrected using the coefficients developed by comparing net and sampler samples (Virro, 1989).

For planktonic ciliates (studied since 1995), 250-ml subsamples of depth-integrated water were preserved with acid Lugol's solution. Ciliate biomass and community composition were determined using the Utermöhl (1958) technique. Ciliates were enumerated and identified with an inverted microscope (Wild Heerbrug M40, Nikon diaphot-TMD, Nikon ECLIPSE Ti) at × 200–600 magnification. The first 20 measurable specimens encountered for each taxon were measured. The biovolume of each taxon was estimated by assuming geometric shapes. Ciliates were identified by consulting several works (e.g. Foissner &

Berger, 1996; Foissner et al., 1999). On several occasions, we used additional live subsamples to aid identification. Silver impregnation techniques were used to identify some species (Foissner et al., 1999).

Daily data on air temperature at the closest weather station to Võrtsjärv (Tõravere) as well as water level data in Võrtsjärv were provided by Estonian Environmental Agency and by the Estonian Meteorological and Hydrological Institute.

For statistical analyses, we used STATISTICA version 12, StatSoft, Inc.

To avoid the problems caused by non-normal distribution of data, we used non-parametric Spearman correlation analysis for relating the biomasses of different fish species with the indices (biomasses and in some cases the individual weight) of lower trophic levels in the food chain (metazooplankton, phytoplankton, and ciliates). For revealing the potential impact of fishery on the lake fish community, we analysed the impact of yearly fish catches on the average fish biomass (WPUE) in the following year.

## Results

### Changes in Võrtsjärv fish community and fisheries

Lake Võrtsjärv has intensive commercial fisheries with well-documented yearly catches for all commercial fish species (Fig. 1). Only in conditions of profound changes in societal and economic life and opening of west market caused a rapid rise in prices (mostly of pikeperch and perch) in late 1980s and early 1990s, fish catches were not correctly registered and part of fish was sold on the black market (Järvalt, 1998). In this period, largest inconsistencies could be noticed between commercial catch and experimental trawl data (Fig. 2). Catches and experimental trawl data (WPUE) correlated significantly only for pikeperch ($r = 0.39$, $P = 0.02$).

Before 2010, the bycatch of mostly small bream, white bream, and roach by fyke nets was 100–250 tonnes per year. This amount of fish was used as food for pigs and other domestic animals. Since 2010, there is no market for this fish anymore. That has caused extensive back-release of bycatch fish by fishermen and the amount of this fish in experimental trawl catches has sharply increased. This is reflected in the increasing total WPUE (Fig. 2D) and is mainly caused by the increasing share of small bream (Fig. 2C).

### Fishery impacts on fish community

Analysis of the relationship between yearly catches and the average biomass (WPUE) in the following year (Fig. 3) revealed a bell-shape relationship in case of pikeperch (Fig. 3A). Low catches of pikeperch (<40 tonnes/year) were likely caused by generally small stocks (the latter being small for other reasons rather than influenced by catch of the year before). During 1979–2013, the catch range of 40–60 tonnes/year was likely optimal for a wealthy pikeperch population as high biomass could follow. At catches >60 tonnes/year, the following-year biomass was low and those could be considered as overcatches for pikeperch in Võrtsjärv. For pike, bream, and total catches, the values exceeding, respectively, 50, 100, and 500 tonnes/year decreased the fish biomass in the following year and could presumably be considered as overcatches for Võrtsjärv (Fig. 3B–D).

### Top-down effects in the food web

We found a negative relationship between phytoplankton biomass (Bphyto) and pikeperch biomass (Fig. 4) indicating a potential top-down cascading effect in the food web (Fig. 6). As supporting evidence to this, we found that

(1) chlorophyll a and biomasses of phytoplankton and cyanobacteria were all negatively correlated with zooplankton biomass (Spearman $r = -0.4$, $P = 0.02$; $r = -0.25$, $P = 0.08$, and $r = -0.27$, $P = 0.05$, respectively). Among zooplankton species, the biomass of *Bosmina coregoni* was most strongly negatively correlated with phytoplankton biomass (Spearman $r = -0.62$, $P < 0.001$), and a significant negative correlation existed also between the biomass of *Chydorus sphaericus* and chlorophyll a concentration (Spearman $r = -0.37$, $P < 0.04$);

(2) the individual weight and biomass of cladocerans was lower in years with high small fish (ruffe + bleak + roach + smelt) biomass (Fig. 5A); the average biomass of the whole metazooplankton community was negatively

