



Fish predation pressure on zooplankton in a large northern temperate lake: impact of adult predators versus juvenile predators

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Abstract. In recent decades, a marked decrease in planktivorous fish (*Osmerus eperlanus eperlanus* m. *spirinchus* Pallas and *Coregonus albula* (L.)) in Lake Peipsi has stimulated research into the potential effect of fish predation on zooplankton. The abundance of planktivorous fish and the abundance and biomass of zooplankton were studied from 1986 to 2014, and the diet of plankton-eating fish was analysed from 2007 to 2013. A linear regression model was used to establish possible trends in the zooplankton assemblages (biomass, abundance, mean weight of individuals) and in the abundance of zooplankton-eating fish. The ANOVA test was used to evaluate differences in the zooplankton assemblages and in fish consumption in the years with large and small fish cohorts. Despite the collapse of the smelt and vendace populations, the abundance of plankton-eating fish remained high due to an increase in the abundance of juvenile fish. Fish juveniles consumed as much as or even more zooplankton than adult planktivores. Since 1986, a significant decrease was observed in the cladoceran and copepod biomass and in the mean body weight of cladocerans. Large cladocerans such as *Leptodora kindtii* (Focke) and *Bythotrephes longimanus* Leydig were rare in zooplankton samples and the biomass of *Bosmina* spp. decreased. Changes in the structure of the zooplankton community were most likely caused by the feeding of juvenile fish as the calculated consumption by fish was high, especially in years with particularly large fish cohorts.

Key words: planktivorous fish, zooplankton, diet of juvenile fish, size of fish cohorts, top-down effect of fish.

INTRODUCTION

Size-selective predation by adult zooplanktivorous fish has a strong impact on the dynamics and structure of the zooplankton communities of temperate lakes (Amundsen et al., 2009; Iglesias et al., 2011). Increased predation by planktivorous fish may result in a multitude of effects, including a decrease in zooplankton abundance (Persson et al., 2004), changes in the community and population structure towards smaller species and smaller individuals within the species (Haberman, 2000; Persson et al., 2004). Therefore, pelagic food webs have long

been considered classical examples of the structuring effects of predation in lakes (Mehner et al., 2016).

Not only adult plankton-eating fish but also young-of-the-year (YOY) fry have a significant effect on the diversity of zooplankton as they mainly prey on them (Mehner, 1996). Juvenile fish may reach high abundances in northern cold temperate lakes in summer; hence they may potentially impact the dynamics of the zooplankton population, especially in late summer (Mehner, 1996). Nevertheless, the abundance of planktivorous individuals varies from year to year depending on the number of factors such as the recruitment success of planktivorous and piscivorous fish (Persson and Crowder, 1998), food availability (Persson and Greenberg, 1990), macrophyte

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coverage (Jeppesen et al., 2002), winter starvation and fish kills under ice (Ruuhijärvi et al., 2010), as well as summer water temperature (Mehner, 2000). Therefore, fluctuations in the abundance of plankton-eating fish can induce major shifts in the size distribution and abundance of zooplankton (Iglesias et al., 2011); moreover, these effects may cascade down to phytoplankton (Jeppesen et al., 2011; Bunnell et al., 2014).

Amundsen et al. (2009) pointed out that most studies of predation effects on zooplankton have been conducted on a short-term scale. Such analyses may lack the power to distinguish weak trends from natural variations (Elliott, 1994). Long-term studies of the predator impact on prey are necessary to obtain information on the mechanisms that drive changes in the prey community, but such studies have rarely been conducted (Strayer et al., 2006). Moreover, it is supposed that in a warming climate the functioning of the food web may start to change (Jeppesen et al., 2010; Iglesias et al., 2011; Ventelä et al., 2016). For example, data from Danish lakes showed enhanced predation on zooplankton at higher temperatures (Jeppesen et al., 2009). Thus, new insights into trophic interactions are needed in order to elucidate the ecosystem functioning in new conditions.

In Lake Peipsi, an abrupt increase in the water temperature was recorded in 1987–1989 (Nõges and Nõges, 2014). A shift from clean- and cold-water species, e.g. vendace (*Coregonus albula* (L.)), Peipsi whitefish (*C. lavaretus maraenoides* Poljakow), and lake (dwarf) smelt (*Osmerus eperlanus eperlanus* m. *spirinchus* Pallas), to species preferring warmer and more eutrophic waters, e.g. pikeperch (*Sander lucioperca* (L.)), in Lake Peipsi had taken place by the turn of the 1980s/1990s (Kangur et al., 2007a; 2007b). Also the zooplankton community was affected by climate warming (Blank et al., 2010; Laugaste et al., 2010). Scheffer et al. (2001) emphasized that climate warming may cause essential shifts in a lake's food web. For example, major shifts might occur in the feeding interactions between fish and zooplankton. Long-term data necessary to reveal such changes exist from Lake Peipsi: the statistics on commercial fisheries date back to 1931, experimental trawling has been conducted since 1986, and zooplankton records date back to the 1960s; in addition, some data are available for the diet of adult planktivorous fish (Tikhomirova, 1974; Ibnejeva, 1983; Salujõe et al., 2008) and fish juveniles (Ginter et al., 2011; 2012). These long-term data sets allow a more precise analysis of the predator impact on prey communities in the changing environment (e.g. climate warming and eutrophication) of Lake Peipsi.

To assess the potential top-down effect of fish predation on zooplankton characteristics in Lake Peipsi, the long-term data on the abundance of adult and

juvenile planktivorous fish were analysed in parallel with zooplankton data. The fish diet was investigated over a seven-year period (2007–2013) and the daily consumption rate was assessed. We hypothesized that (1) the numbers of juvenile fish have significantly increased, (2) the abundance and biomass of copepods and cladocerans have decreased, and (3) the zooplankton consumption by juvenile fish is higher than that by adult planktivores.