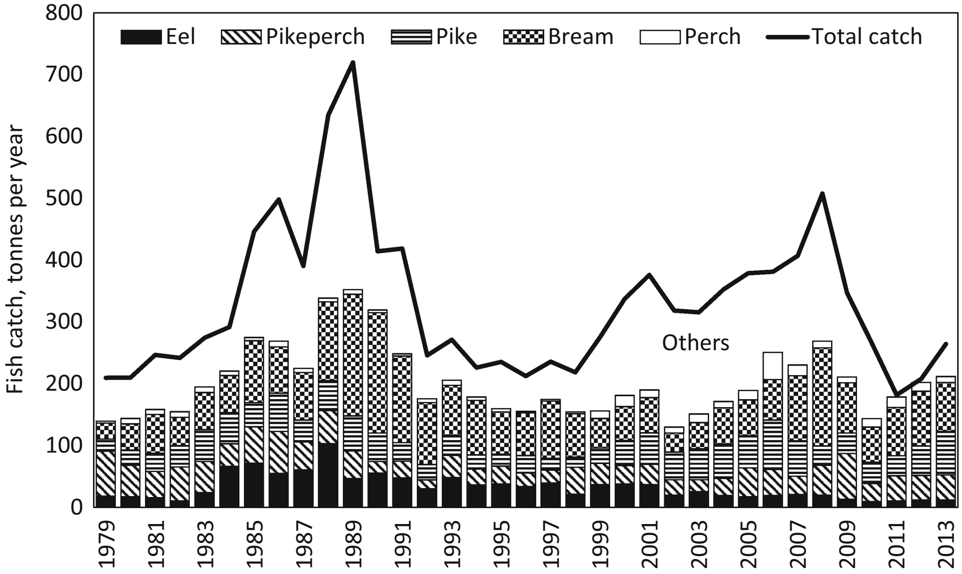

**Fig. 1** Composition of commercial catches in Lake Võrtsjärv during 1979–2013. "Others" denote the sum of smelt, bleak, ruffe, roach, burbot, and white bream. (See more detailed fish composition data from experimental trawlings in Supplementary Material)

correlated with small fish biomass (Fig. 5B); the negative relationship of small fish (bleak) WPUE and zooplankton individual weight was most clearly expressed for *Daphnia cucullata* and *C. sphaericus* (Fig. 5C);

(3) at high biomasses (WPUE) of small fish, ciliate domination over metazooplankton increased (Fig. 5B) demonstrating increasing predation pressure on metazooplankton and consequent enhancement of the microbial food web. Biomass of ciliates was rather strongly negatively correlated with biomass of rotifers (Fig. 5D);

(4) although we could not find significant correlations between piscivorous fish (pikeperch and pike) and small fish in our database, the top-down food web impact of piscivores was, however, manifested at zooplankton level in a positive correlation of pikeperch biomass with the biomass of dominating cladoceran species *B. coregoni* (Spearman $r = 0.59$, $P < 0.001$) and with the individual weight of copepods (Spearman $r = 0.32$, $P < 0.06$).

Multiple stepwise regression explained nearly 40% of the variability of the May–October mean phytoplankton biomass by changes in annual average pikeperch WPUE and May–October mean TP as significant determinants, and average May–Oct air temperature and annual mean water level as non-significant determinants (Table 1).

## Discussion

The cascading food-chain effect of fish community is a well-known phenomenon and forms the basis of the biomanipulation method for recovering aquatic ecosystems (Shapiro et al., 1975; Jeppesen et al., 2012). A prerequisite for the cascading, however, is efficient predation and grazing occurring along the food web—zooplankton has to be able to graze down phytoplankton. In Võrtsjärv where large filamentous cyanobacteria dominate in phytoplankton and ciliates, small-sized crustaceans and rotifers prevail in zooplankton, it is presumed that the grazing is inefficient. Due to inefficiency of grazing food chains, the total production of herbivorous metazooplankton and benthic macroinvertebrates in Võrtsjärv is 40 times lower than phytoplankton primary production. The extremely high production of bacteria, being equal to 70% of primary production, reflects the importance of microbial food chains (Nõges et al., 2004b). Võrtsjärv has a very abundant protist community (Zingel, 1999; Zingel & Nõges, 2010), and it is evident that the

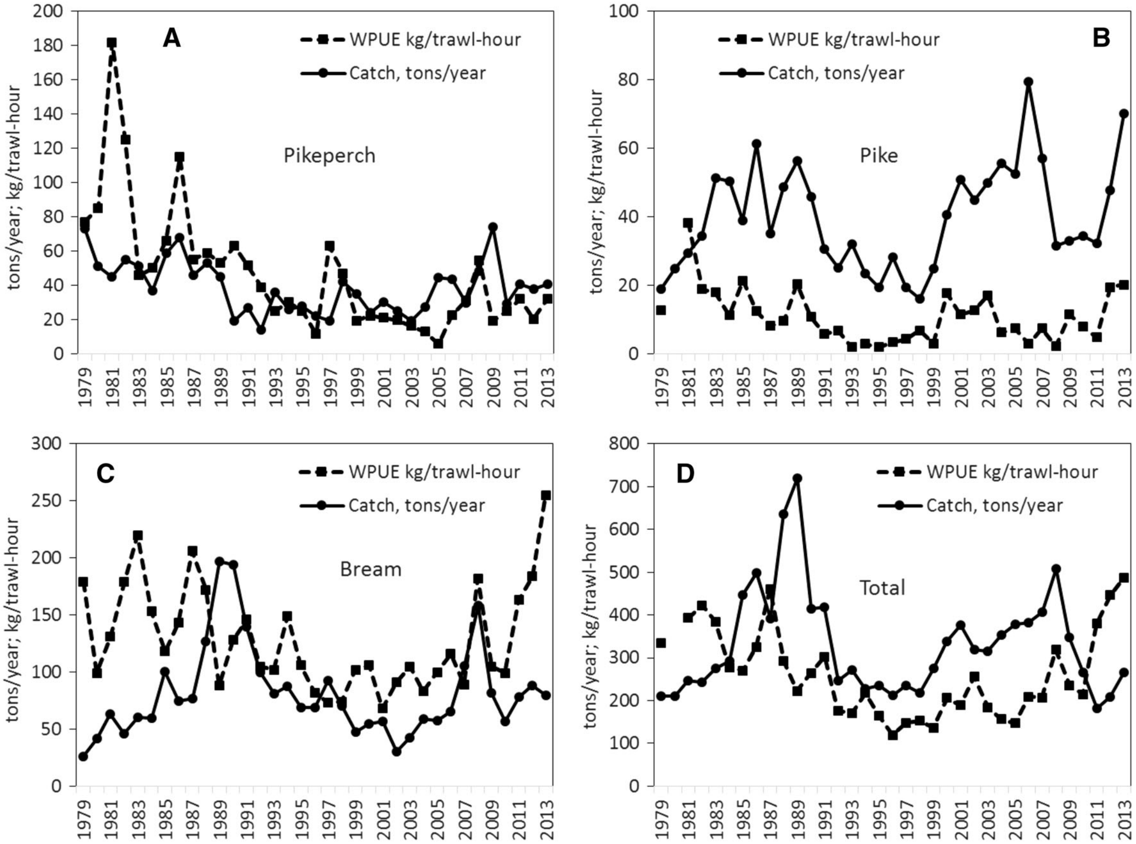

**Fig. 2** Commercial catch data vs experimental trawling weight catch per unit effort (WPUE) of main commercial fish species in Lake Võrtsjärv during 1979-2013. **A** pikeperch, **B** pike, **C** bream, and **D** total catch

majority of the organic matter produced by phytoplankton is not consumed by herbivores. Most of algal material assumingly turns into detritus and is consumed via microbial loop and benthic food chain. The efficiency of predatory links in the food web of Võrtsjärv seems much higher than that of grazing links. The efficiency of grazing was estimated to be about 2.5% of the total production of phytoplankton, as the production of herbivorous zooplankton and benthic macroinvertebrates was 40 times lower than the primary production of phytoplankton. The production of predatory zooplankton constituted more than 10% of the herbivorous zooplankton, the production of non-predatory fish made up 12% of the production of its food items (zooplankton, benthic invertebrates), and the production of predatory fish formed 13% of the production of non-predatory fish (Nõges et al., 2004b). Based on the high feeding pressure by small fish on zooplankton, its grazing efficiency was low and we assumed that the cascading impact of top predatory fish in regulating phytoplankton abundance was minor. In such conditions, the bottom-up factors, such as water level and nutrients, should be the leading factors that control phytoplankton.

However, this study demonstrated that a predator (pikeperch) could exert control over phytoplankton biomass in Võrtsjärv. Our analysis revealed a significant negative correlation between phytoplankton biomass and pikeperch WPUE (Fig. 4), most likely caused by a cascading top-down effect in the food web. Supporting this, we found also negative correlations between phytoplankton and zooplankton biomasses and a shift in zooplankton size structure at different pikeperch biomasses—smaller rotifers and larger copepods when pikeperch was abundant. Also the individual weight of crustacean zooplankton was lower in the years of high abundance of small fish;