MATERIALS AND METHODS

Study site

Lake Peipsi, situated on the Estonian–Russian border (Fig. 1), is the fourth largest lake in Europe with a surface area of 3555 km². The present study was carried out in the largest and deepest northern part of the lake, Lake Peipsi *sensu stricto* (area 2611 km², mean depth 8.3 m, maximum depth 12.9 m). This part of Lake Peipsi is eutrophic with a mean total phosphorus concentration of 40 mg P m⁻³ and a total nitrogen concentration of 658 mg N m⁻³ in the ice-free period (Kangur and Möls, 2008). According to earlier limnological time-series data, the quality of the lake's water has deteriorated (Kangur et al., 2009; 2013b) while the data for recent years indicate a modest improvement (Blank et al., 2017).

In the quantitative zooplankton samples from the pelagial of Lake Peipsi, 57 species of cladocerans and 28 species of copepods were found, in which the characteristic species of oligo-mesotrophic and eutrophic waters co-dominated. In 1985–1999, the lake was quite rich in zooplankton, its biomass being on average 3 g m⁻³ (in wet mass) in summer (July–August; Haberman, 2001). Since the early 2000s the average summer biomass of zooplankton decreased; at the same time the biomass dominants were cladoceran species of the genera *Bosmina*

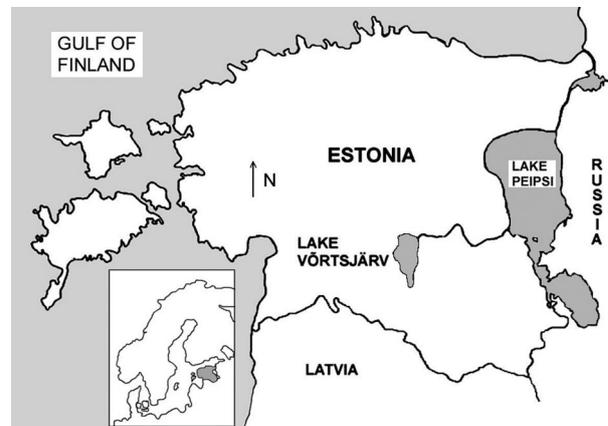


Fig. 1. Location of Lake Peipsi.

Table 1. Dominating fish species in commercial catch in Lake Peipsi with their percentage of total commercial catch (according to the Estonian Ministry of Rural Affairs)

1931–1940	1981–1990	2005–2009	2010–2014
Smelt 43%	Smelt 27%	Pikeperch 27%	Eurasian perch 33%
Roach 16%	Vendace 17%	Eurasian perch 24%	Common bream 22%
Eurasian perch 7%	Eurasian perch 12%	Common bream 20%	Pikeperch 21%
Common bream 7%	Roach 6%	Roach 14%	Roach 11%

(recently *B. gibbera* Schoedler) and *Daphnia* (mainly *D. galeata* Sars), copepods of *Eudiaptomus gracilis* (Sars), and juvenile *Mesocyclops* (Haberman et al., 2008; 2010).

Lake Peipsi is characterized by high fish production and a large number of fish species: it is inhabited by 37 fish species (Kangur et al., 2008). Over the past 80 years, none of the species has disappeared from the lake; on the other hand, there is no information about the invasion of any new species into the fish community. However, shifts in the catches of commercial fisheries since 1931 demonstrate several marked changes in the composition of the fish assemblages (Kangur et al., 2013a; Ginter et al., 2015; Table 1).

Sampling

Zooplankton sampling was conducted monthly (in mid-month) during the ice-free period in the northern part of the lake. A series of two-litre samples was taken with a Van Dorn sampler at one-metre intervals from the surface to approximately 0.5 m above the sediments. These samples were pooled in a water tank. For zooplankton samples, 20 L of mixed water was screened through a plankton net with a mesh size of 48 µm. The plankton samples were preserved with Lugol's (acidified iodine) solution.

The biomass and community composition of zooplankton were studied by conventional quantitative methods (Kiselev, 1956). Subsamples of 4 ml were analysed under a stereomicroscope (Nikon SMZ1500) in a Bogorov chamber at up to 120× magnification. Zooplankton taxa accounting for 20% or more of the number and biomass were considered dominants (Haberman, 1977). When possible, at least 10 individuals from each species were measured for the determination of the wet biomass per sample. Crustacean length was converted to weight after Studenikina and Cherepakhina (1969) and Balushkina and Winberg (1979). The biomass of zooplankton was calculated from the abundance and wet weight of individual zooplankters.

The abundance of zooplanktivorous fish from 1986 to 2014 was assessed by trawl sampling using a bottom trawl (height 2 m, width 12 m, knot-to-knot mesh size at the cod-end 10–12 mm). The trawl was towed by a ship

for 15 min per haul at a speed of 5.5–6.2 km h⁻¹. Trawl sampling was carried out monthly at noon, in the pelagic zone of the northern lake part. All fish were identified and their standard length (SL) was measured to the nearest millimetre. Moreover, relative abundance was found, therefore the catches per unit effort (CPUE) was calculated for all fish species. The 0+ fish density per cubic metre was also calculated. The relative abundance of juvenile fish in the trawl samples in autumn served as the basis on which the size of the cohorts was assessed. The ages of juvenile fish were estimated from the length frequency distribution of the 0+ and 1+ age groups (e.g. Kangur et al., 2013a). A large cohort was defined as a cohort that was at least twice as large as an average cohort, starting from 1986.