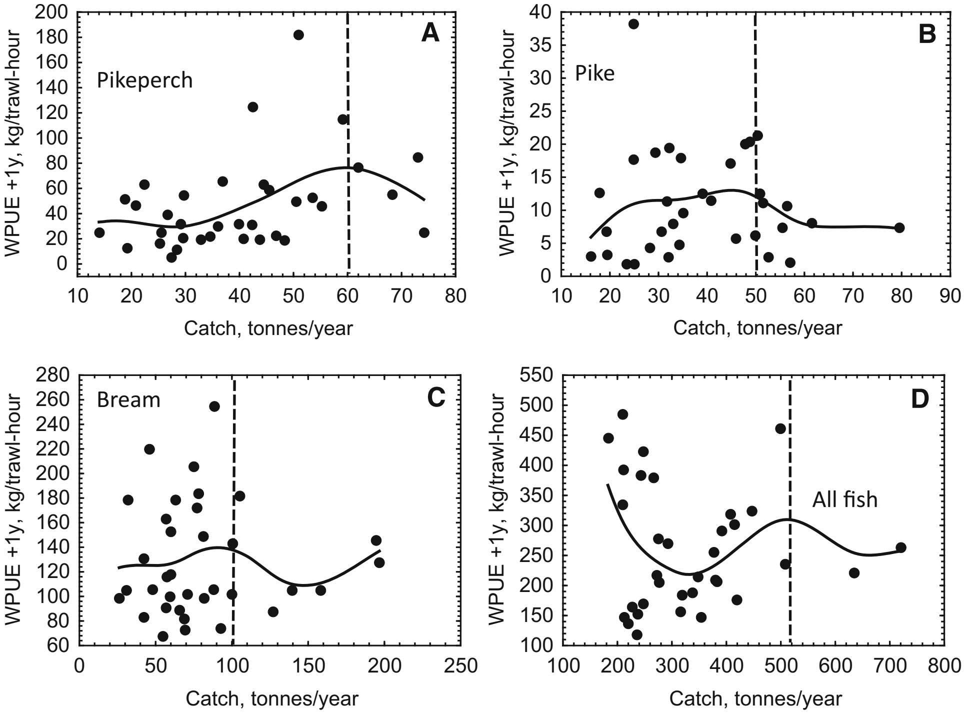

**Fig. 3** Impact of the annual catch on the biomass (experimental trawling weight per unit effort WPUE) of pikeperch (**A**), pike (**B**), bream (**C**), and all fish (**D**) in the following year in Lake Võrtsjärv during 1979–2013. *Solid line* denotes the distance-weighted least square fitting, and *dashed line* denotes the proposed upper border of the annual catch presumably not harming the stock

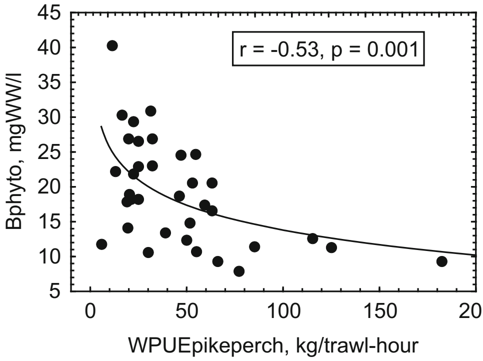

**Fig. 4** Average May–October phytoplankton biomass (Bphyto) versus annual average pikeperch WPUE

high small fish biomasses also stimulated ciliate domination over metazooplankton and thus enhanced the domination of the microbial food web. Our former mesocosm studies in Võrtsjärv (Agasild et al., 2013; Zingel et al., 2016) have shown that removal of metazooplankton caused an increase in large predacious ciliates such as haptorians from genera *Dileptus* and *Paradileptus*. Metazooplankters, especially cyclopoids, assumingly control the biomass of these large haptorian ciliates through direct grazing. A similar effect could appear in the lake when high planktivorous fish pressure on large-sized metazooplankton leads to an increase of large predacious ciliates. As a result, the biomass of ciliates could increase and thus advance also the ciliate domination over metazooplankton at higher planktivorous fish WPUE. Large-sized haptorians, which become more numerous at higher fish biomasses in Võrtsjärv, can additionally reduce the abundance of small-sized metazoans, such as rotifers (Vd'ačný & Foissner, 2012). This could have caused the inverse relationship between ciliates and rotifers found in our study (Fig. 5D), demonstrating an additional pathway explaining ciliate domination over metazooplankton at higher fish biomasses.

Still, the question remains how the cascading effect of the fish could reach phytoplankton if our assumption

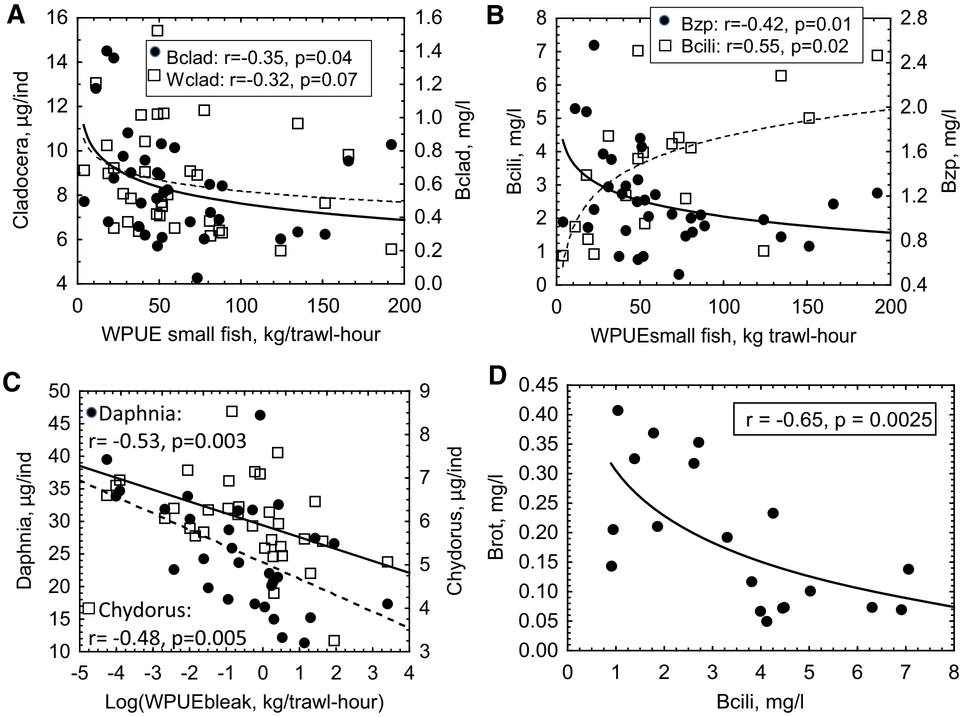

**Fig. 5** Average biomass and individual weight of cladocerans (**A**), biomass of metazooplankton (Bzp) and ciliates (**B**) versus small fish (ruffe + smelt + bleak + roach) biomass (WPUE); individual weight of *Daphnia cucullata* and *Chydorus sphaericus* vs WPUE of bleak (**C**); and the relationship of the biomasses of rotifers and ciliates (**D**) in Lake Võrtsjärv during 1979–2013. Vegetation period (May–October) averages are used for zooplankton and annual average WPUE for fish

**Table 1** Multiple stepwise regression for determining mean phytoplankton biomass (Bphyto, mgWW/l) in vegetation period (May–Oct) by changes in annual average pikeperch WPUE (kg/trawl-hour), average total phosphorus concentration (TP, mg/m$^3$) and air temperature (AT, °C) in May–Oct, and annual mean water level (WL, m above sea level): *r*—correlation coefficient, *b*—regression coefficient, *P*—significance level, *R*$^2$—determination coefficient

Dependent variable LogBphyto, $R^2 = 0.453$, adjusted $R^2 = 0.369$, $P < 0.0027$, $n = 31$

| | *r* | *b* | *P* |
|---|---|---|---|
| Intercept | | −44.507 | 0.049 |
| LogWPUEpikeperch | −0.479 | −0.292 | 0.008 |
| LogTP | 0.455 | 0.754 | 0.012 |
| LogWL | 0.360 | 12.072 | 0.058 |
| LogAT | 0.182 | 1.180 | 0.249 |

on the inability of small zooplankton to graze on filamentous cyanobacteria holds? A number of studies, however, have disputed this assumption including a case described in Võrtsjärv (Nõges & Nõges, 1999) where late fish spawning in 1996 delayed the onset of predation pressure of fish larvae on zooplankton enabling the latter to reach exceptionally high biomass and suppress the growth of commonly dominating filamentous *Limnothrix* species. Also Schaffner et al. (1994) demonstrated that early onset of zooplankton growth could suppress N-fixer dominance in the phytoplankton community. Recent grazing experiments in Sweden showed that cyclopoid copepods and small cladocerans suppressed the growth of *Anabaena,*