Analysis of the diet of zooplanktivorous fish was conducted from 2007 to 2013. For this, fish samples were frozen after capture. Each fish was dissected, its stomach content was analysed under microscope, and the food items were identified and counted. Data for prey weight (individual biomass values for the zooplankton species) were drawn from long-term research on zooplankton (Haberman, 2000; Haberman and Laugaste, 2003). In total, we examined the digestive system of 635 pikeperch, 350 Eurasian perch *Perca fluviatilis* L., 265 ruffe *Gymnocephalus cernuus* (L.), 13 roach *Rutilus rutilus* (L.), 20 common bream *Abramis brama* (L.), 10 vendace, and 21 smelt with a SL between 4 and 15 cm.

Data analysis

To find out major prey species in the diet of the plankton-eating fish in Lake Peipsi, the following indices were calculated:

- percentage of prey number (the number of each prey species *i* expressed as the percentage of all observed prey):

$$N(\%) = 100 * \sum ni / \sum n; \quad (1)$$

- percentage of prey weight (the weight of each prey species *i* expressed as the percentage of all observed prey):

$$W(\%) = 100 * \sum Vi / \sum V. \quad (2)$$

The average zooplankton abundance and biomass in stomach per fish body weight of all individual fish analysed during eight years (2007–2014) were calculated. Moreover, the zooplankton abundance and biomass per fish body weight in summer (June–July) and autumn (August–October) were analysed in detail. Also, daily consumption was calculated according to the formula provided by Eldridge et al. (1981):

$$PT = A \cdot AT / S, \quad (3)$$

where PT is daily consumption per fish, A is average zooplankton biomass in the stomach, AT is active feeding period, and S is digesting time. The active feeding period was set at 20 h according to Karjalainen (1992), and the digesting time was set at 4 h according to Sutela and Huusko (1997). To assess the consumption of all fish, we multiplied PT by the abundance of juveniles (ind. m⁻³); in the calculations the diet of all fish species and the relative abundance of different fish species in a particular year were treated separately.

A linear regression model was used to establish possible trends in the abundance of zooplankton-eating fish since 1986; moreover, trends in the abundance of both smelt and YOY fish (pikeperch, perch, ruffe) were analysed in detail. A linear regression model was used to establish changes in the zooplankton assemblages (biomass, abundance, mean weight of zooplankton individual) in summer (June–July) and autumn (August–October) starting from 1992. An ANOVA test was used to evaluate the possible impact of the changing fish

population on the zooplankton community. Various zooplankton characteristics were compared for two time periods: 1992–2001, with the domination of smelt in the zooplankton-eating niche, and 2002–2013, with the domination of the YOY fish. An ANOVA test was employed to evaluate differences in the zooplankton assemblages and in fish consumption between the years with large and small fish cohorts. In statistical analysis, only pairwise analyses were used as the data were too limited for multivariate analysis. All analyses were carried out using the procedures available in the program R version 3.2.4 (R Core Team, 2016).

RESULTS

Fluctuations in the relative abundance of zooplanktivorous fish

According to the data of trawl sampling, smelt and vendace were the most abundant (CPUE) fish preying on zooplankton in Lake Peipsi in the late 1980s (Fig. 2). At the end of the 1980s, the vendace population collapsed while smelt continued to dominate up to 2001. Smelt relative abundance (CPUE) peaked in several years with up to ~3500 individuals per trawl hour. The large smelt cohort of 2001 was followed by a steep decline in the abundance, and from 2007 the population of this fish was extremely small, approximately 3 individuals per trawl hour (Fig. 2). When the population of smelt declined ($P < 0.01$, $R^2 = 0.3$, $F_{1,21} = 6.9$) to the lowest level ever

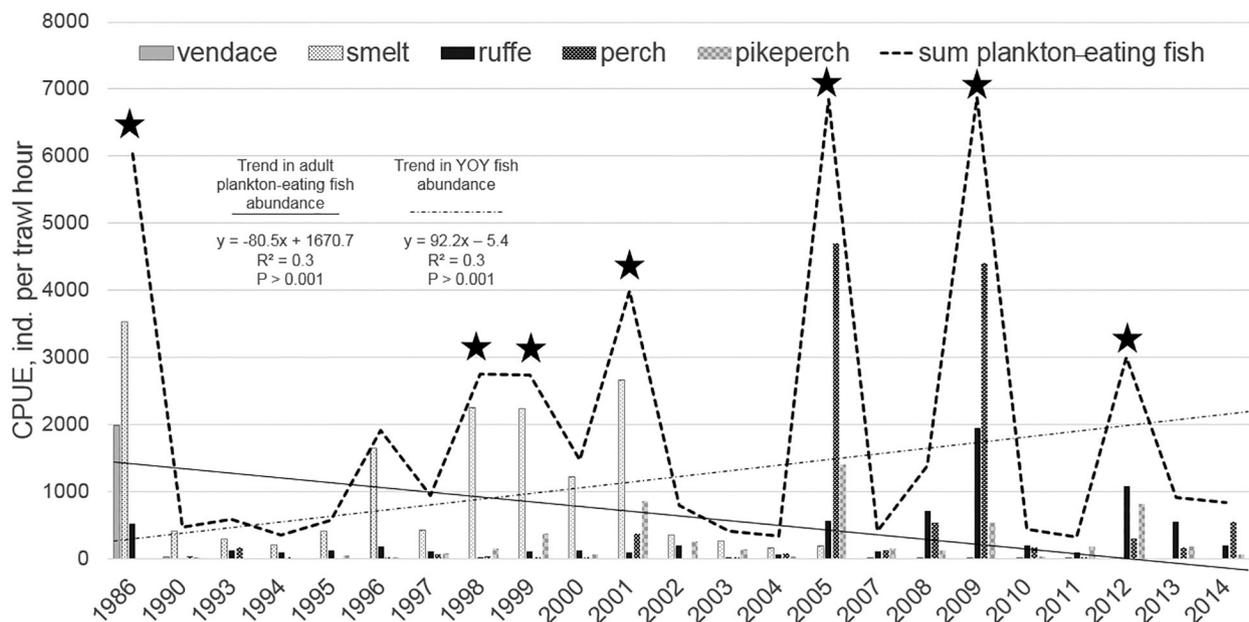


Fig. 2. Trends in the abundance (CPUE) of fish. The stars (★) denote particularly large cohorts of plankton-eating fish.