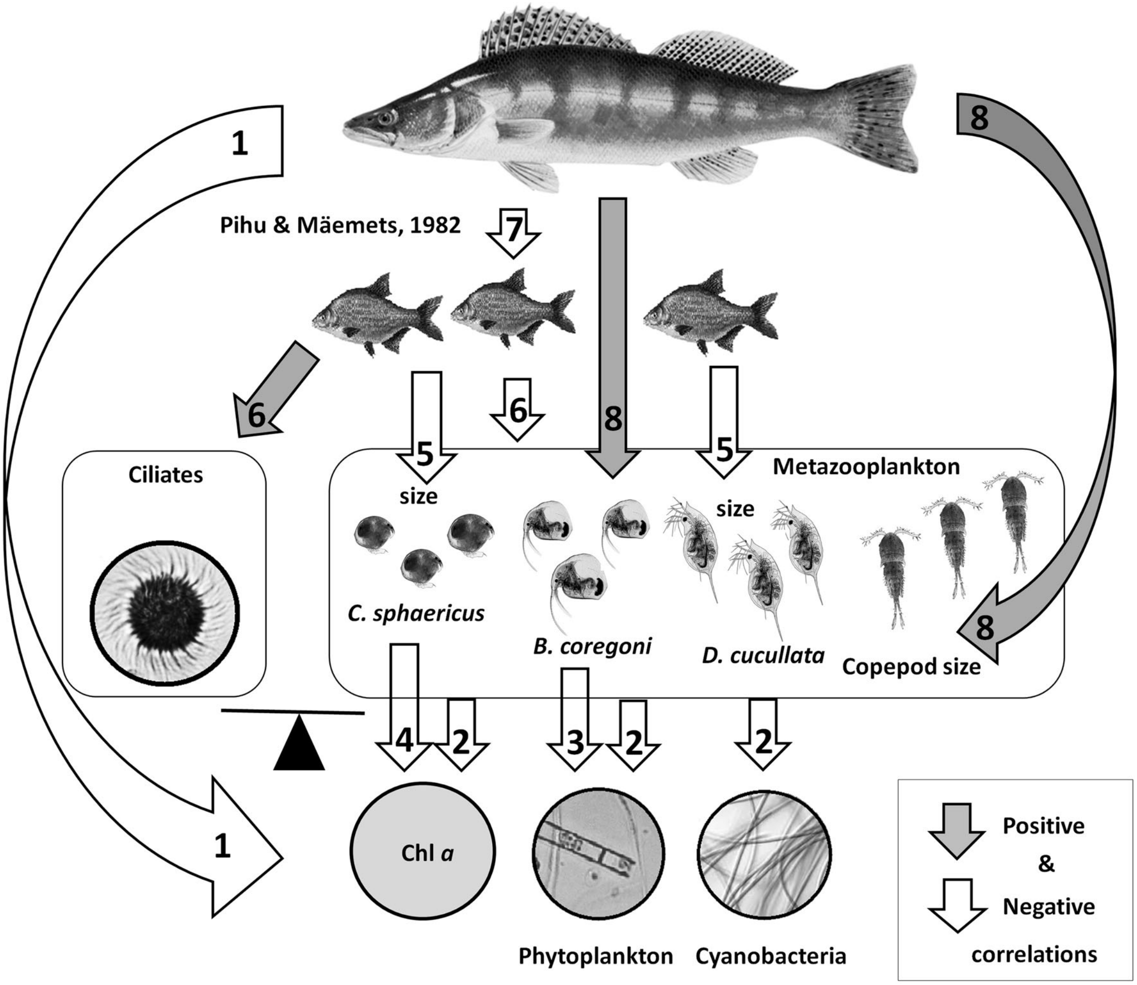

**Fig. 6** Evidence for top-down cascading effects in the food web of Lake Võrtsjärv. Negative relationship was found between phytoplankton and pikeperch biomasses (*1*). Chlorophyll a and biomasses of phytoplankton and cyanobacteria were negatively correlated with zooplankton biomass (*2*). Among zooplankton species, the biomasses of *Bosmina coregoni* (*3*) and *Chydorus sphaericus* (*4*) were negatively correlated with phytoplankton biomass/chlorophyll *a* concentration. The individual weights of metazooplankton and cladocerans, most clearly that of *Daphnia cucullata* and *Ch. sphaericus*, were all negatively correlated with small fish (ruffe + bleak + roach + smelt) biomass (*5*). At high biomasses (WPUE) of small fish, ciliate domination over metazooplankton increased (*6*). The relationship between piscivorous fish and small fish (*7*) has been proved earlier by Pihu & Mäemets (1982). The top-down food web impact of piscivores was reflected in positive correlations of pikeperch biomass with *B. coregoni* biomass and the mean individual weight of copepods (8)

*Microcystis*, and *Planktothrix* species under bloom conditions in late summer (Urrutia-Cordero et al., 2015). Grazing of crustaceans on filamentous cyanobacteria in Võrtsjärv was confirmed by a recent study on phytoplankton pigments in zooplankton guts (Tõnno et al., 2016) showing that about half of the phytoplankton diet of *D. cucullata* and *Bosmina* spp. originated from cyanobacteria and also the filamentous forms were ingested. This corresponds well with the negative correlation between some cladocerans' (*D. cucullata*, *B. coregoni*, and *C. sphaericus*) and phytoplankton biomasses found in this study.

Although we could not demonstrate the link between predatory and non-predatory or small fish based on our data, the existence of this link in Võrtsjärv was proved in practice in the 1970s when after banning of the small-meshed fishing gear, predatory fish efficiently suppressed previously dominant ruffe and roach populations (Pihu & Mäemets, 1982).