documented, the abundance of juvenile fish increased significantly ($P < 0.008$, $R^2 = 0.3$, $F_{1,21} = 8.5$). Juveniles of ruffe, perch, and pikeperch, especially of perch (total abundance reaching a peak of up to 4500 individuals per trawl hour in several years), were the most abundant fish juveniles in the pelagic zone of Lake Peipsi *s.s.* The abundance of roach and bream juveniles was lower, approximately 38 and 6 individuals per trawl hour, respectively. During the investigation period (1986–2014), the abundance of zooplanktivorous fish (smelt, vendace, and juveniles of ruffe, roach, pikeperch, and bream) did not change significantly.

In seven years (1986, 1998, 1999, 2001, 2005, 2009, 2012; Fig. 2) throughout the study period, fish cohorts were very large. The maximum density of juvenile fish in the study period reached 0.2 ind. m^{-3} (in 2005 and 2009), while the average density was only 0.06 ind. m^{-3} . In 1986, 1998, 1999, and 2001, smelt was the most abundant among the plankton-eating fish (Fig. 2). In 2005 perch and pikeperch, in 2009 perch and ruffe, and in 2012 pikeperch and ruffe were the most abundant among the YOY fish (Fig. 2).

Changes in the zooplankton assemblage

Both summer and autumn zooplankton biomass decreased significantly (regression analysis, $P < 0.001$, $R^2 = 0.5$, $F_{1,16} = 20.7$) from 1992 to 2014. In 1992–2001, when smelt dominated in the zooplankton-eating niche, the total summer zooplankton biomass was on average 2.1 g m^{-3} . In 2002–2013, when the plankton-eating niche was dominated by the YOY fish, the total summer zooplankton biomass was on average only 1.1 g m^{-3} (Table 2). Similarly, in autumn, total zooplankton biomass was on average 1.7 g m^{-3} in 1992–2001 and 0.7 g m^{-3} in 2002–2013.

Also, the biomass of cladocerans and copepods decreased ($P = 0.002$, $R^2 = 0.4$, $F_{1,16} = 13.3$ and $P < 0.001$,

$R^2 = 0.3$, $F_{1,16} = 9.3$, respectively) from 1992 to 2013 (Table 2). Comparison of the abundance and biomass of different zooplankton species revealed marked changes between the 1990s and 2000s (Table 3). In the 1990s (August–October), zooplankton biomass was dominated by *Daphnia cucullata* Sars, *D. galeata*, *D. cristata* Sars, *Diaphanosoma brachyurum* (Liéven), *Limnospira frontosa* Sars, *Bythotrephes longimanus* Leydig, *E. gracilis*, and juveniles of copepods. The species of the genus *Bosmina* (*B. berolinensis* Imhof, *B. coregoni coregoni* Baird, and *B. gibbera*) were abundant. In the 2000s (August–October), the former dominating species *D. cristata*, *B. berolinensis*, *B. c. coregoni*, and *L. frontosa* almost disappeared from zooplankton. Also, adult *B. longimanus* and *Leptodora kindtii* (Focke) were almost absent from the zooplankton samples, and their juveniles became particularly rare. Moreover, even the occurrence of smaller cladocerans was lower; *Bosmina longirostris* (Müller) and *B. c. coregoni* were quite infrequent in the zooplankton samples. Zooplankton biomass was dominated by juveniles of cyclopoid copepods, mainly of *Mesocyclops leuckarti* (Claus). Copepodites with a mean individual weight of 6 μg accounted for 16% of the total zooplankton biomass, nauplii (mean weight 1.4 μg) accounted for 8%, and the calanoid copepod *E. gracilis* (mean weight 29 μg) accounted for 19%. Large egg-carrying females of *M. leuckarti*, *Acanthocyclops viridis* (Jurine), and *E. gracilis* were rare in the zooplankton samples. Species of the genera *Daphnia* and *Bosmina* made up only 10% and 4% of the total zooplankton biomass, respectively.

A significant decrease in the mean individual cladoceran weight (regression analysis, $P = 0.02$, $R^2 = 0.2$, $F_{1,16} = 5.7$) was observed from 1992 to 2013 (Table 3). The mean cladoceran weight was 30.4 μg in 1992–2001 and 26.0 μg in 2002–2013. The decrease in the mean copepod weight from 9.2 μg in 1992–2001 to 6.0 μg in 2002–2013 was not statistically significant.

Table 2. Biomass (g m^{-3}) and abundance (thous. ind. m^{-3}) change of total zooplankton and its groups in summer (August–September) and autumn (October) for two time periods: the period with smelt dominating the fish assemblage (1992–2001) and the period after the collapse of the smelt population (2002–2013)

Period	Zooplankton	August–September		October	
		Abundance	Biomass	Abundance	Biomass
1992–2001	Total	895	2.07	467	1.65
	Cladocera	34	0.71	53	0.70
	Copepoda	122	0.71	60	0.67
2002–2013	Total	191	1.06	82	0.67
	Cladocera	17	0.34	18	0.31
	Copepoda	86	0.42	31	0.33

Table 3. Main shifts in the zooplankton community in Lake Peipsi in August–October for two time periods: the period with smelt dominating the fish assemblage (1992–2001) and the period after the collapse of the smelt population (2002–2013)