Based on our previous knowledge, we assumed that the impact of different fisheries management strategies in Võrtsjärv would not cascade down to the plankton level and that the effect on water quality would be negligible due to the poorly performing grazing food chain. Our present study showed, however, that predatory fish (pikeperch) could have a cascading impact down the food web in this lake that has to be considered in fisheries management. As we showed, the recently introduced legal requirement to sort out small fish and report it in fishery statistics has caused extensive back-release of small fish by fishermen and was one of the likely reasons why the amount of small fish, including small bream, has sharply increased in the lake. The fishery management measures that could increase small plankti- and benthivorous fish biomass have to be avoided as having a cascading negative effect on the ecosystem health of Lake Võrtsjärv. An increase in the planktivorous fish (roach, bleak, smelt) abundance enhances feeding pressure on zooplankton and therefore favours phytoplankton development and blooms (Laugaste et al., 2007). An increase in the abundance of benthivorous fish such as bream and ruffe brings about more intensive bottom sediment bioturbation and nutrient release that decreases water transparency and intensifies phytoplankton production (Tarvainen et al., 2005).

## Conclusions

Contrary to our expectations, our analysis revealed that the biomass (WPUE) of pikeperch could be an important factor contributing to the control over phytoplankton biomass in a shallow lake dominated by filamentous cyanobacteria. Our study showed that fish impacts down the food chain were often nonstationary depending on the abundance of fish size groups and catch intensities. In a eutrophic lake, the food web becomes so complex and seasonally changing that the trophic levels and their interactions can be delineated by holistic approaches taking into account rather the signs of a number of medium strength correlations (as judged by the *r* values) than any single direct relationship which become blurred by the numerous interfering factors in the system. All relationships between food-chain components revealed in our study contributed to a general picture (Fig. 6) showing the importance of top-down control of predatory fish in the system. New insights into the potential role of cyanobacteria in the grazing food chain and into fisheries' impact on lower trophic levels gained in this study showed that fishery management measures that could increase small plankti- and benthivorous fish biomass have to be avoided.

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## References

Agasild, H., P. Zingel, K. Karus, K. Kangro & T. Nõges, 2013. Does metazooplankton regulate the ciliate community in a shallow eutrophic lake? Freshwater Biology 58: 183–191.

Balushkina, E. B. & G. G. Vinberg, 1979. Зависимость между массой и длнной тела у планктонных животных. Г. Г. Винберг (ред), Обшие основы изучения водных экосистем. Ленинград: 169–172.

Foissner, W. & H. Berger, 1996. 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 Biology 35: 375–482.

Foissner, W., H. Berger & J. Schaumburg, 1999. Identification and ecology of limnetic plankton ciliates. Informationsberichte des Bayerischen Landesamtes für Wasserwirtschaft 3(99): 1–793.

Grasshoff, K. E. & M. K. Kremling, 1983. Methods of seawater analysis. Verlag Chemie, Weinheim.

Haberman, J., 1998. Zooplankton of Lake Võrtsjärv. Limnologica 28: 49–65.

Haberman, J. & M. Haldna, 2014. Indices of zooplankton community has valuable tools in assessing the trophic state and water quality of eutrophic lakes: long term study of Lake Võrtsjärv. Journal of Limnology 73(2): 61–71.

Järvalt, A., 1998. Estimation of fishing mortality and abundance of pikeperch *Stizostedion lucioperca* (L.) in Lake Võrtsjärv, Estonia, by Virtual Population Analysis. Limnologica 28(1): 109–113.

Järvalt, A., A. Kangur, K. Kangur, P. Kangur & E. Pihu, 2004. Fishes and fisheries management. In Haberman, J., E. Pihu & A. Raukas (eds), Lake Võrtsjärv. Estonian Encyclopaedia Publishers, Tallinn: 281–295.

Jeppesen, E., M. Sųndergaard, T. L. Lauridsen, T. A. Davidson, Z. Liu, N. Mazzeo, C. Trochine, K. Özkan, H. S. Jensen, D. Trolle, F. Starling, X. Lazzaro, L. S. Johansson, R. Bjerring, L. Liboriussen, S. E. Larsen, F. Landkildehus & M.

Meerhoff, 2012. Biomanipulation as a restoration tool to combat eutrophication: recent advances and future challenges. Advances in Ecological Research 47: 411–487.

Laugaste, R., J. Haberman, T. Krause & J. Salujõe, 2007. Significant changes in phyto- and zooplankton in L. Peipsi in recent years: what is the underlying reason? Proceedings of Estonian Academy of Sciences. Biology and Ecology 56: 106–123.

Nõges, T. & P. Nõges, 1999. The effect of extreme water level decrease on hydrochemistry and phytoplankton in a shallow eutrophic lake. Hydrobiologia 408(409): 277–283.

Nõges, P. & T. Nõges, 2012. Võrtsjärv Lake in Estonia. In Bengtsson, L., R. W. Herschy & R. W. Fairbridge (eds), Encyclopedia of Lakes and Reservoirs. Springer, New York: 850–861.