	1992–2001	2002–2013
<i>Daphnia</i> spp. abundance, thous. ind. m ⁻³	0.3	0.07
<i>Daphnia</i> spp. biomass, g m ⁻³	6.0	1.8
<i>Bosmina</i> spp. abundance, thous. ind. m ⁻³	10.9	3.9
<i>Bosmina</i> spp. biomass, g m ⁻³	0.2	0.05
<i>Mesocyclops</i> spp. abundance, thous. ind. m ⁻³	1.8	1.0
<i>Mesocyclops</i> spp. biomass, g m ⁻³	0.03	0.01
<i>Bythotrephes longimanus</i> abundance, thous. ind. m ⁻³	0.2	0
<i>B. longimanus</i> biomass, g m ⁻³	0.8	0
Zooplankton dominants in August–October	<i>Daphnia cucullata</i> <i>D. galeata</i> <i>D. cristata</i> <i>Diaphanosoma brachyurum</i> <i>Limnospida frontosa</i> <i>Bosmina berolinensis</i> <i>B. c. coregoni</i> <i>B. gibbera</i> <i>Eudiaptomus gracilis</i>	Juveniles of cyclopoid copepods, mainly of <i>Mesocyclops leuckarti</i>
Mean cladoceran weight, µg	30.4	26.0
Mean copepod weight, µg	9.2	6.0

Diet of zooplanktivorous fish

Lake Peipsi is inhabited by two fish species that are zooplanktivorous as adults: smelt and vendace. Additionally, numerous juvenile fish species (perch, ruffe, pikeperch, roach, and bream) feed on zooplankton.

In the first two growing seasons, until reaching a standard length of about 11 cm, perch fed mainly on zooplankton; zoobenthos was rarely picked. In terms of weight, *L. kindtii* (*W* 37%, *N* 10%), *B. longimanus* (*W* 22%, *N* 7%), and *D. galeata* (*W* 18%, *N* 14%) dominated in the diet (Fig. 3). However, also large egg-carrying *M. leuckarti* (*W* 14%, *N* 33%), *B. gibbera* (*W* 7%, *N* 14%), and *B. longirostris* (*W* 4%, *N* 12%) were abundant in its diet.

In the first growing season, pikeperch consumed largely zooplankton; in terms of weight, *L. kindtii* (*W* 60%, *N* 29%) dominated in its stomach (Fig. 3). Large egg-carrying *M. leuckarti* was also an abundant prey object (*W* 4%, *N* 33%) while smaller cladocerans like *Bosmina* spp. and *Chydorus sphaericus* Müller were unimportant (*N* 0.8% and *N* 0.6%, respectively). The shift of pikeperch to the fish diet occurred in most cases in the second spring.

In the first two growing seasons, the diet of ruffe consisted of zooplankton and zoobenthos; the role of zoobenthos increased with the growth of the fish. Regarding weight, its diet was dominated by various chironomid species (*W* 66%, *N* 1.5%). The most important

zooplankton prey item in terms of weight and number was *B. c. coregoni* (*W* 16%, *N* 50%). Large egg-carrying *M. leuckarti* was also abundantly (*N* 21%) represented.

Bream, too, fed on zooplankton in the first growing season. In terms of weight and number, its most important prey was *B. c. coregoni* (*W* 97%, *N* 66%). Other prey objects, e.g. *M. leuckarti* (*W* 3%, *N* 21%), *B. longirostris* (*W* 5%, *N* 17%), and *D. galeata* (*W* 1.4%, *N* 0.6%), were less chosen.

During the first two growing seasons, roach fed on zooplankton and phytoplankton. Its diet consisted largely of small zooplankters, most abundant being *M. leuckarti* (*N* 71%, *W* 46%), followed by *B. longirostris* (*N* 12%, *W* 10%), *B. gibbera* (*N* 8%, *W* 6%), and *C. sphaericus* (*N* 8%, *W* 4%).

Smelt preys on zooplankton throughout its whole life cycle, up to 3 years, in Lake Peipsi. Its most essential prey object was *D. galeata* (*W* 63%, *N* 75%) and, regarding weight, also *L. kindtii* (*W* 25%, *N* 4%) was important. Small cladocerans were unimportant (*N* ~5%), and *M. leuckarti* was not very abundant, either (*W* 2%, *N* 11%).

Similarly, vendace preys on zooplankton throughout its whole life cycle. In terms of numbers, its most important prey object was large egg-carrying *M. leuckarti* (*N* 57%, *W* 4%), and in terms of weight, *B. longimanus* (*W* 54%, *N* 18%). Small cladocerans such as *B. gibbera* (*W* 10%, *N* 14%) and *C. sphaericus* (*W* 3%, *N* 16%) were its less chosen food objects.