Nõges, P. & L. Tuvikene, 2012. Spatial and annual variability of environmental and phytoplankton indicators in Lake Võrtsjärv: implications for water quality monitoring. Estonian Journal of Ecology 61: 227–246.

Nõges, P., R. Laugaste & T. Nõges, 2004a. Phytoplankton. In Haberman, J., E. Pihu & A. Raukas (eds), Lake Võrtsjärv. Estonian Encyclopedia Publishers, Tallinn: 217–231.

Nõges, T., J. Haberman, A. Kangur, K. Kangur, P. Kangur, H. Künnap, H. Timm, P. Zingel & P. Nõges, 2004b. Food webs in Lake Võrtsjärv. In Haberman, J., E. Pihu & A. Raukas (eds), Lake Võrtsjärv. Estonian Encyclopaedia Publishers, Tallinn: 335–345.

Nõges, P., T. Nõges & A. Laas, 2010a. Climate-related changes of phytoplankton seasonality in large shallow Lake Võrtsjärv. Estonia. Aquatic Ecosystem Health & Management 13(2): 154–163.

Nõges, P., U. Mischke, R. Laugaste & A. G. Solimini, 2010b. Analysis of changes over 44 years in the phytoplankton of Lake Võrtsjärv (Estonia): the effect of nutrients, climate and the investigator on phytoplankton-based water quality indices. Hydrobiologia 646: 33–48.

Pihu, E. & A. Mäemets, 1982. The management of fisheries in Lake Võrtsjärv. Hydrobiologia 86: 207–210.

Post, J. R., 2012. Resilient recreational fisheries or prone to collapse? A decade of research on the science and management of recreational fisheries. Fisheries Management and Ecology 20(2–3): 99–110.

Ruttner-Kolishko, A., 1977. Suggestions for biomass calculation of planktonic rotifers. Archiv für Hydrobiologie 8: 71–76.

Schaffner, W. R., N. G. Hairston & R. W. Howarth, 1994. Feeding rates and filament clipping by crustacean zooplankton consuming cyanobacteria. Internationale Vereinigung für Theoretische und Angewandte Limnologie Verhandlungen 25(4): 2375–2381.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke & B. Walker, 2001. Catastrophic shifts in ecosystems. Nature 413: 591–596.

Shapiro, J., V. Lamarra & M. Lynch, 1975. Biomanipulation: an ecosystem approach to lake restoration. Proceedings of a Symposium on Water Quality and Management through Biological Control, Gainesville: 85–96.

Studenikina, E. I. & M. M. Tserepahina, 1969. Средний вес основных зоопланктона Азовского моря. Гидробиологический журнал 5: 89–91.

Tarvainen, M., A.-M. Ventelä, H. Helminen & J. Sarvala, 2005. Nutrient release and resuspension generated by ruffe (Gymnocephalus cernuus) and chironomids. Freshwater Biology 50: 447–458.

Tõnno, I., H. Agasild, T. Kõiv, R. Freiberg, P. Nõges & T. Nõges, 2016. Algal Diet of Small-Bodied Crustacean Zooplankton in a Cyanobacteria-Dominated Eutrophic Lake. PloS One 11(4): e0154526.

Urrutia-Cordero, P., M. K. Ekvall & L.-A. Hansson, 2015. Response of cyanobacteria to herbivorous zooplankton across predator regimes: who mows the bloom? Freshwater Biology 60: 960–972.

Utermöhl, H., 1958. Zur Vervollkommung der quantitativen Phytoplanktonmethodik. Mitteilungen Internationale Vereiningung fuer Theoretische und Angewandte Limnologie 9: 1–38.

Vd'ačný, P. & W. Foissner, 2012. Monograph of the dileptids (Protista, Ciliophora, Rhynchostomatia). Land Oberösterreich, Biologiezentrum/Oberösterreichische Landesmuseen.

Virro, T., 1989. The comparison of sampling methods of planktonic rotifers (Rotatoria) on the example of Lake Peipsi. Proceedings of Academy of Sciences of Estonian SSR, Biology 38: 119–122. **(in Russian)**.

Zingel, P., 1999. Pelagic ciliated protozoa in a shallow eutrophic lake: community structure and seasonal dynamics. Archiv für Hydrobiolgie 146: 495–511.

Zingel, P. & T. Nõges, 2010. Seasonal and annual population dynamics of ciliates in a shallow eutrophic lake. Fundamental and Applied Limnology 176: 133–143.

Zingel, P. H., K. Agasild, K. Karus, H. Kangro, I. Tammert, T. Feldmann Tõnno & T. Nõges, 2016. The influence of zooplankton enrichment on the microbial loop in a shallow, eutrophic lake. European Journal of Protistology 52: 22–35.