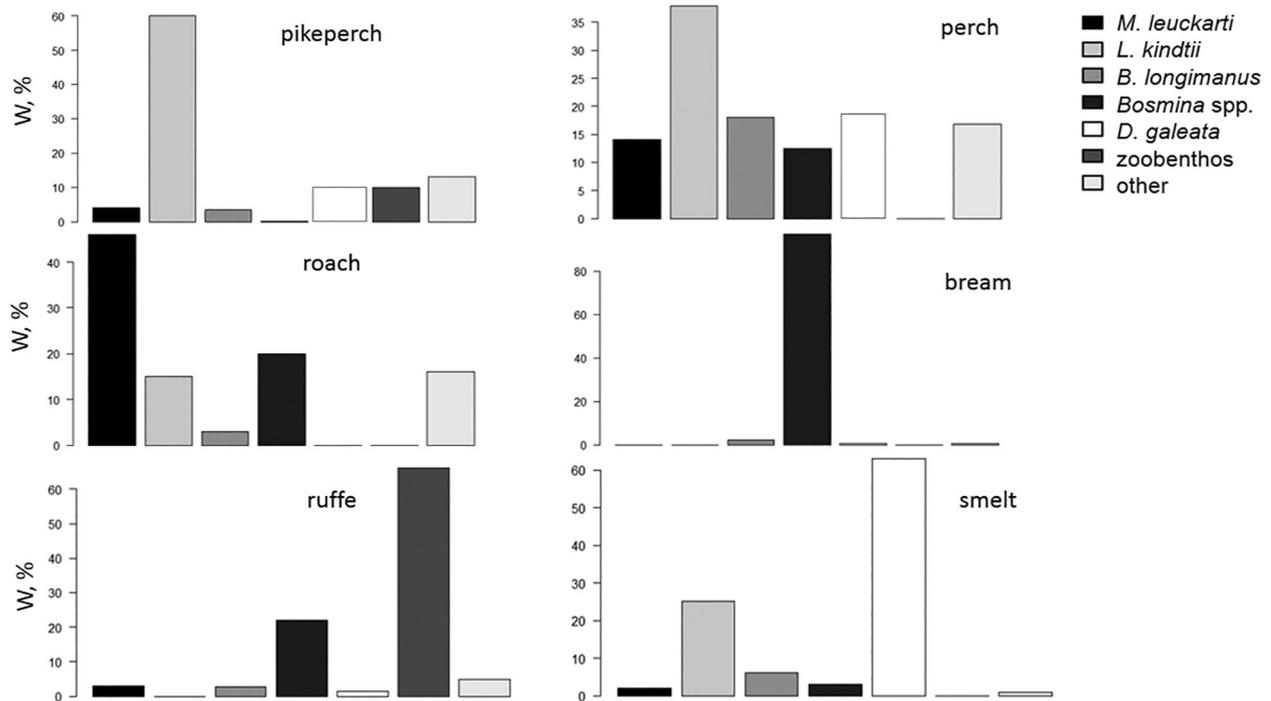


Fig. 3. The most important prey objects of plankton-eating fish in terms of weight (W, percentage of the given prey category of the total food weight of all fish) in Lake Peipsi during 2007–2013.

The stomach content biomass relative to the body mass of adult planktivores (smelt and vendace) was somewhat lower than the stomach content biomass relative to the 0+ fish body mass. Juvenile pikeperch, perch, and ruffe consumed on average 0.2, 0.7, and 0.4 mg copepods per 1 g fish body mass; and 1.6, 5.3, and 3.4 mg cladocerans per 1 g fish body mass, respectively. The consumption of smelt and vendace was 0.3 and 0.2 mg copepods per 1 g fish body mass and 3.4 and 0.8 mg cladocerans per 1 g fish body mass, respectively. Hence, the stomach content biomass relative to the fish body mass was significantly higher for perch fry than the corresponding indicator for the other plankton-eating fish. For all investigated fish species, the stomach content biomass relative to fish body mass was significantly higher in autumn (August–October) than in summer (June–July; t -test, $P < 0.001$; Table 4). Towards autumn, the number and biomass of cladocerans in the diet increased by 62% and 70%, respectively, and the number and biomass of copepods increased by 6% and 8%, respectively. Nevertheless, the species composition of zooplankters in the stomach of adult planktivores and juvenile fish did not differ significantly in summer and autumn months.

The zooplankton biomass consumed by plankton-eating fish per day was significantly higher (ANOVA,

$P < 0.001$, $F_{1,16} = 38.2$) in years with large cohorts of these fish (Fig. 2). Small cohorts consumed zooplankton on average 0.02 g m^{-3} per day and large cohorts, 0.3 g m^{-3} per day. The daily consumption of copepods and *Bosmina* spp. increased and that of *Daphnia* spp. somewhat decreased in the study period. The calculated daily consumption of different zooplankton species (*M. leuckarti*, *Daphnia* spp., *Bosmina* spp.) may exceed their biomass in the water (Fig. 4).

Comparison of the two periods (1992–2001 and 2002–2013) revealed a statistically significant difference ($P < 0.001$, $F_{1,12} = 121$) in many zooplankton characteristics. The first period was characterized by the dominating role of smelt in the zooplankton-eating niche and the second period by the prevalence of YOY fish. In parallel with the shift in the fish assemblages, dominant species in the zooplankton community changed. Large cladocerans (*L. kindtii*, *B. longimanus*, *D. galeata*) were replaced by juvenile copepods. A significant decline was evident even in smaller cladocerans (*Bosmina* spp., especially *B. c. coregoni*) ($P < 0.001$, $R^2 = 0.5$, $F_{1,16} = 16.68$). At the same time, the abundance of ruffe, the main predator of *Bosmina* spp., increased (Fig. 5).

Table 4. The stomach content biomass (μg) relative to fish body mass (g) of given fish species calculated as an average of all individual fish analysed in summer and autumn during seven years (2007–2013)

Fish species	Copepods		<i>Bosmina</i> spp.		<i>Daphnia</i> spp.		<i>L. kindtii</i>	
	Summer	Autumn	Summer	Autumn	Summer	Autumn	Summer	Autumn
Ruffe	440 \pm 13	418 \pm 10	742 \pm 41	5234 \pm 41	83 \pm 6	398 \pm 24	56 \pm 7	394 \pm 16
Perch	1341 \pm 27	401 \pm 8	13 \pm 1.2	979 \pm 20	62 \pm 4	4095 \pm 87	224 \pm 22	879 \pm 19
Pikeperch	787 \pm 29	87 \pm 0.6	0.8 \pm 0.1	5 \pm 0.1	68 \pm 4	308 \pm 3	26 \pm 5	1219 \pm 9
Smelt	228 \pm 81	138 \pm 5	0	214 \pm 9	192 \pm 60	2210 \pm 95	0	1100 \pm 47
Vendace		169		91		6		0

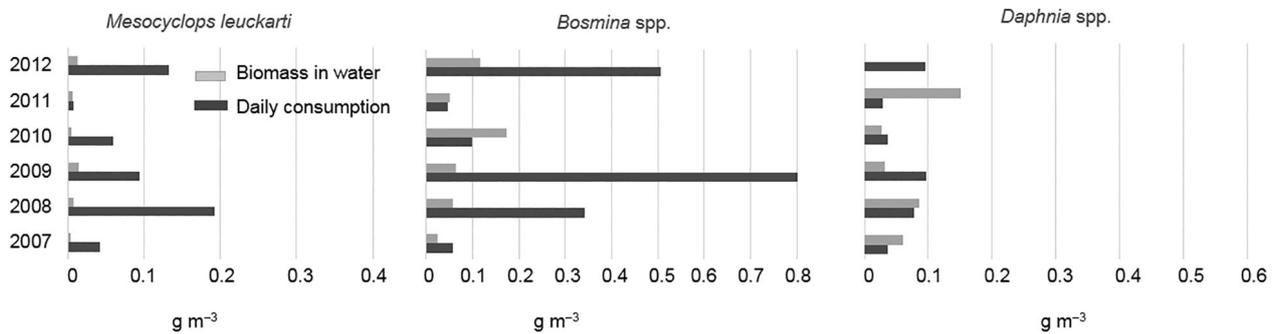


Fig. 4. Daily consumption (g m^{-3}) by plankton-eating fish of different zooplankton species and their abundance in water (g m^{-3}).

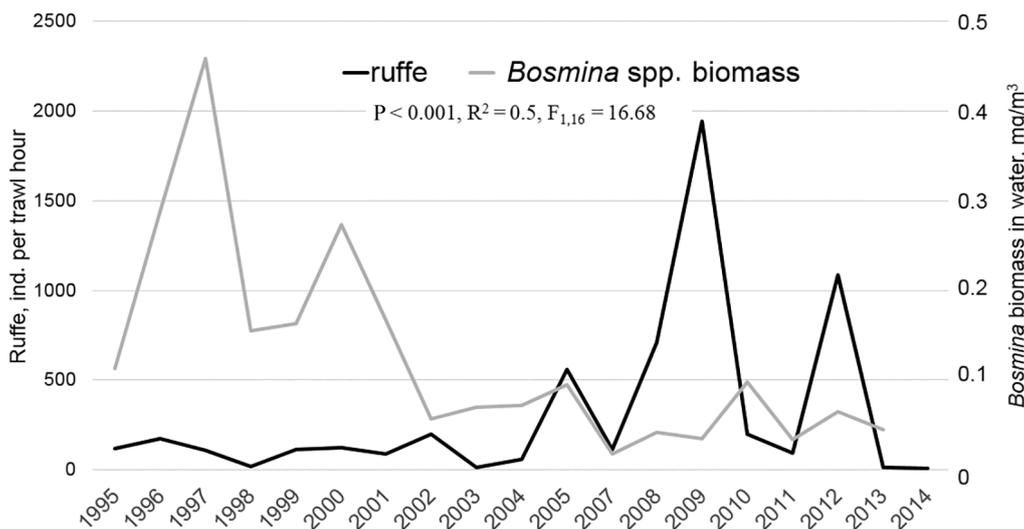


Fig. 5. The biomass (g m^{-3}) of *Bosmina* spp. in autumn (August–October) in water and the abundance (individuals per trawl hour) of ruffe (*Gymnocephalus cernuus* (L.)) in Lake Peipsi.

DISCUSSION

Our study demonstrated essential changes in the zooplankton community starting from 1986. First, the summer mean zooplankton biomass decreased markedly, from 2.1 g m^{-3} in 1986–2001 to 1.1 g m^{-3} in 2002–2013. Second, the biomass of cladocerans, the most preferred

food object for fish, decreased. Third, the earlier dominating large-bodied cladocerans (*D. cristata*, *B. berlinensis*, *B. c. coregoni*, *B. longimanus*, *L. kindtii*, *L. frontosa*) almost disappeared from the zooplankton samples. Moreover, *B. longimanus* and *L. kindtii* (the favourable food objects of fish) only occurred as juvenile forms. Also the copepod community (mainly the genus

Mesocyclops) was largely dominated by juveniles, nauplii, and copepodites while adult copepods were modestly represented and large egg-carrying females (*M. leuckarti*, *A. viridis*, *E. gracilis*) were rare. As a consequence, the mean cladoceran weight and the mean copepod weight decreased (see Table 3). The disappearance of large zooplankton specimens from the plankton samples can be attributed to fish predation as is the case in several other water bodies (Iglesias et al., 2011; Bunnell et al., 2014). Sarvala et al. (1998) even outlined that fish predation can be particularly intensive in shallow lakes without a deep-water refuge for cladocerans. At the same time, the impact of changes in the trophic state of a lake (Haberman and Laugaste, 2003; Jeppesen et al., 2010; Haberman and Haldna, 2014) and in water temperature (Straile, 2015) may be important. The current data of Estonian national monitoring indicate, however, that the water temperature in Lake Peipsi has been quite stable after an abrupt increase recorded in 1987–1989 (Nõges and Nõges, 2014).

According to the analysis of the trawl samples, the abundance of adult planktivores (smelt and vendace) significantly decreased in Lake Peipsi during the past two decades. Despite the significant decline in the vendace and smelt populations, the abundance of plankton-eating fish remained high as the abundance of juvenile fish (mainly perch, pikeperch, and ruffe) increased, and unusually large cohorts were frequent in the last decade. Moreover, our previous research showed a marked juvenilization of the pikeperch population due to the heavy fishing pressure and climate change (Ginter et al., 2015). At the same time, the shift of pikeperch to fish diet was delayed (Ginter et al., 2011). Thus, despite the collapse of the smelt and vendace populations, the fish predation pressure on zooplankton remained considerable.

According to the stomach content analysis of planktivorous fish, the majority of abundant juveniles (perch and ruffe) consumed more zooplankton per fish body weight than adult planktivores did. Similarly, Romare and Bergman (1999) found that after the removal of planktivorous fish, the predation pressure on zooplankton increased up to 2–3 times as the abundance of YOY fish increased. Also Hewett and Johnson (1992) found that among several fish species, including percids and cyprinids, YOY fish show higher mass specific consumption rate than older fish. Persson et al. (2004) reported the cascading effects of the abundance of both roach and YOY perch on zooplankton and phytoplankton dynamics. Likewise, we suppose that after the collapse of adult planktivores in Lake Peipsi, it was the YOY fish that induced significant shifts in the size distribution and species composition of zooplankton.

Romare and Bergman (1999) reported that average densities of 0.3 ind m^{-3} of the YOY fish can affect the recovery of *Daphnia*, and the latter will be totally suppressed at YOY fish densities of 0.7 ind m^{-3} . In Lake Peipsi, the average density of the YOY fish was estimated at about 0.2 ind m^{-3} in the years with very large fish cohorts. In such years, the calculated rate of the daily consumption of zooplankton by fish was very high compared to the zooplankton biomass in the water. In the real world, the consumption of zooplankters cannot exceed the zooplankton biomass in the water. The diet of plankton-eating fish varied among different species, but the most important target species were the same: large cladocerans (*L. kindtii*, *B. longimanus*, *D. galeata*), also smaller cladocerans (*Bosmina* spp., mainly *B. c. coregoni*, and *B. longirostris*) and large egg-carrying copepods (mainly *M. leuckarti*). Similar target species in the diet of planktivorous smelt and YOY fish in Lake Peipsi were observed also by Tikhomirova (1974), Ibnejeva (1983), and Salujõe et al. (2008). Hence, as the prey species of plankton-eating fish are similar, their mutual relationships can be tense and the pressure on zooplankton may increase. Nonetheless, plankton-eating fish can have a profound top-down effect on zooplankton, especially on the larger target species and particularly in years with large fish cohorts.

Simultaneous changes were detected in the fish and zooplankton assemblages in the large and shallow Lake Peipsi: a marked increase in the YOY fish was accompanied by a significant decrease in the abundance and biomass of copepods and cladocerans. Currently, both the zooplankton and fish assemblages are simultaneously affected by multiple, possibly partly conflicting stressors: rise of water temperature and increased frequency of extreme weather events (Blank et al., 2009; Laugaste et al., 2010; Kangur et al., 2013a), changing nutrient loads (Kangur and Möls, 2008; Blank et al., 2009; Nõges et al., 2010; Jeppesen et al., 2012; Blank et al., 2017), blooms of toxic cyanobacteria (Haberman et al., 2010), overexploitation of fish (Ginter et al., 2015), etc. In a situation where both fish and zooplankton are constantly subject to a huge number of stress factors (Iglesias et al., 2011), it is extremely difficult to disentangle the effects of co-occurring stressors that influence interactions between species (Battarbee et al., 2012; Bunnell et al., 2014). Nevertheless, in recent decades the feeding pressure of YOY fish possibly contributed to the changes in the zooplankton community of Lake Peipsi. This can be explained by the fact that juvenile fish consumed more zooplankton compared with adult planktivores when particularly large cohorts of YOY fish were frequent.

CONCLUSIONS

Our study highlights that in the large northern temperate shallow Lake Peipsi the structuring effect of fish on zooplankton remained important despite a significant decline in adult planktivorous vendace and smelt. This was because the predation pressure by the YOY fish correspondingly increased. Long-term data indicate that the summer mean zooplankton biomass and the proportion of large cladocerans in zooplankton declined, the earlier dominating large-bodied cladocerans and egg-carrying copepods almost disappeared, and the mean individual weight of cladocerans and copepods decreased in Lake Peipsi. Because of the high number of juvenile fish, especially in the years with large cohorts, the top-down pressure by fish on zooplankton remained considerable. Thus, prospects for the improvement of water quality in Lake Peipsi as a result of the cascading effect of planktivorous fish on plankton remain modest.

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Kalade toitumissurve zooplaktonile suures põhjapoolses parasvöötme järves: täiskasvanud kalade versus noorkalade mõju zooplanktonile

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Planktontoiduliste kalade, peipsi tindi (*Osmerus eperlanus eperlanus* m. *spirinchus* Pallas) ja rääbise (*Coregonus albula* (L.)) arvukuse vähenemine Peipsi järves tõstatab küsimuse, kuidas zooplankton reageerib sellisele olulisele muutusele veekogu ökosüsteemis. Kas zooplanktoni hulk väheneb? Perioodil 1986–2014 uuriti Peipsi järve pelagiaali planktontoiduliste kalade ja zooplanktoni arvukust ning perioodil 2007–2013 planktontoiduliste kalade toitumist. Uuring näitas, et täiskasvanud planktontoiduliste kalade (tindi ja rääbise) arvukuse vähenemisele vaatamata jäi planktontoiduliste kalade arvukus järves jätkuvalt suureks. Planktontoiduliste kalamaimude arvukus suurenes ja nad sõid sama palju zooplanktonit kui tint ning rääbis, mõned liigid (ahven, koha, särg) isegi rohkem. Surve zooplanktonile jäi suureks. Zooplanktonis vähenes vesikirbuliste (Cladocera) ja aerjalgsete (Copepoda) kalade meelistoidu biomass, samuti zooplankterite keskmine kaal. Paljud suuremad zooplankterid kas peaaegu kadusid zooplanktonist või muutusid haruldasteks: *Leptodora kindtii* (Focke) ja *Bythotrephes longimanus* Leydig. Uuring näitas, et neid muutusi põhjustasid suurenenud arvukusega kalamaimud. Ühesuviste kalamaimude poolt päevas söödud zooplanktoni hulk ületas vees oleva zooplanktoni biomassi, eriti kalamaimude suurte põlvkondadega aastatel. Ühesuvised kalamaimud kujundavad oluliselt nii zooplanktoni hulka kui ka koostist.